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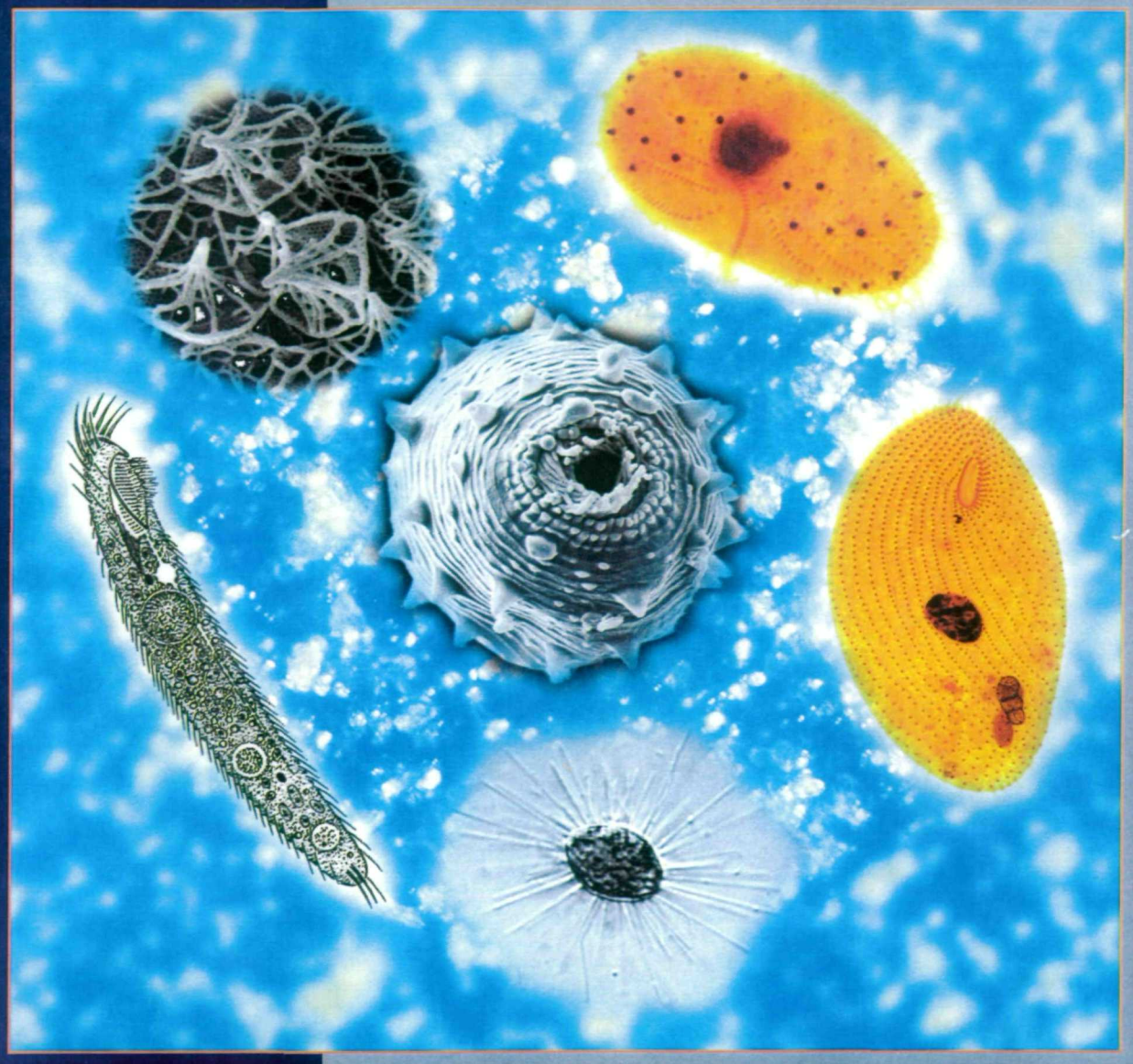

W. Foissner, S. Agatha & H. Berger

Soil Ciliates (Protozoa, Ciliophora) from Namibia (Southwest Africa), with Emphasis on two Contrasting Environments, the Etosha Region and the Namib Desert

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Soil Ciliates (Protozoa, Ciliophora) from Namibia (Southwest Africa), with Emphasis on Two Contrasting Environments, the Etosha Region and the Namib Desert

PART I: Text and Line Drawings

Wilhelm FOISSNER, Sabine AGATHA and Helmut BERGER

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Preface, Authorship, and Acknowledgements

Namibia (Southwest Africa) is well-known for its contrasting environments, especially the Namib Desert and the Etosha National Park. Thus, after a holiday travelling through Namibia in February 1994, I came back to Austria with 73 well-sorted soil samples, on which I worked, with some interruptions, for seven years, with the indispensable help of Dr. Sabine AGATHA, Dr. Brigitte MOSER, and Prof. Dr. Helmut BERGER, to describe the over 200 rare and new species found.

The resulting monograph is unique in many ways. For the first time since the unforgotten monographs by MÜLLER (1786), EHRENBERG (1838), STEIN (1859, 1867), PENARD (1922), and KAHL (1930-35), almost 150 new species are described in a single publication. The list from the 73 samples comprises 365 painstakingly identified species and is by far the largest number ever published in a single study from a comparatively small area. Thus, this list will be an invaluable document for ecologists and biodiversity researchers. All species are described by a combination of classic (live observation) and modern (silver impregnation, scanning electron microscopy) methods, and many are illustrated by a multitude of excellent micrographs, and, last but not least, all are documented by silver-impregnated types stored in an acknowledged repository. Thus, we hope that our study will serve as an example for ciliate community studies and will be as long-lived as those of the pioneers mentioned above.

Authors are listed in the order they contributed to the monograph. This statement and the details mentioned below are important for historical reasons, the estimation of data quality and, last but not least, fairness. *However, I state that, if not otherwise indicated, all nomenclatural acts (new species, new genera, new combinations etc.) have to be cited as:* FOISSNER, AGATHA & BERGER, 2002.

WILHELM FOISSNER made all species lists, the live observations with the raw illustrations, the silver preparations, the light and scanning electron micrographs (with the invaluable assistance of Dr. BRIGITTE MOSER, financed by the Austrian Science Foundation), the general section, and the 158 species indicated in table 3. Further, FOISSNER critically checked the work done by Dr. AGATHA and Dr. BERGER. SABINE AGATHA completed (refined live illustrations; morphometry, illustrations and description) the 39 species indicated in table 3. Further, she was responsible for the layout. Dr. AGATHA was financed by the Austrian Science Foundation from 01.01.1998–30.06.2001. HELMUT BERGER completed, like AGATHA, the 33 hypotrichs indicated in table 3. He was financed from FOISSNER's private funds.

Financial support was provided by the Austrian Science Foundation, based on reviews by three unknown colleagues. Without this grant, the work would have been impossible. We are also very grateful to Prof. Dr. Hofrat Franz SPETA, head of the Museum of Natural History in Linz, Austria, who made it possible to publish the work in full length and excellent quality. All together, but without FOISSNER's ordinary salary, $ 200,000 US were needed for this book!

Further, I am indebted to Dr. Eva HERZOG for typing part of the manuscript; Dr. Remigius GEISER for help with nomenclature; Mag. Eric STROBL and Dr. Steve WICKHAM for refining the English; and Dr. Wolf-Dietrich KRAUTGARTNER for ensuring the smooth operation of the scanning electron microscope.

Wilhelm FOISSNER

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Soil Ciliates (Protozoa, Ciliophora) from Namibia (Southwest Africa), with Emphasis on Two Contrasting Environments, the Etosha Region and the Namib Desert

Wilhelm FOISSNER, Sabine AGATHA and Helmut BERGER

Abstract: A highly diverse ciliate community was found in 73 samples from terrestrial and semiterrestrial habitats of Namibia, Southwest Africa, one of the world's driest countries. The ciliate, respectively, their resting cysts, were re-activated from air-dried samples using the non-flooded Petri dish method. Species were determined by combining live observations, silver impregnation, and scanning electron microscopy.

A total of 365 species were identified, of which 128 (35%) were undescribed, including a new order and suborder, three new families, and 34 new genera and subgenera. These new and many insufficiently known taxa, altogether more than 200 species and subspecies and over 300 populations, are described in the present monograph (see chapter 3.2.1 for a summary of names and nomenclatural acts); 800 type slides have been deposited in (LI). Further, ontogenesis was investigated in 20 species.

The Namibian soil ciliate community shows some remarkable differences to the world community. Specifically, raptorious gymnostomatids and filamentous cyanobacteria feeding nassulids are over-represented, while hypotrichs and peritrichs are underrepresented. Nassulids obviously profit from the cyanobacteria covering wide areas of the Etosha region and the crust soils in the arid areas. Hypotrichs are more k- than r-selected and thus cannot develop optimally in the harsh Namibian climate. Likewise, the sandy soils are disadvantageous for sessile peritrichs. Generally, however, the Namibian soil ciliate biota are unexpectedly rich, that is, more diverse than those from central Europe, likely because they had at least 55 million years to evolve adapted populations and species. 200 of the 365 ciliate species identified occur at only one or two sites, showing a very patchy distribution of most species and a high proportion of possibly rare species. Most of the 11 most frequent ($\geq$ 40%) species are common in soils globally, except for *Exocolpoda augustini*, which is adapted to hyperarid conditions by a special life cycle and an extraordinarily thick-walled (dormant) resting cyst. Using total species numbers and the proportions of undescribed species, four local ciliate diversity centres were discovered: Etosha region (19 samples with 216 species, of which 61 were undescribed); dune sea Namib Desert (15 samples with 150 species, of which 32 were undescribed); *Aloe dichotoma* forest and Bukaos River floodplain near the town of Keetmanshoop (2 samples each with 11 new species); road puddles in the Bambatsi Guest Farm (1 sample with 126 identified and 15 unidentified species, of which at least 40 were undescribed).

We estimate that there are about 1000 soil ciliate species in Namibia, of which 350 are undescribed, including an unknown number of endemic species. Thus, our monograph contains only one third of the species actually living in the highly diverse terrestrial habitats of this country. We show that there must be many more free-living ciliate species globally than the 3000 estimated by FINLAY. His estimation is flawed by biased literature evaluation, doubtful synonymies, unusual taxonomic practices and, partially, false theoretical concepts. Undersampling is **the** key to understanding protist diversity.

Key words: Adaptation, ciliate ecology, ciliate systematics, ciliate taxonomy, ciliate endemism, ciliate biodiversity, global number of free-living ciliates, neotypification, new species, ontogenesis, saline desert, dune desert, undersampling.

CONTENTS

1. INTRODUCTION

Soil Protozoa were neglected for a long time and the species "identified" as a part of the freshwater or even activated sludge community (FOISSNER 1987d). It was only between the sixties and nineties that BONNET (1964) and FOISSNER (1987d) renewed the interest and showed that soil testate amoebae and ciliate biota are fundamentally different from the limnetic ones. This view, which is now widely accepted, is emphasized by the present study which describes not only many new species, but also a considerable number of new organization types (genera), as yet unknown from freshwater. Unfortunately, the interest in soil protozoa is decreasing again, although many studies showed their importance in bioindication and the soil energy cycle (EKELUND & RØNN 1994, FOISSNER 1987d, 1999e).

There is now much research and discussion on biodiversity and its application in conservation, seemingly indicating a flourishing alpha-taxonomy (= investigation and description of species), the basestone of biodiversity research. Unfortunately, appearances are deceptive: species describers and faunists who do the "hard work", that is, identify and eventually describe new species, are decreasing in number, expertise, and social reputation, partially because the large biodiversity programs are misused by other disciplines to acquire money for purely ecological and/or conservation research (COTTERILL 1995, PRANCE 1995).

As concerns ciliates, ecologically and taxonomically orientated biodiversity researchers reach entirely different conclusions about the number of free-living ciliate species: "As protozoans species are probably globally ubiquitous, there is every reason to believe that all species of freshwater protozoa could eventually be discovered in one small pond" (FINLAY & ESTEBAN 1998). FOISSNER (1999c), in contrast, states: "It is unlikely that total diversity of free-living ciliates is close to 3000 or 4000 species, as proposed by FINLAY and FENCHEL. A more likely figure is 30,000". Certainly, both statements are weakly founded and need more objective discussion (FOISSNER 1999d). Generally, however, it is our belief that there is only one way to get the truth, viz., the critical investigation of representative biomes by **experienced** taxonomists. The present monograph is the only recent example available. The immense amount of work required can hardly be done by the few experts left, even if the financial resources were available!

Thus, we shall probably not find out whether there are 3000 or 30,000 free-living ciliate species during the coming centuries. But our study shows a high number of undescribed species. This is emphasized by the following calculation: 643 ciliate species are known to occur in terrestrial habitats, and more than half of them are likely confined to such environments (FOISSNER 1998a). With the species described here and some others from the literature, we arrive at 800 species. This is half the number likely living in soil (FOISSNER 1997c). Considering that a single working group increased the number of species from about 270 in 1987 to 800 in 2001, the estimated 1600 total appears reasonable (FOISSNER 1997c).

FINLAY et al. (1996) state that the main biotopes of the Earth have already been sufficiently investigated for free-living ciliates. Clearly, this is not the case. Neither have ciliates been investigated, for instance, in Namibia (BARNARD 1998), Australia (BLATTERER & FOISSNER 1988) and South America nor in the 25 world species diversity hotspots selected by MYERS et al. (2000), except of the Mediterranean Basin. As concerns Namibia, we found only one small paper describing *Fabrea salina* and *Condylostoma* sp. from saline Flamingo pools on the outskirts of Walvis Bay (BRAIN 1980).

2. MATERIALS AND METHODS, SPECIES CONCEPT, TYPES

2.1 Material

2.1.1 General Site Description

2.1.1.1 Brief Overview of Namibia (Fig. 1, 2)

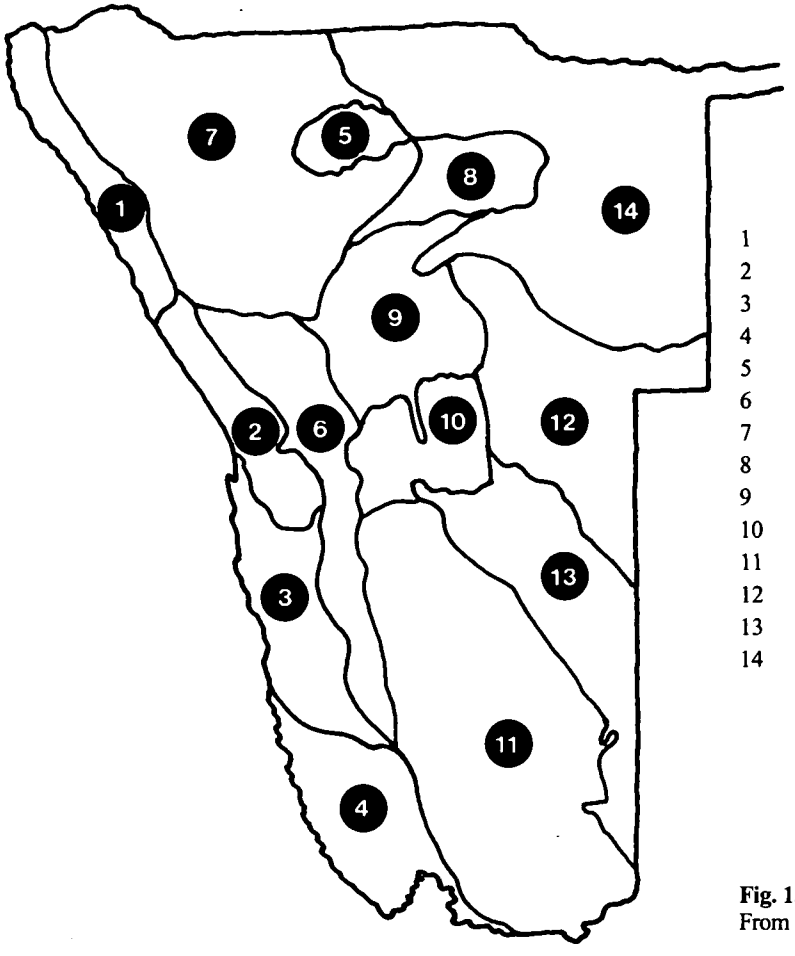
There is no need to describe Namibia in detail because many excellent travel guides are available and the centres of our sampling activity are treated in some detail in the paragraphs below and the site descriptions.

Namibia, or Southwest Africa, extends for about 1000 km on the southwest coast of Africa from about 17° to 29° south of the equator, and it is divided by the Tropic of Capricorn. Thus, the region belongs to the subtropics. The land area is 823,988 km^2, 45% of which is flat and covered by bushveld in the central plateau at 1600 to 1800 m above sea level. Namibia has 1.6 million human inhabitants and a hyper-arid (west) to dry subhumid (east) climate. Rainfall is mostly in summer and increasingly variable towards the west coast. It determines the three main biomes of Namibia: desert, savannah, and woodland.

The overwhelming two features of Namibia's climate are the scarcity and unpredictability of rainfall. Within Africa, the climate is second in aridity only to the Sahara. The country-wide average rainfall of under 250 mm per year is coupled with annual mean evaporation of up to 3700 mm. Overall, 69% of the country is regarded as semi-arid, and 16% as arid. Most of Namibia's rain falls in summer, from November to April; only the south western part of the country also has winter rain, sustaining a diverse succulent flora. The combination of a cold, subantarctic upwelling on the Atlantic coast and a hot subtropical interior have led to hyper-arid, bleak coastal conditions in the Namib Desert, similar to those of Chile's Atacama Desert and of Baja California, Mexico. Temperatures in Namibia can also be extremely variable with values well over 50° C and under 0° C recorded in the same parts of the country. However, in the tropical northeast and along the coast, daily highs and lows can differ by as little as 2–5° C (BARNARD 1998).

Our soil ciliate samples represent roughly a quarter of Namibia's land area (Fig. 2) and are from three contrasting environments, viz., an ephemeral wetland, that is, the Etosha Pan and surroundings; the Namib Desert and Namib Escarpment; and savannahs. Certainly, this is only a minor portion of the environments present in Namibia! For instance, freshwaters, the "classic" habitats for ciliates, were not investigated at all, although Namibia has quite a lot of nice riverine, lacustrine, palustrine and estuarine habitats (see the excellent overview by BARNARD 1998). Further, the most productive region, the Caprivi Stripe at the northeast of Namibia was not sampled, as the water-holes around the Etosha Pan. Likewise, the many microhabitats present in any biome were rarely collected selectively, although they contain many undescribed species, for instance, bark from trees, mud and soil from ephemeral rivers and pools, and the many types of crust soil in the hyper-arid environments. Thus, the majority of ciliate species present in Namibia is likely unknown, and certainly includes many new species. Some of the above and other habitats were sampled during a second journey in January 2001.

Sampling was possible due to Permits 09938P and 37213P of the Namibian Ministry of Environment and Tourism.



1 Northern Namib
2 Central Namib
3 Southern Namib
4 Desert and succulent steppe
5 Saline desert with dwarf shrub savannah
6 Semi-desert and savannah transition
7 Mopane savannah
8 Mountain savannah and karstveld
9 Thornbush savannah
10 Highland savannah
11 Dwarf shrub savannah
12 Camelthorn savannah
13 Mixed tree and shrub savannah
14 Forest savannah and woodland

Fig. 1. The 14 major vegetation types of Namibia. From BARNARD (1998) after GIESS (1970).

2.1.1.2 The Etosha Pan (Fig. 1–3; 244–261)

The Etosha Pan (large, white place, according to the natives) is an ephemeral wetland famous for its wildlife (the "big five": elephant, rhino, lion, leopard, giraffe) and habitat diversity ranging from the saline Pan Desert to the ordinary savannah woodland. Sufficient rainfall (about 430 mm/year) and steep gradients in soil physical and chemical parameters produced a rich, sharply zonated flora and fauna. BERRY (1982), for instance, reports 689 plant species belonging to 165 families, and about 150 vertebrates occur. Thus, the Etosha Pan was chosen as one of the main areas for sampling soil ciliates. All samples (nos. 53–71) were taken at the south edge of the Pan. The following paragraphs provide a brief general overview; for details on sample sites (vegetation and soil types, rainfall etc.), see site description in chapter 2.1.2.

The Etosha National Park is located between 14°30' and 17°E, and 18°30' and 19°30'S. The overall size is 22270 km^2, of which salt pans occupy 23%; the main Pan measures about 120 × 55 km and covers an area of 5000 km^2. The northwest corner (Ekuma) is 1073 m above sea-level, the southwest corner "Okerfontein" 1086 m. Mean annual rainfall is about 430 mm, and most rain falls between December and April. Mean annual temperature is about 22° C,

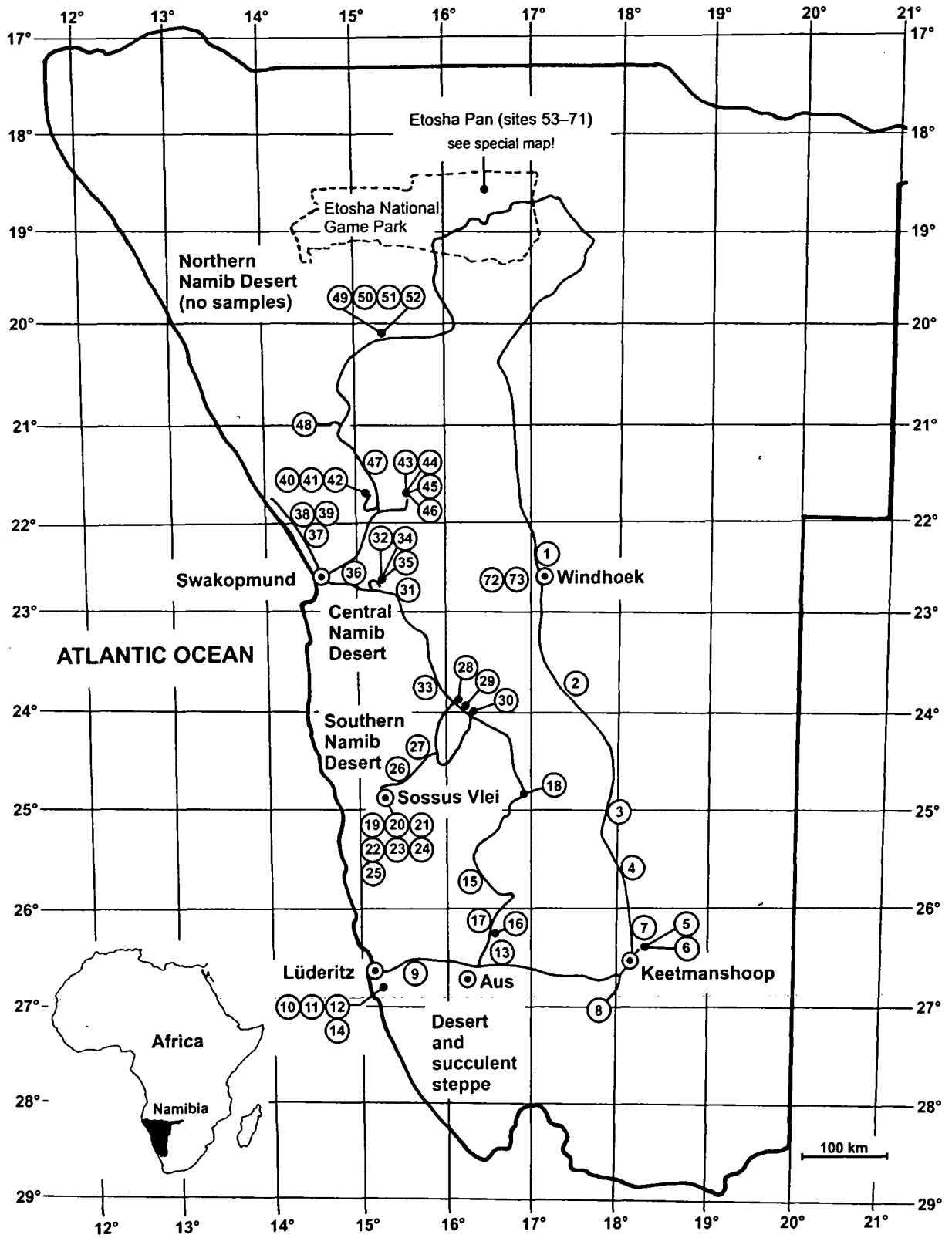


Fig. 2. Location of Namibia in Africa (lower left) and sample sites (numbers 1–73) along the travel route.

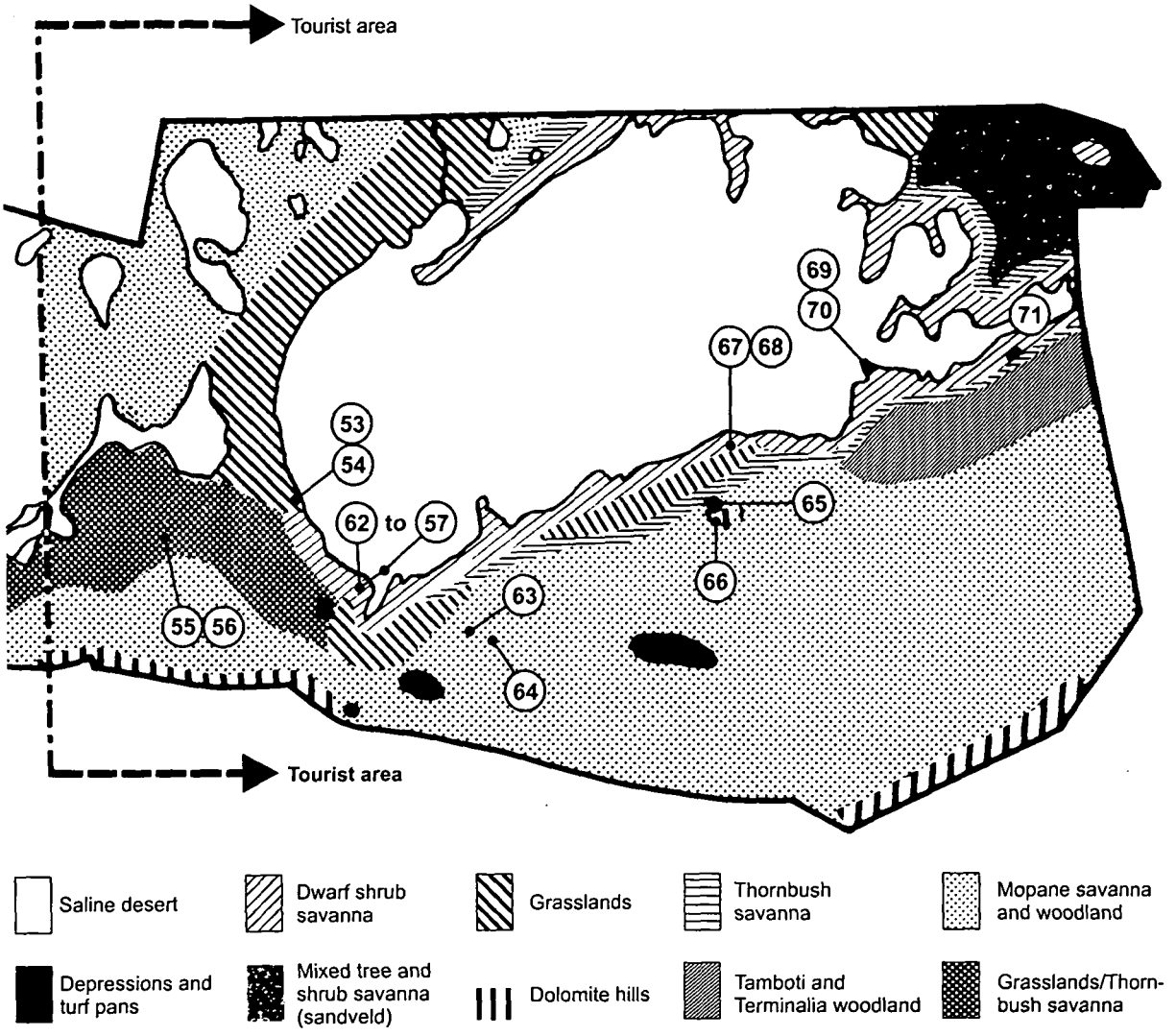


Fig. 3. Map of the Etosha National Park, divided into nine major vegetation types. Numbers 53–71 are the sample sites for soil ciliates. Sites 57–63 represent a fine-scaled transect from the saline desert (57) to the Mopane savannah (63).

with extremes ranging from about 0° C to 40° C. January to April are humid and hot; May to August are dry and cold; September to December are dry and hot (HERDTFELDER 1984).

The Etosha region is flat with up to 500 m high dolomitic hills. The south margin of the Pan, where the ciliate samples were taken, is dominated by rather young limestone tables. The Pan has several inflows but no outflow. Its geological formation possibly evolved two to ten million years ago, during the Pliocene epoch, when the Cunene River flowed into the Ekuma Lake, of which the Etosha Pan was an extension. Later, the Cunene River changed course towards the Ruacana Falls in the west, thus cutting off the water supply of the lake. During the drying period, the soil of the pan became very brackish. Wind erosion deepened the depression and in places impermeable clay up to 240 m deep formed on the floor.

Soils (Fig. 246–251, 255, 256): A soil map of the Etosha National Park has been published by BUCH et al. (1994). They differentiate 26 types distributed over five main associations: soil from deep (> 1 m) sandy substrates; shallow to moderately deep (< 1 m) sandy to sand-loamy soils; shallow to moderately deep sandy-loamy to loamy-clayey soils from the fluvial sediments; and saline, sodium-rich soils. Of special interest are the alkaline (pH up to 10! see sample descriptions in chapter 2.1.2) and saline (up to 130 ‰) soils of the Solonchak and Solonetz-type in the Pan and, especially, at the Pan margin. These vary conspicuously in salinity seasonally, horizontally and vertically, providing an endless number of habitats for soil microorganisms (detailed measurements, see sample descriptions in chapter 2.1.2, HERDTFELDER 1984, and GANSSEN 1963). Indeed, about half of the ciliate species found in these habitats were undescribed.

Vegetation (Fig. 1; 244, 252–261; and shortened text from BERRY 1982): Nine vegetation types have been distinguished in the Etosha National Park. The following paragraphs provide a brief description of the six types from which soil ciliate samples were taken.

Saline desert (Pan sensu stricto): During the rainy season, the Pan may be partially flooded, most of the water coming from two rivers in the north. The Pan water is unfit for human or animal consumption, as it may contain twice as much salt as sea-water. However, there are many freshwater springs at the Pan margin. Nevertheless, it supports a rich growth of blue-green algae, which in good rainy seasons attracts a million or more flamingos. When the water dries up, little vegetation grows on the Pan, with exception of a specific halophytic grass *Sporobolus salsus*. Areas adjoining the Pan have a very brackish soil and support only halophytic vegetation such as the grasses, *Sporobolus spicatus* and *Odyssea paucinervis*, and a small shrub, *Suaeda articulata*.

Dwarf shrub savannah: The fringes surrounding the Pan support a variety of small shrubs such as *Salsola etoschensis, Petalidium engleranum, Monechma genistifolium, Monechma tonsum, Leucosphaera bainesii* and *Cyathula hereroensis* which cover large areas of alkaline soils. *Acacia nebrownii* and *Aloe littoralis* occur close to the edge of the Pan, and in the vicinity of Salvadora.

Grasslands: These are mainly at the perimeter of the Pan on sandy soils overlying limestone. Annual and perennial grasses are interspersed with clumps of *Acacia nebrownii, Acacia luederitzii* var. *luederitzii, Acacia reficiens* sspec. *reficiens* and *Catophractes alexandri*. The winter grazing areas, which sustain less palatable grasses, are the Halali plains, extending from Charitsaub to Nuamses and Gemsbokvlakte, covering an area of almost 30.000 ha. The dominant grass here is the perennial *Monelytrum luederitzianum*.

Thorn bush savannah: This vegetation type is dispersed throughout Etosha, close to the Pan, on limestone and alkaline soils. The most common thorn tree species are water acacia (*Acacia nebrownii*), bastard umbrella-thorn (*Acacia luederitzii* var. *luederitzii*), false umbrella-thorn (*Acacia reficiens* sspec. *reficiens*), hook-thorn (*Acacia mellifera* sspec. *detinens*), candle acacia (*Acacia hebeclada*) and umbrella-thorn (*Acacia tortilis* sspec. *heteracantha*) as well as a few albizia (*Albizia anthelmintica*). Both the white-flowering "Gabbabos" or the rattle tree (*Catophractes alexandri*) and the sickel-bush (*Dichrostachys cinerea* sspec. *africana*) often form dense thickets. Good examples of the vegetation type can be seen on the road to Gemsbokvlakte and on the fringe of the Pan near Namutoni, in the Okerfontein area.

Mopane savannah and woodland: The mopane, *Colophospermum mopane*, is the dominant species of this veld type and also the most common tree in the Etosha National Park. It has

been estimated that 80% of all Etosha's trees are mopane. Typical mopane woodland occurs in the Halali area where trees of 6 m and higher are common. This veld type is interspersed with red bush-willow (*Combretum apiculatum* sspec. *apiculatum*), purple-pod terminalia (*Terminalia prunioides*) and leadwood (*Combretum imberbe*).

Dolomite hills: Along the south-eastern and western borders of Etosha there is a ridge of dolomite hills which rises sharply above the surrounding, flat bushveld. The low range near Andersson entrance gate bears the picturesque name of "Ondundozonanandana" meaning "the place to which the young calves went and from which they never returned" implying that the hills are the haunt of leopards. The only hill of this type which is accessible to the tourist is inside the Halali camp. The vegetation there, as well as on the nearby "Twee Koppies" (twin hills), is typified by fat-stemmed moringo (*Moringa ovalifolia*), bird plum (*Berchemia discolor*) and red bush-willow. Purple-pod terminalia mingle with yellow-bark acacia (*Acacia erubescens*), scented thorn, sheperd's tree, common commiphora, and a few sour plum shrubs (*Ximenia americana*). Four different *Grewia* species grow on the Halali Hill, as well as sickle-bush and the climbing shrub *Combretum mossambicense*, which displays masses of flowers in spring.

2.1.1.3 The Namib Desert and Namib Escarpment (Fig. 1, 2; 222–243)

The Namib Desert and its east margin, both famous for the high endemism of flora and fauna, were one of the centres chosen for investigating soil ciliates. Thus, the region is described in some detail, based on BARNARD (1998); for details on sampling sites (vegetation and soil types, rainfall etc.), see site description in chapter 2.1.2. Further readings on details of climate, soil, fauna and flora: CRAVEN & MARAIS (1992), FLETCHER & MARTIN (1948), GIESS (1989), KAYSER (1973), LANCASTER & LANCASTER (1984), SCHOLZ (1968, 1972), SEELY (1988); see also the comprehensive bibliography in BARNARD (1998). The following samples belong to this area: 9–17, 19–48 (Fig. 2).

The combination of a cold, subantarctic upwelling on the Atlantic coast and a hot subtropical interior have led to hyper-arid, bleak coastal conditions in the Namib Desert, similar to those of Chile's Atacama Desert and of Baya California, Mexico. The zone between cold sea and hot desert is narrow. A thin stripe of coastal fog, seldom reaching more than 30 km inland, frequently blows over the hyper-arid coast and sustains life there in the absence of rainfall.

The Namib as a geo-ecological zone extends about 2000 km from the Carunjamba River in Angola to the Olifants River in South Africa. Bounded sharply in the west by the Atlantic coast, its eastern reaches (Namib Escarpment) are ill-defined. The Namib reaches 80 to 200 km inland, roughly coinciding with the 100-mm annual rainfall line, that is, the 1000 m altitude contour line, or the Namib Escarpment. It covers about 15% of Namibia's land area. There are three desert landforms: (1) the Southern Namib, with spectacular "dune sea" and "islands" of black outcrops and inselbergs; (2) the Central Namib, with gravel plains between the Ugab and Kuiseb Rivers; (3) the Northern Namib, with rugged mountains and dune fields reaching northwards into Angola (no samples were taken from this part).

The succulent steppe in the Southern Namib (Lüderitz and south) is fed by winter rainfall and is a hot-spot of plant diversity dominated by succulent shrubs of the family Mesembryanthemaceae. Perennial grasses such as *Stipagrostis sabulicola* characterize the Namib mobile dunes, while annual herbs and grasses including other *Stipagrostis* species occur on the gravel

plains of the Central Namib. The Namib Escarpment is a narrow, sometimes poorly defined transition zone between the desert and the central highland plateau. Thus, it is termed a semi-desert savannah transition zone. Many unique, Namibian endemic vertebrates, invertebrates and plants are found in this zone, which also harbours many relics from wetter periods in the past.

The Namib is widely called the world's oldest desert. Today, the major centres of endemism are not in the tropical northeast, but in the arid northwest escarpment and southern winter-rainfall zone. There is ample evidence that the Namib has been semi-arid to arid for at least 55 and possibly up to 80 million years, while the Benguela Current was forced northward along the southwest African coast only about 5–10 million years ago. The slow continental breakup of west Gondwana, 130–145 million years ago, set the conditions for the regions's aridity, by shifting southern Africa to its present position, astride the Tropic of Capricorn, and slowly readjusting adjacent marine currents and prevailing winds. In effect, the region has been an island of aridity in a "sea" of more changeable climes.

2.1.1.4 Savannahs (Fig. 1, 2)

Most of Namibia is covered by savannah, especially thorny shrub and tree savannah. The dwarf shrub and succulent savannah of the south is of the Karoo type and a regional centre of endemism (BARNARD 1998). The Hottentot term Karoo is given to barren (treeless) tracts in South Africa, consisting of extensive elevated plateaus with a clayey soil, which during the dry season are entirely waterless and arid. Mountain, Thornbush and Highland Savannahs dominate the central highlands, while Mopane Savannah surrounds Etosha in the north.

Savannahs grow on Lithosoils (BARNARD 1998), which are red and deep when old (terra rossa), while brown, flat and stony when more recent (terra fusca); further, grey, clayey soils develop in depressions (SCHOLZ 1968a). Lithosoils are poor in plant nutrients and humus and thus very sensitive and rather unproductive (GANSSEN 1963, GANSSEN & MOLL 1961). However, they are frequently covered with a rather thick litter layer providing rich and diverse habitats for soil microorganisms and mesofauna.

Many of our samples belong to this biome type in one way or the other: highland savannah (nos. 1, 72, 73), dwarf shrub savannah ~ Karoo (2–8, 18), Mopane savannah (49–52), and some samples from the Etosha National Park, viz., the thorny shrub and mopane savannah (55, 56, 62, 63, 64, 66). Furthermore, many samples from the Namib Escarpment are associated with this biome type.

2.1.2 Description of Individual Samples, Remarks on Species Numbers, and Minor Observations on Species Not Treated in the Description Section (Fig. 1–3)

General description of main sample regions, see chapter 2.1.1. Geographic coordinates are approximate because a detailed map and GPS were not available. Data on rainfall and vegetation types are from BARNARD (1998). Salinity was measured with a refractometer. The species mentioned are indexed.

Site 1: West margin of the town of Windhoek (22°40'S 17°E); highland savannah. Soil wet, reddish, very sandy, and covered with a moist algal mat. Material collected: litter, algal mat,

roots and soil from 0–10 cm; pH 7.2. Number of species identified: 39, of these 2 described as new in this book; number of unidentified species: 3, all likely undescribed (new); total number of species: 42. Remarks: annual rainfall 350–400 mm; collected on 14.02.1994, investigated on 16.11.1994. *Sorogena stoianovitchae* identified according to the characteristic shape of body and oral dome. One of the 2 new species has its type location here. Two of the undescribed species (*Terricirra* sp., *Enchelyodon* sp.) are rare; the third, likely an unusual *Holosticha*, was not separated from *Lamtostyla decorata* in vivo.

Site 2: About 50 km north of the town of Kalkrand (23°40'S 17°30'E); dwarf shrub savannah at margin of main road to the town of Windhoek. Soil dry, red, with many fine roots. Material collected: litter, roots and soil from 0–5 cm plus surface litter from dry bed of a streamlet; pH 5.4. Number of species identified: 24, of these 1 described as new in this book; number of unidentified species: 0; total number of species: 24. Remarks: annual rainfall 200–250 mm; collected on 14.02.1994, investigated on 16.02.2000. The smooth and ribbed variety of → *Nivaliella plana* occur. The new species has its type location elsewhere.

Site 3: About 50 km south of the town of Mariental (25°S 18°E); flooded (if much rain) dwarf shrub savannah near main road. Soil dry, red, contains many roots from green grass cushions. Material collected: litter, roots and soil from 0–5 cm; pH 6.8, moderately saline. Number of species identified: 24, of these 1 described as new in this book; number of unidentified species: 0; total number of species: 24. Remarks: annual rainfall 100–150 mm; collected on 14.12.1994, investigated on 16.11.1994. *Woodruffides terricola* with about 20 adoral organelles. Transverse cirral row distinctly shorter than in Austrian type population. The new species has its type location elsewhere.

Site 4 (Fig. 222): About 80 km north of the town of Keetmanshoop (25°40'S 18°10'E); floodplain of the Bukaos River near the main road in the dwarf shrub savannah. Material collected: litter sieved off a dry sand bank; pH 6.2. Number of species identified: 80, of these 11 described as new in this book; number of unidentified species: 10, of these 6 likely undescribed (new); total number of species: 90. Remarks: annual rainfall 100–150 mm; collected on 14.02.1994, investigated on 27.12.1999. A rich sample! *Bryophyllum loxophylliforme* with monilate macronucleus. *Colpoda orientalis* amicronucleate. → *Colpodidium caudatum* shows transitions to the Chinese variety. Four of the 10 new species have their type location here.

Site 5 (Fig. 223, 224): Gariganus Guest Farm, about 30 km northeast of the town of Keetmanshoop (26°30'S 18°25'E); *Aloe dichotoma* forest in the dwarf shrub savannah. Stony, there is only a thin (0–3 cm) humous litter/soil layer. Material collected: litter and humous layer from under some *Aloe* trees; pH 6.7. Number of species identified: 43, of these 11 described as new in this book; number of unidentified species: 3, of these 2 likely undescribed (new); Total number of species: 46. Remarks: annual rainfall 100–150 mm; collected on 14.02.1994, investigated on 27.12.1999. A local biodiversity centre! *Uroleptus notabilis* invariably with only two transverse cirri.

Site 6: As in site 5; thin, paper-like bark from *Aloe dichotoma* trees; pH 5.1. Number of species identified: 10, of these 0 described as new in this book; number of unidentified species: 1; total number of species: 11. Remarks: annual rainfall 100–150 mm; bdelloid rotifers and *Peranema* sp. became numerous a month after rewetting.

Site 7: Surroundings of Gariganus Guest Farm, about 50 km north of Keetmanshoop in the dwarf shrub savannah (26°25'S 18°20'E). Material collected: rotting *Aloe* sp. and moder/soil

between rotting parts; pH 5.1. Number of species identified: 8, of these 1 described as new in this book; number of unidentified species: 0; total number of species: 8. Remarks: annual rainfall 100–150 mm; collected on 15.02.1994, investigated on 01.10.1999. The new species has its type location elsewhere.

Site 8: Löwen River, about 100 m downstream of the "Naute" dam in the dwarf shrub savannah (26°55'S 17°55'E); dry part of river bed. Material collected: litter from river, roots from sedges, and mud from dry rock-pools; pH 6.7, highly saline (20‰). Number of species identified: 35, of these 4 described as new in this book; number of unidentified species: 2, all likely undescribed (new); total number of species: 37. Remarks: annual rainfall 50–100 mm; collected on 15.02.1994, investigated on 17.03.2000. *Lamtostyla hyalina* lacks single bristle composing dorsal bristle row 1. Only 1 of the 4 new species has its type location here.

Site 9: Southern Namib Desert and succulent steppe, about 50 km east of the town of Lüderitz, at main road traversing the Namib Desert (26°40'S 15°40'E). Material collected: litter, mud, and sand of a flat, dried puddle near the road, litter mixed with excrements of small mammals; pH 6.2. Number of species identified: 36, of these 1 described as new in this book; number of unidentified species: 0; total number of species: 36. Remarks: annual rain fall 50–100 mm; collected on 16.02.1994, investigated on 01.10.1999. *Dileptus terrenus*: extrusomes only in right half of proboscis; large extrusomes rod-shaped to slightly fusiform, about 7 µm long; small extrusomes rod-shaped, 2.5 µm long. The new species has its type location elsewhere.

Site 10 (Fig. 225): Southern Namib Desert and succulent steppe in the surroundings of the town of Lüderitz (26°40'S 15°10'E); Atlantic coast, Flamingo Bay. Soil very sandy and covered with a thin layer of filamentous green algae or cyanobacteria. Material collected: litter, roots of halophytes, and sand with algal cover; pH 7.5, highly saline (> 20‰). Number of species identified: 1; total number of species: 1. Remarks: annual rain fall 0–50 mm; collected on 16.02.1994, investigated on 03.11.1994. This sample probably contained too much salt; repeated change of the soil solution (water) did not alter the result.

Site 11 (Fig. 226, 227): Southern Namib Desert and succulent steppe in the Great Bay at the town of Lüderitz, about 1 km inshore from the Atlantic sea coast, in the area of the "living stones", a special kind of succulent plants that look like stones (26°40'S 15°10'E). Material collected: crust soil, mainly a thin algal layer, from small (5–20 cm) quartz stones and small, humous sand aggregates from the margin of the stones. The quartz stones are transparent and thus a rather rich algal flora ("window" flora; RUMRICH et al. 1989) can develop on the stone surface which is embedded in the sand; water is provided by fog condensing on the stones; pH 7.2, highly saline (20‰). Number of species identified: 17, of these 4 described as new in this book; number of unidentified species: 2; total number of species: 19. Remarks: annual rainfall 0–50 mm; collected on 17.02.1994, investigated on 27.06.1994. A rich ciliate fauna considering the poorness of the habitat and the extreme salinity. Soil percolate was changed several times because the sample soon became putrid, and to stimulate growth of ciliates at lower salt concentrations; furthermore, small quantities of the dry sample were suspended in distilled water. Only 2 of the 4 new species have their type location here.

Site 12: As in site 11. Material collected: litter and small stones sieved off sand accumulated around cushion plants plus plant roots with a thick mantle of sand and peeled epidermal cells; pH 6.2, highly saline (15‰). Number of species identified: 18, of these 3 described as new in this book; number of unidentified species: 0; total number of species: 18. Remarks: annual

rainfall 0–50 mm; collected on 17.02.1994, investigated on 11.10.1999. *Protospathidium serpens* with thick oral bulge, as described in the Antarctic population (FOISSNER 1996a). Sample became putrid, and thick iron-moulds developed two weeks after rewetting; thus soil solution was replaced by fresh tap water. The 2 new species have their type location elsewhere.

Site 13: Namib Escarpment in the desert and succulent steppe between the towns of Goageb and Aus, that is, at main road to the town of Lüderitz (26°40'S 16°50'E); semi-desert and savannah transition. Material collected: litter, roots and red soil between and under large cushions (about 1 × 1 m) of *Euphorbia* sp.; pH 6.5. Number of species identified: 16, of these 1 described a new in this book; number of unidentified species: 0; total number of species: 16. Remarks: annual rainfall 50–100 mm; collected on 16.12.1994, investigated on 02.08.1999. Micronucleus of *Colpoda edaphoni* as conspicuous as in type population.

Site 14: As in site 11. Material collected: lichens from succulent bushes; pH 6.6, highly saline (20‰). Number of species identified: 5, of these 1 described as new in this book; number of unidentified species: 0; total number of species: 5. Remarks: annual rain fall 0–50 mm; collected on 17.02.1994, investigated on 13.10.1994. The percolating soil water was replaced by tap water one week after rewetting to reduce salt concentration, whereupon *Rostrophrya namibiensis maldivensis* and *Colpoda ecaudata* appeared. The new species has its type location elsewhere.

Site 15: Escarpment of the southern Namib Desert, Sinclair Guest Farm, about 50 km northwest of the town of Helmeringhausen (25°40'S 16°20'E); semi-desert and savannah transition. Material collected: litter and soil between tree branches and pieces of the thick, fibrous bark of four camel-thorn trees (*Acacia erioloba*); pH 5.2. Number of species identified: 21, of these 0 described as new in this book; number of unidentified species: 0; total number of species: 21. Remarks: annual rainfall 100–150 mm; collected on 18.02.1994, investigated on 01.10.1999. The smooth variety of *Nivaliella plana* occurs. *Amphisiella magnigranulosa* small and posteriorly not narrowed.

Site 16: Dry roadside ditch at main road between the towns of Aus and Helmeringhausen at the escarpment of the southern Namib Desert (26°20'S 16°25'E); semi-desert and savannah transition. Material collected: litter, roots, and 0–2 cm mud and sand layer of the ditch; pH 6.2. Number of species identified: 30, of these 3 described as new in this book; number of unidentified species: 0; total number of species: 30. Remarks: annual rainfall 50–100 mm; collected on 18.02.1994, investigated on 31.05.1999. Soil solution (water) replaced by tap water one week after rewetting because of mass development of bacteria. *Urosomoida antarctica* has only 5–6 transverse and pretransverse cirri, while the type population has 7. *Gonostomum affine* has ellipsoidal cortical granules and lacks transverse cirri, indicating that it is a new species; but the matter is complicated (FOISSNER et al. 2001). The new species have their type location elsewhere. *Hemimastix amphikineta* FOISSNER et al., 1988 occurs.

Site 17: Sand dune at the escarpment of the southern Namib Desert between the towns of Aus and Helmeringhausen (26°05'S 16°35'E); semi-desert and savannah transition; dune overgrown by the dune grass *Stipagrostis* sp. and nicely populated by a variety of insects, especially tenebrionids. Material collected: plant remnants and roots sieved off the sand around *Stipagrostis* shrubs at a depth of 0–10 cm; ph 5.4. Number of species identified: 17, of these 2 described as new in this book; number of unidentified species: 2; total number of species: 19. Remarks: annual rainfall 50–100 mm; collected on 18.02.1994, investigated on 21.12.1998.

Soil solution replaced by tap water three weeks after rewetting, whereupon the 2 new species developed. *Hemimastix amphikineta* FOISSNER et al., 1988 occurs.

Site 18: Wet soil from around a pond in the dwarf shrub savannah near the town of Maltahöhe (24°55'S 16°55'E); soil dark and anoxic below 2 cm. Material collected: litter, roots, and 0–2 cm soil layer around sedges shrubs; pH 9.2, highly saline (20‰). Number of species identified: 12, of these 2 described as new in this book; number of unidentified species: 0; total number of species: 12. Remarks: annual rainfall 150–200 mm; collected on 19.02.1994, investigated on 16.11.1994. A really extreme biotope where 2 new species were found, of which 1 has its type location in the USA. In vivo, *Semiplatyophrya foissneri* looks rather different to the original figure; thus, it will be redescribed later.

Site 19: Southern Namib Desert, small pan in southwest area of the Sossus Vlei (24°50'S 15°20'E). Material collected: upper 0–3 cm soil layer, that is, yellowbrown clay without any recognizable organic residues or roots; pH 6.3. Number of species identified: 2, of these 0 described as new in this book; number of unidentified species: 0; total number of species: 2. Remarks: annual rainfall 0–50 mm; collected on 20.02.1994, investigated on 15.03.1999. A very poor sample; no further species appeared when it was enriched with a few crushed wheat grains after three weeks.

Site 20: Southern Namib Desert, southwest region of Sossus Vlei (24°50'S 15°20'E). Material collected: plant residues, clay, and sand agglomerated during the last flood of the vlei; pH 7.0. Number of species identified: 15; of these 1 described a new in this book; number of unidentified species: 0; total number of species: 15. Remarks: annual rainfall 0–50 mm; collected on 20.02.1994, investigated on 25.07.1994. *Colpoda maupasi*, *E. augustini*, and *Peranema* sp. became very numerous three weeks after rewetting. The new species has its type location elsewhere.

Site 21 (Fig. 228): Southern Namib Desert, Death Vlei, that is, a vlei no longer flooded by the river, which changed the bed (24°50'S 15°20'E). Material collected: upper 0–3 cm soil layer, that is, yellowbrown clay without any recognizable organic residues or roots; pH 6.2. Number of species identified: 2, of these 0 described as new in this book; number of unidentified species: 0; total number of species: 2. Remarks: annual rainfall 0–50 mm; collected on 20.02.1994, investigated on 15.03.1999. A very extreme biotope without any green plants. The 2 species found, are r-selected colpodids. The sample was enriched with some crushed wheat grains three weeks after rewetting, but no further species developed.

Site 22 (Fig. 228): As in site 21. Material collected: pieces of decaying bark and wood from dead camel-thorn trees (*Acacia erioloba*); pH 6.2. Number of species identified: 7, of these 0 described as new in this book; number of unidentified species: 0; total number of species: 7. Remarks: annual rainfall 0–50 mm; collected on 20.02.1994, investigated on 19.10.1998. *Lamtostyla islandica* 70–120 µm long, that is, larger than the specimens from type population; nuclear apparatus and infraciliature, however, typical.

Site 23 (Fig. 229–231): Southern Namib Desert, centre of Sossus Vlei (24°50'S 15°20'E). Material collected: plant remnants sieved off the sand under *Nara* shrubs; pH 7.7; moderately saline. Number of species identified: 26, of these 5 described as new in this book; number of unidentified species: 1; total number of species: 27. Remarks: annual rainfall 0–50 mm; collected on 20.02.1994, investigated on 29.03.1994. This rather rich sample contained 5 new

species, of which 2 have their type location here. *Circinella filiformis* might be a distinct subspecies because the ventral cirral row is about twice as long as in the Austrian type.

Site 24: As in site 23. Material collected: sieved litter and humous sand under a camel-thorn tree (*Acacia erioloba*), up to a depth of 15 cm. Number of species identified: 21, of these 4 described as new in this book; number of unidentified species: 0; total number of species: 21. Remarks: annual rain fall 0–50 mm; collected on 20.02.1994, investigated on 18.12.1998. A rather rich sample with several new species, 2 of which have their type location here. The smooth variety of *Nivaliella plana* occurs.

Site 25: As in site 23. Material collected: dusty bark of camel-thorn trees (*Acacia erioloba*); pH 6.4. Number of species identified: 2, of these 1 described as new in this book; number of unidentified species: 0; total number of species: 2. Remarks: annual rainfall 0–50 mm; collected on 20.04.1994, investigated on 21.12.1998. Soil percolate was replaced by tap water after one week because bacteria became very numerous. *Nudiamphisiella interrupta* reproduced strongly. The new species has its type location here.

Site 26 (Fig. 232): Southern Namib Desert, dune 45 at road to the Sossus Vlei (24°50'S 15°30'E). Material collected: *Stipagrostis* and shrub remnants sieved off the sand, sample composed of about 80% plant residues and 20% sand; pH 6.2. Number of species identified: 31, of these 3 described as new in this book; number of unidentified species: 3; total number of species: 34. Remarks: annual rainfall 0–50 mm; collected on 20.02.1994, investigated on 06.07.1998. Ciliates were very numerous six days after rewetting the sample, especially *Pedohymena australiensis*, *Nivaliella plana* (both the smooth and ribbed variety), and *Spathidium namibicola*. This and the fairly high number of species show that ciliates may play an important role in the energy cycle of Namibian sand dunes. *Pseudoholophrya terricola* has rod-shaped extrusomes, as described originally. The new species have their type location elsewhere.

Site 27 (Fig. 233): Escarpment of the southern Namib Desert, small dune about 23 km west of the main gate in Sesrim village, near the road over the Sesrim Canyon (24°30'S 15°50'E); semi-desert and savannah transition; dune rather densely overgrown with *Stipagrostis*. Material collected: *Stipagrostis* (dune grass) and shrub remnants sieved off the sand, sample composed of about 95% plant residues and 5% sand; pH 5.4. Number of species identified: 24, of these 1 described as new in this book; number of unidentified species: 0; total number of species: 24. Remarks: annual rainfall 0–50 mm; collected on 20.02.1994, investigated on 15.03.1999. Soil solution (water) replaced by tap water after one week because of strong development of bacteria. The new species has its type location elsewhere.

Site 28 (Fig. 234): Surroundings of Büllsport Guest Farm in the escarpment of the southern Namib Desert (23°55'S 16°15'E); semi-desert and savannah transition; pass at begin of Aubschlucht (Aub Canyon) at about 1750 m sea-level. Material collected: bark from a vine-like, succulent plant; pH 6.6. Number of species identified: 23, of these 2 described as new in this book; number of unidentified species: 0; total number of species: 23. Remarks: annual rainfall 150–200 mm; collected on 21.02.1994, investigated on 09.07.1999. *Pseudouroleptus procerus* differs slightly from the original description in having at least three bristles in dorsal kinety 1 and minute (< 0.5 µm), pale cortical granules around the bases of the cirri and dorsal bristles. The new species have their type location elsewhere.

Site 29 (Fig. 235): As in site 28; mid-region of Aubschlucht. Material collected: mud from dry rock-pools along the stream in the Aubschlucht; pH 7.5. Number of species identified: 41, of these 5 described as new in this book; number of unidentified species: 2; total number of species: 43. Remarks: annual rainfall 150–200 mm; collected on 21.02.1994, investigated on 02.11.1994. *Maryna atra* matches the Italian population described by FOISSNER (1993a), however, specimens are rather distinctly flattened. *Vermioxytricha muelleri* lacks cortical granules. Extrusomes of *Dileptus terrenus* very similar to those of → *D. mucronatus*. One of the 5 new species has its type location here. A rare, conspicuous flagellate occurred: *Tetradimorpha* sp.

Site 30 (Fig. 236): As in site 28; near end of Aubschlucht, at the so-called Riedloch, a small, pond-like inflation of the stream in the centre of the Aubschlucht. Material collected: 0–10 cm soil layer from around the pond, which is surrounded by sedges and *Ficus* trees; soil dark, very humous, with much litter and some roots; pH 7.7. Number of species identified: 65, of these 7 described as new in this book; number of unidentified species: 3, of these 1 likely undescribed (new); total number of species: 68. Remarks: annual rainfall 150–200 mm; collected on 21.02.1994, investigated on 02.11.1994. A very rich sample with many rare and new species. *Bryophyllum loxophylliforme* with about 10 macronuclear nodules. Extrusomes of *Pseudoholophrya terricola* rod-shaped, as in type population. Extrusomes of *Spathidium anguilla* fusiform, macronucleus, however, a tortuous strand. Three of the 7 new species have their type location here.

Site 31 (Fig. 237, 238): Central Namib Desert, at road margin between Welwitschia drive and Bloedkoppie, about 100 km east of Swakopmund (22°45'S 15°25'E); a very meagre, tree-less region with few plants. Material collected: litter and 0–2 cm soil layer under *Welwitschia* shrubs and decaying blossoms from a succulent shrub; pH 6.4; slightly saline (5‰). Number of species identified: 27, of these 5 described as new in this book; number of unidentified species: 0; total number of species: 27. Remarks: annual rainfall 0–50 mm; colleted on 22.02.1994, investigated on 04.05.1998. A rather rich sample containing 4 of the new species described in this book. *Lamtostyla islandica* has only 1–2 transverse cirri. Extrusomes of *Enchelys terrenum* exactly as in type population. *Colpoda maupasi* become numerous 10 days after rewetting the sample. Only 1 of the 5 new species has its type location here.

Site 32 (Fig. 237, 238): Central Namib Desert, Welwitschia Plain (drive), about 80 km east of Swakopmund (22°40'S 15°15'E); a treeless area containing a rather high number of *Welwitschia mirabilis* individuals; soil poor, that is, a mixture of sand, gravel, and *Welwitschia* litter. Material collected: decaying leaves from *Welwitschia* trunks; pH 5.4. Number of species identified: 15, of these 1 described as new in this book; number of unidentified species: 0; total number of species: 15. Remarks: annual rainfall 0–50 mm; collected on 22.02.1994, investigated on 08.12.1998. The smooth variety of *Nivaliella plana* occurs. When we visited the site again in January 2001, many shrubs and plants were flowering. The new species has its type location elsewhere.

Site 33: Escarpment of central Namib Desert, about 20 km north of the village of Solitaire (23°50'S 16°E); semi-desert and savannah transition; a beautiful dune rich in plant debris and insects at west margin of main road. Material collected: organic debris and living roots of *Stipagrostis* sp. (dune grass) sieved off the sand to a depth of 10 cm; pH 7.6, slightly saline (5–10‰). Number of species identified: 47, of these 7 described as new in this book; number of unidentified species: 2, all likely undescribed (new); total number of species: 49. Remarks:

annual rainfall 50–100 mm; collected on 22.02.1994, investigated on 29.03.1994. A rich sample containing 7 of the new species described in this book; 4 of them even have their type location here, and the 2 unidentified species are also very likely undescribed, including a new colpodid genus. Unfortunately, these 3 rare species were not recognized in vivo and thus cannot be described. All 9 new species occurred a week after rewetting the sample! Later, diversity significantly decreased, possibly due to the intense sampling at day 7.

Further remarkable observations: The sample contains two "typical" freshwater species, viz., *Cinetochilum margaritaceum* and *Chilodonella uncinata*, which are rare in soil, especially the latter. The protargol preparations show that they are morphologically indistinguishable from the European freshwater strains, as described and illustrated in FOISSNER et al. (1991, 1994). *Protospathidium arenicola* and *Spathidium procerum* are easily confused in vivo, but distinct in the protargol slides due to the different shape of the circumoral kinety. Likewise, *Paragonostomum rarisetum* and *P. binucleatum* are easily confused, even in the protargol preparations. One of the unidentified species has the same size, shape, and nuclear apparatus as → *Apoenchelys bamforthi*, but possesses a distinct circumoral kinety and thus belongs to *Enchelyodon*! Another remarkable species is *Pleuroplitoides smithi* FOISSNER, 1996a, a rare species found in Namibia only in this sample; small individuals are easily confused with → *Diplites arenicola*!

Site 34 (Fig. 237, 238): As in site 32. Material collected: dry, decaying *Welwitschia* leaves; pH 5.4. Number of species identified: 13, of these 0 described as new in this book; number of unidentified species: 0; total number of species: 13. Remarks: annual rainfall 0–50 mm; collected on 22.02.1994, investigated on 18.12.1998. The water added for rewetting became a dark-brown, bacteria-rich soup and was thus replaced by tap water on days 7 and 20. *Colpoda steinii* was covered by epicortical bacteria. *Lamtostyla australis* was numerous and as described by BLATTERER & FOISSNER (1988). *Exocolpoda augustini* became very numerous seven days after rewetting the sample.

Site 35 (Fig. 237, 238): As in site 32. Material collected: litter and sandy soil under *Welwetschia* plants to a depth of 10 cm; pH 6.0. Number of species identified: 10, of these 0 described as new in this book; number of unidentified species: 0; total number of species: 10. Remarks: annual rainfall 0–50 mm; collected on 22.02.1994, investigated on 14.11.1998. The water added for wetting became a dark-brown, bacteria-rich soup and was thus replaced by tap water on day 2.

Site 36 (Fig. 239): Central Namib Desert, "Moon landscape" near the river oasis Goanikontes, about 25 km east of the town of Swakopmund (22°40'S 14°45'E); a very meagre basaltic (?) landscape with only a few grasses, ground however covered by a thin, greenish layer of lichens and algae because the region is heavily influenced by the Atlantic fog. Material collected: greenish crust soil as described above from small and large gravel; pH 6.0, moderately saline (10‰). Number of species identified: 8, of these 2 described as new in this book; number of unidentified species: 0; total number of species: 8. Remarks: annual rainfall 0–50 mm; collected on 22.02.1994, investigated on 27.12.1999. The water added for rewetting became a brown, gelatinous soup and was thus replaced by tap water on day 3. Two new species occurred at this extreme site, 1 has its type location here. In January 2001, the site was drier and looked poorer. One of the 2 new species has its type location here.

Site 37: Central Namib Desert, about 40 km north of the town of Swakopmund (22°10'S 14°25'E); conspicuously orange lichen lawn (*Teloschistes capensis*) at main road, about 1 km

inshore from the Atlantic. Material collected: lichen litter and the 0–2 cm soil layer under lichen carpets; pH 5.4, slightly saline (1‰). Number of species identified: 12, of these 2 described as new in this book; number of unidentified species: 1, likely a new *Colpoda* species related to *E. augustini*; total number of species: 13. Remarks: annual rainfall 0–50 mm; collected on 23.02.1994, investigated on 31.05.1999. The new species have their type location elsewhere.

Site 38: Central Namib Desert, Cape Cross, about 120 km north of the town of Swakopmund (21°50'S 14°E), road to seal colony. Material collected: various lichens, including *Teloschistes capensis* from ground, and gravel surface up to a depth of 2 cm. Soil brownish, sandy; pH 5.1, slightly saline (8‰). Number of species identified: 10, of these 0 described as new in this book; number of unidentified species: 0; total number of species: 10. Remarks: annual rainfall 0–50 mm; collected on 22.01.2001, investigated on 15.02.2001. A rich lichen flora stabilizes the soil surface.

Site 39 (Fig. 240): As in site 37, but a few km north in the central area of the lichen (*Teloschistes*) lawn; pH 5.8, saline (16‰). Number of species identified: 11, of these 2 described as new in this book; number of unidentified species: 0; total number of species: 11. Remarks: annual rainfall 0–50 mm; collected on 22.01.2001, investigated on 15.02.2001. The new species have their type location elsewhere.

Site 40: Escarpment of the central Namib Desert, Spitzkoppe area about 120 km northeast of the town of Swakopmund (21°45'S 15°08'E); semi-desert and savannah transition. Material collected: pieces from a decaying *Cyphostemma currorii* tree; pH 7.2. Number of species identified: 28, of these 1 described as new in this book; number of unidentified species: 0; total number of species: 28. Remarks: annual rainfall 50–100 mm; collected on 24.02.1994, investigated on 14.12.1999. Soil solution (water) replaced by tap water on days 3 and 20 after rewetting the sample because it soon became a darkbrown, mucous soup. *Gonostomum affine* unusual because it has highly refractile cortical granules about 1 × 0.5 µm in size and lacks transverse cirri. Extrusomes of *Pseudoholophrya terricola* rod-shaped, as in type population. *Sorogena stoianovitchae* easily recognized by the typical body shape and oral dome; sorocarps not observed; fed exclusively on *Colpoda elliotti*. Macronucleus of *Epispathidium ascendens* as in type population, that is, tortuous at ends, straight in mid-region. The new species has its type location elsewhere.

Site 41 (Fig. 241): As in site 40; granitic rock-pools partially covered with grasses (e.g., *Aponogeton desertorum*) and/or containing conspicuous branchiopods. Material collected: mud and grass roots from deep, dry rock-pools; pH 5.8. Number of species identified: 55, of these 6 described as new in this book; number of unidentified species: 1; total number of species: 56. Remarks: annual rainfall 50–100 mm; collected on 24.02.1994, investigated on 16.02.2000. A rich sample containing 6 of the new species described in this monograph. Both the smooth and ribbed variety of *Nivaliella plana* occur. The extrusomes of → *Trachelophyllum apiculatum* are simple, about 10 µm long rods, and the mucilaginous cortical layer is very inconspicuous. *Halteria grandinella* often has three bristles posteriorly, resembling *Pelagohalteria*. *Circinella filiformis* deviates rather distinctly from the Austrian type: frontoventral row longer, two cirri left of frontoventral row, buccal cirrus composed of four cilia, micronuclei distinctly ellipsoidal. The unidentified species is likely a new colpodid genus. Two of the 6 new species have their type location here.

Site 42: As in sites 40 and 41. Material collected: mud from flat rock-pools without grass; pH 6, not saline. Number of species identified: 27, of these 1 described as new in this book; number of unidentified species: 3, of these 1 likely undescribed (new); total number of species: 30. Remarks: annual rainfall 50–100 mm; collected on 24.02.1994, investigated on 17.03.2000. The new species has its type location elsewhere.

Site 43 (Fig. 242): Escarpment of the central Namib Desert, surroundings of the Ameib Guest Farm, about 120 km northeast of the town of Swakopmund (21°50'S 15°35'E); on way to Phillips cave with rock paintings; semi-desert and savannah transition. Material collected: plant litter and 0–5 cm soil layer with grass roots under trees and shrubs; soil very sandy and rather humous; pH 6.2. Number of species identified: 52, of these 9 described as new in this book; number of unidentified species: 7, of these 2 likely undescribed (*Sikorops* spp.); total number of species: 59. Remarks: annual rainfall 150–200 mm; collected on 25.02.1994, investigated on 31.01.2000. A rich sample containing 8 of the new species described in this book. Both the smooth and ribbed variety of *Nivaliella plana* occur. *Gonostomum kuehnelti* has, like the type population, four transverse cirri in quadrangular pattern. Left polykinetid of *Bresslaua insidiatrix* composed of 10–12 kineties. *Dileptus americanus* has two size-types of extrusomes: type 1 rod-shaped, 5–6 µm long and rather thick; type 2 rod-shaped, 2 µm long and very fine. Two of the 8 new species have their type location here.

Site 44: As in site 43. Material collected: grass roots with an up to 5 mm thick cover of sand and peeled root cells; pH 6.0. Number of species identified: 16, of these 0 described as new in this book; number of unidentified species: 1 (a suctorian swarmer); total number of species: 17. Remarks: annual rainfall 150–200 mm; collected on 15.02.1994, investigated on 31.01.2000. The ribbed variety of *Nivaliella plana* and *Hemimastix amphikineta*, a peculiar flagellate, occur.

Site 45: As in site 43. Material collected: flaky bark from *Sterkulia africana* trees; pH 5.4. Number of species identified: 18, of these 1 described as new in this book; number of unidentified species: 0; total number of species: 18. Remarks: annual rainfall 150–200 mm; collected on 25.02.1994, investigated on 07.03.2000. The new species has its type location here.

Site 46: As in site 43; in the garden of the Guest Farm. Material collected: paper-like bark from *Cyphostemma currorii* trees plus some soil from in between tree branches; pH 5.1. Number of species identified: 19, of these 0 described as new in this book; number of unidentified species: 0; total number of species: 19. Remarks: annual rainfall 150–200 mm; collected on 25.02.1994, investigated on 14.12. 1999. Soil solution became slightly putrid after one week and was thus replaced by tap water. Sample was kept rather dry three and four weeks after rewetting, but only 1 further species developed (*Platyophrya vorax*). *Colpoda maupasi* reached high numbers in the fourth week.

Site 47: Escarpment of the central Namib Desert, Omaruru River, where it crosses the main road between Spitzkoppe and the village of Unis Myn (21°25'S 15°05'E); semi-desert and savannah transition. Material collected: bark from a large *Combretum imberbe* (leadwood) tree. Number of species identified: 16, of these 1 described as new in this book; number of unidentified species: 0; total number of species: 16. Remarks: annual rainfall 100–150 mm; collected on 26.02.1994, investigated on 07.03.2000. The ribbed variety of *Nivaliella plana* occurs. The new species has its type location elsewhere.

Site 48: Escarpment of the central Namib Desert, at end of road to the Brandberg, a granitic island mountain at the northeast margin of the central Namib Desert (21°S 14°35'E); semi-desert and savannah transition. Material collected: 0–12 cm litter layer under a large *Combretum imberbe* (leadwood) tree; litter connected by many fungal hyphae; pH 6.7. Number of species identified: 43, of these 4 described a new in this book; number of unidentified species: 2, of these 1 likely undescribed (new); total number of species: 45. Remarks: annual rainfall 100–150 mm; collected on 26.02.1994, investigated on 17.03.2000. A rich sample with many rare and new species. The smooth variety of *Nivaliella plana* occurs. The extrusomes of *Pseudoholophrya terricola* are rod-shaped, as in the type population. Although numerous, *Opercularia curvicaule* did not form colonies. Two of the 4 new species have their type location here.

Site 49: Bambatsi Guest Farm between the towns of Khorixas and Outjo, 1150 m above sea-level (20°10'S 15°25'E); Mopane savannah. Material collected: dark grey mud and 0–2 cm soil layer, grass roots, and the orange and green algal cover from dry and wet puddles of roads within the farm; pH 6.7, not saline. Number of species identified: 126, of these 34 (!) described as new in this book; number of unidentified species: 15, of these 13 likely undescribed (new); total number of species: 141. Remarks: annual rainfall 250–300 mm; collected on 27.02.1994, investigated on 27.12.1999. The richest sample in the whole collection and that we ever had with many new and rare species. As the other samples from this region are also rich, the area is a local diversity centre. When we revisited the site in January 2001, all puddles were filled with sand and gravel because the roads had been upgraded. Thus, the type location of the new species found there disappeared. This population of *Plagiocampa pentadactyla* also has epicortical bacteria. A red and a red-blue variety of *Blepharisma steini* occur.

Site 50: As in site 49; alluvial grassland within the *Colophospermum mopane* forest surrounding the farm. Soil dark, very humous, with much litter and grass roots. Material collected: litter and soil up to a depth of 10 cm; pH 6.7. Number of species identified: 51, of these 3 described as new in this book; number of unidentified species: 2; total number of species: 53. Remarks: annual rainfall 250–300 mm; collected on 27.02.1994, investigated on 31.01.2000. *Balantidioides dragescoi* and *Enchelyodon terrenus* considerably smaller than in type populations. Extrusomes of *Pseudoholophrya terricola* rod-shaped and 5-6 µm long. The new species have their type location elsewhere.

Site 51: As in site 49. Material collected: thick, flaky bark from *Colophospermum mopane* trees; pH 6.0. Number of species identified: 46, of these 4 described as new in this book; number of unidentified species: 2, of these 1 likely undescribed (new); total number of species: 48. Remarks: annual rainfall 250–300 mm; collected on 27.02.1994, investigated on 07.03.2000. *Gonostomum affine* with distinct, rod-shaped cortical granules. The smooth variety of *Nivaliella plana* occurs. The macronuclear nodules of *Gonostomum kuehnelti* contain conspicuous protein crystals. *Spathidium spathula* as in population I in FOISSNER (1984). Three of the 4 new species have their type location here.

Site 52 (Fig. 243): As in site 49. Material collected: fresh cow dung globules made by a large *Scarabaeus* sp. in the Mopane forest; pH 6.7. Number of species identified: 28, of these 5 described as new in this book; number of unidentified species: 2, of these 1 likely undescribed (new); total number of species: 30. Remarks: annual rainfall 250–300 mm; collected on 27.02.1994, investigated on 07.03.2000. A rather rich sample considering the material investigated. One of the 5 new species has its type location here.

Site 53: Etosha National Park – Wolfsnes water-hole near the margin of the Etosha Pan (19°S 15°50'E); small salt bush (*Suaeda articulata*) island very near to the pan margin. Soil classification according to BUCH et al. (1994): (Hyper) calcaric Regosol - (Hyper) calcaric Arenosols - Haplic Calcisols (petrocalcic phase) from calcareous sediments above Etosha Limestone and Andoni Sand-/Siltstone. Soil in collection area is a loamy sand mixed with plant debris and covered by a thin layer of cyanobacteria. Material collected: litter and 0–5 cm soil layer; pH 8.9, highly saline (18‰). Number of species identified: 20, of these 6 described as new in this book; number of unidentified species: 2, of these 1 likely undescribed (new); total number of species: 22. Remarks: annual rainfall 350–400 mm; collected on 28.02.1994, investigated on 01.08.1994. Water-hole dry at collection time.

Site 54: As in site 53. Material collected: litter and soil from around decaying grass shrubbery about 500 m off pan margin; pH 8.0, highly saline (15‰). Number of species identified: 53, of these 16 (!) described as new in this book; number of unidentified species: 4, of these 2 likely undescribed (new); total number of species: 57. An outstanding sample containing 16 new species and subspecies, of which 5 have their type location here. Remarks: annual rainfall 350–400 mm; collected on 28.02.1994, investigated on 25.07.1994.

Site 55 (Fig. 244): Etosha National Park – Ghost tree (*Moringa ovalifolia*) forest (19°S 15°40'E). Material collected: paper-like bark and decaying wood from living and dead *Moringa* trees; pH 6.7, moderately saline. Number of species identified: 11, of these 1 described as new in this book; number of unidentified species: 0; total number of species: 11. Remarks: annual rainfall 350–400 mm; collected on 28.02.1994, investigated on 01.08.1994. The curious *Vorticella* (*Echinovorticella*) *echini* occurs in this habitat. The new subspecies has its type location here.

Site 56 (Fig. 244): As in site 55. Soil classification according to BUCH et al. (1994): (Lithi) Eutric/(Calcaric) Fluvisoils – Calcaric Regosols – Lithi/Rendzic Leptosols above/from Etosha Limestone. Soil at collection site grey and dust-like, very hard. Material collected: litter, grass roots, and soil from 0–5 cm; pH 7.8, slightly saline (< 10‰). Number of species identified: 55, of these 10 described as new in this book; number of unidentified species: 4, of these 1 likely undescribed (new); total number of species: 59. Remarks: annual rainfall 350–400 mm; collected on 28.02.1994, investigated on 29.03.1994. A rich sample, in spite of the meagre appearance of the soil. *Ilsiella palustris* (conspicuously egg-shaped), *Maryna antarctica* (length around 40 µm), and *M. minima* were already active 7h after rewetting, but encysted after about 20h! *Enchelyodon nodosus* as in population II described by BERGER et al. (1984). Five of the 10 new species have their type location here.

The following samples (57, 59, 60, 61, 62, 63) are a transect extending from the pan to the *Colophospermum mopane* forest. There is a strong gradient in all parameters, such as plant communities and soil salinity. Likewise, strong vertical gradients occur, as evident from salinity measurements in a hill around a *Suaeda* bush: 0–1 cm depth 130‰, 1–3 cm 55‰, 3–5 cm 18‰, 5–10 cm 8%, 10–20 cm 8‰. Obviously, salt accumulates in the upper 5 cm soil layer due to the strong evaporation. Soil classification according to BUCH et al. (1994) for sites 57–62: (Gleyi) – Verti – (Hyper) calcari (Hyper) salic Fluvisols above Andoni Sand-/Siltstone. Vegetation, see figure 1. A lot of new species occur in these samples, especially in the saline habitats. Certainly, there are many more!

Site 57 (Fig. 245–251): Etosha National Park – lookout site "Pan" (19°10'S 15°55'E); about 100 m inside the pan, which was dry on the surface but wet underneath. The pan is a saline desert sparsely grown with grass (*Sporobolus salsus*) and partially covered with a thin layer of cyanobacteria. The pan soil is a particular mixture of clay, lime, and salt having a pH around 9; when dry, the mass is like a stone, but doubles its volume and becomes a fluffy pancake when saturated with water (Fig. 250, 251). The surface of the non-flooded Petri dish cultures was covered by a mat of filamentous and coccal cyanobacteria, providing an ideal biotope for cyanobacteria-feeding ciliates (Fig. 247–249). Material collected: soil and grass roots from 0–20 cm plus scraping from the soil surface with the cyanobacterial crust; pH 8.7, highly saline (15‰). Number of species identified: 34, of these 11 described as new in this book; number of unidentified species: 2, of these 1 likely undescribed (a new *Sikorops* with monilate macronucleus and conspicuous bulge); total number of species: 36. Remarks: annual rainfall 350–400 mm; collected on 01.03.1994, investigated on 09.05.1994. A considerable number of species, of which 11 (!) are described as new in this book, considering the extremity of the biotope. *Oxytricha granulifera quadricirrata* contained pieces of filamentous cyanobacteria in the food vacuoles. Only 3 of the 11 new species have their type location here.

Site 58 (Fig. 252): Etosha National Park – lookout site "Pan" (19°10'S 15°55'E). Material collected: dry and moist crusts of cyanobacteria at pan margin, that is, between sites 57 and 59; pH 8.7; extremely saline (20‰). Number of species identified: 8, of these 2 described as new in this book; number of unidentified species: 0; total number of species: 8. Remarks: annual rainfall 350–400 mm; collected on 01.03.1994, investigated on 09.05.1994. Rather few species, although the cyanobacteria grew well in the non-flooded Petri dish culture. *Plagiocampides halophilus* became very numerous a week after rewetting. *Homalogastra setosa* has a single macronuclear nodule. The new species have their type location elsewhere.

Site 59 (Fig. 253–256): Etosha National Park – lookout site "Pan" (19°10'S 15°55'E); salt bush (*Suaeda articulata*, *Salsola etoshensis* etc.) girdle 10–20 m off pan margin. Soil a sandy loam mixed with much darkbrown plant debris providing the mass a spongy consistency. Material collected: litter, roots, and soil around and under salt bushes up to a depth of 20 cm; pH 9.0; extremely saline (80‰). Number of species identified: 7, of these 4 described as new in this book; number of unidentified species: 1 (likely undescribed); total number of species: 8. Remarks: annual rainfall 350–400 mm; collected on 01.03.1994, investigated on 09.05.1994. Three of the 7 species identified are described as new in this book and 1 was described earlier (*Arcuospathidium vlassaki* FOISSNER, 2000d)! Two of the 4 new species have their type location here.

Site 60 (Fig. 253, 257): Etosha National Park – lookout site "Pan" (19°10'S 15°55'E); mixed grass (*Sporobolus* sp.) and salt bush (*Suaeda articulata* etc.) girdle about 100 m off pan margin. Soil red or grey, depending on microhabitat, covered by a crust of filamentous cyanobacteria, contains many roots. Material collected: soil and roots around and under grass and salt bush shrubbery plus some pieces of the cyanobacterial crust; pH 8.6, slightly saline (10‰). Number of species identified: 49, of these 9 described as new in this book; number of unidentified species: 0; total number of species: 49. Remarks: annual rainfall 350–400 mm; collected on 01.03.1994, investigated on 09.05.1994. A very rich sample containing 9 of the new species described in the book! Four of the 9 new species have their type location here. The ribbed variety of *Nivaliella plana* occurs.

Site 61: Etosha National Park – lookout site "Pan" (19°10'S 15°55'E); about 10 m wide sedge girdle between sites (59) and (60). Sedges grow on a limestone plate about 10 cm under soil surface. Soil is a yellow, sandy loam. Material collected: litter from soil surface, sedge roots, and soil up to 10 cm; pH 9.0, extremely saline (40‰). Number of species identified: 15, of these 8 described as new in this book; number of unidentified species: 5; total number of species: 20. Remarks: annual rainfall 350–400 mm; collected on 01.03.1994, investigated on 30.05.1994. Five of the 8 new species have their type location here. Two of the 5 unidentified species are likely undescribed. Thus, half of the 20 species found are new!

Site 62 (Fig. 258): Etosha National Park – lookout site "Pan" (19°10'S 15°55'E); thorn-bush girdle (savannah; *Acacia nebrownii* [dominant], *Cyathula hereroensis*, *Leucosphaera bainesii*, *Petalidium engleranum*, *Salsola etoshensis*) about 1 km off pan margin. Soil grey and dusty, little litter and humus. Material collected: litter, roots, and soil from 0–10 cm depth; pH 7.7, not saline. Number of species identified: 28, of these 1 described as new in this book; number of unidentified species: 2, of which 1 likely undescribed (a new *Urosoma* with conspicuous cortical granules); total number of species: 30. Remarks: annual rainfall 350–400 mm; collected on 01.03.1994, investigated on 09.05.1994. Soil solution (water) became putrid and was thus replaced by tap water one week after rewetting. The smooth and ribbed variety of *Nivaliella plana* occurs. Cortical granules of *Amphisiella magnigranulosa* very conspicuous (large). The new species has its type location elsewhere.

Site 63 (Fig. 259): Etosha National Park – Aus water-hole (19°10'S 16°10'E); *Colophospermum mopane* girdle about 15 km off pan margin. Soil classification according to BUCH et al. (1994): Calcaric Fluvisol – Calcaric Regosols above Etosha Limestone and Calcrete. Soil brown and humous at collection site, base rock dolomitic. Material collected: litter, roots, and soil from 0–10 cm depth; pH 7.7, not saline. Number of species identified: 35, of these 0 described as new in this book; number of unidentified species: 2, of these 1 likely undescribed (new); total number of species: 37. Remarks: annual rainfall 400–450 mm; collected on 01.03.1994, investigated on 30.05.1994. *Bresslaua insidiatrix* and *Colpoda orientalis* exactly as described in FOISSNER (1993c).

Site 64: Etosha National Park – Aus water-hole (19°10'S 16°10'E); waterhole dry and overgrown with grasses, some sedges and limestone blocs in centre. Material collected: litter, roots, and soil from 0–5 cm in central area of water-hole; pH 6.3, slightly saline (0.5‰). Number of species identified: 36, of these 2 described as new in this book; number of unidentified species: 4, of these 2 likely undescribed (new); total number of species: 40. Remarks: annual rainfall 400–450 mm; collected on 01.03.1994, investigated on 21.12.1998. Although there was considerable growth of filamentous cyanobacteria in the rewetted sample, only 2 nassulids developed. *Protospathidium serpens* as described by FOISSNER (1996a) from Antarctica. Two varieties of *Spathidium claviforme* occur: one as described by FOISSNER (1987b) and a more slender, almost cylindroidal form with 4 µm long extrusomes and about 10 ciliary rows. One of the 2 new species has its type location here.

Site 65 (Fig. 260, 261): Etosha National Park – road to the Halali rest camp (18°55'S 16°25'E); small, saline pan with many nice halophyte shrubs and grass in between. Soil classification according to BUCH et al. (1994): Calcaric Fluvisols – Calcaric Regosols above Etosha Limestone and Calcrete. Soil loamy and covered with a green algal crust at collection site. Material collected: litter, algal crust, grass and shrub roots, and soil from 0–10 cm; pH 8.0, extremely saline (20‰). Number of species identified: 36, of these 7 described as new in this

book; number of unidentified species: 4, of these 1 likely undescribed (new); total number of species: 40. Remarks: annual rainfall 400–450 mm; collected on 01.03.1994, investigated on 30.05.1994. Although extremely saline, a rich sample containing 7 of the new species described in this book. *Holosticha stueberi* lacks distinct transverse cirri and has 7–9 dorsal kineties, indicating that it might be a distinct subspecies. *Pseudoplatyophrya saltans* distinctly jumps, but has the cortex as deeply furrowed as *Grossglockneria hyalina*.

Site 66: Etosha National Park – Halali rest camp (19°S 16°30'E); dolomitic rock-pools between *Moringa ovalifolia* trees on a dolomitic Inselberg in the camp. Material collected: leaf litter and soil-like mud from bottom of rock-pools; pH 7.2. Number of species identified: 16, of these 1 described as new in this book; number of unidentified species: 0; total number of species: 16. Remarks: annual rainfall 400–450 mm; collected on 01.03.1994, investigated on 25.07.1994. This is a rather low number of ciliate species for such a biotope, possibly because the mud is full of rotifers, several of which are fully active a few minutes after rewetting the sample; indeed, when these species are air-dried on a slide in a drop of water, they become active again within a few minutes after water is added; this game can be repeated several times! KOSTE (1996) identified 24 rotifer species in this sample, including 4 new species: *Dissotrocha decembullata* n. sp., *D. hertzogi aculeata* n. ssp., *Otostephanus jersabeki* n. sp., and *Philodina foissneri* n. sp. As concern ciliates, → *Wolfkosia loeffleri* is remarkable because this curious species was known only from the Costa Rican type location.

Site 67: Etosha National Park – lookout "Etosha" (18°50'S 16°30'E); *Sporobolus* girdle about 1 km off pan margin. Soil classification according to BUCH et al. (1994): (Psammi) Lithic/Rendzic Leptosol – (Hyper) calci Sodic Solonchaks – (Hyper) calcaric Regosols from Etosha Limestones, partly from calcareous sediments above Etosha Limestone. Soil at collection site loamy and covered with a slimy, green algal layer, which becomes orange when dry. Material collected: grass litter, roots, and soil from 0–5 cm; pH 9.7, extremely saline (20‰). Number of species identified: 19, of these 8 described as new in this book; number of unidentified species: 5, of these 3 likely undescribed (new); total number of species: 24. Remarks: annual rainfall 400–450 mm; collected on 02.03.1994, investigated on 13.05.1994. A conspicuous number of species, including many new ones, considering the extremity (pH 9.7) of the habitat! Four of the 7 new species have their type location here.

Site 68: As in site 67. Material collected: dry algal crust as described at site 67; pH 9.4, extremely saline (> 20‰). Number of species identified: 2, of these 1 described as new in this book; number of unidentified species: 0, total number of species: 2. Remarks: annual rainfall 400–450 mm; collected on 02.03.1994, investigated on 01.08.1994. Only bacteria developed during the first week after rewetting; thus, the highly saline run-off was replaced by tap water, whereupon 2 species appeared. The new species has its type location elsewhere.

Site 69: Etosha National Park – Okerfontein water-hole (18°45'S 16°45'E); swamp around spring. Soil classification according to BUCH et al. (1994): (Psammi) Lithic/Rendzic Leptosols – (Hyper) calci Sodic Solonchaks – (Hyper) calcaric Regosols from Etosha Limestone, partly from calcareous sediments above Etosha Limestone. Material collected: litter and dark, wet soil around sedges and grass shrubbery from 0–5 cm plus pieces of the dry, orange algal crust on the soil surface; pH 9.7; extremely saline (20‰). Number of species identified: 13, of these 3 described as new in this book; number of unidentified species: 2, of these 1 (an *Apertospathula*) undescribed (new); total number of species: 15. Remarks: annual rainfall

450–500 mm; collected on 02.03.1994, investigated on 13.05.1994. Interestingly, the water is not saline.

Site 70: Etosha National Park – Okerfontein water-hole (18°45'S 16°45'E); salt-bush (*Suaeda* spp.) and grass (*Sporobolus* spp.) girdle near the toilet. Soil classification, see site 69. Material collected: litter with cyanobacteria crusts, roots, and soil up to 5 cm depth; pH 8.4, highly saline (15‰). Number of species identified: 69, of these 17 described as new in this book; number of unidentified species: 6, of these 1 likely undescribed (new); total number of species: 75. Remarks: annual rainfall 450–500 mm; a very rich sample containing 15 of the new species described in this book! Two of the 17 new species have their type location here. Identifications of *Euplotes muscicola* and *Pseudovorticella sphagni* were checked in silver nitrate preparations. Collected on 2.3.1994, investigated 1.8.1994.

Site 71: Etosha National Park – margin of Fischer's Pan, near bridge (18°45'S 16°55'E). Material collected: decaying aquatic plants and cyanobacterial crusts from pan margin; pH 7.6, extremely saline (20‰). Number of species identified: 10, of these 2 described as new in this book; number of unidentified species: 2, both likely undescribed; total number of species: 12. Remarks: annual rainfall 450–500 mm; collected on 02.03.1994, identified on 30.05.1994. Sample became a bacteria/nematode soup after three weeks.

Site 72: Windhoek, Daan Viljoen Game Park (22°35'S 17°05'E). Material collected: bark from a camel-thorn tree (*Acacia erioloba*) in the highland savannah; pH 5.4. Number of species identified: 14, of these 0 described as new in this book; number of unidentified species: 0; total number of species: 14. Remarks: annual rainfall 350–400 mm; collected on 04.03.1994, investigated on 02.08.1999. *Colpoda steinii* has a conspicuous preoral bulge; such a variety was observed also in Venezuela and might be a distinct subspecies. The macronucleus of *Plagiocampa difficilis* has a central nucleolus, as in the type population. The ribbed variety of *Nivaliella plana* occurs.

Site 73: As in site 72; granitic rock-pools in a stream below the dam. Material collected: dry and moist mud from rock-pools; pH 6.2. Number of species identified: 35, of these 6 described as new in this book; number of unidentified species: 6, of these 4 likely undescribed (new); total number of species: 41. Remarks: annual rainfall 350–400 mm; collected on 04.03.1994, investigated on 02.08.1999. A rather rich sample containing 6 of the new species described in this book, 3 of them have their type location here.

2.2 Methods

2.2.1 Sampling and Sample Processing

The material collected usually included mineral top soil (0–5 cm, rarely up to 10 cm depth) with fine plant roots, the humic layer, and the deciduous and/or grass litter from the soil surface. In soil with few organic materials and very sandy habitats, especially in the Namib Desert, litter was sieved off the sand with an ordinary kitchen sieve (1 mm mesh-size), so that the final sample consisted of about 80% litter and 20% sand and gravel. Usually, 10 small subsamples were collected with a small shovel from an area of about 100 m^2 and mixed to a composite sample. Bark samples were usually taken from one to three trees. The bark was

collected with a knife, selecting for regions grown with mosses or lichens and/or containing some soil.

Generally, a "good" sample consists of 50% litter, humus and roots and 50% mineral soil. The litter and humus are very important because they release many nutrients when the sample is rewetted, stimulating growth of bacteria, fungi, flagellates, and amoebae, that is, the main food of ciliates. The nutrient increase obviously decouples microbiostasis, as explained in FOISSNER (1997d).

All samples were air-dried for at least one month and then sealed in plastic bags. Such samples can be stored for years without any significant loss of species, provided they are from arid or temperate environments (FOISSNER 1997d). This is emphasized by the present investigations: there is no correlation between storage time and species number; indeed, the richest samples (nos. 4, 49) are those stored for over four years (details, see chapter 3.1.1).

All collections were analysed with the "non-flooded Petri dish method", as described by FOISSNER (1987d, 1992). The technique is not perfect, but likely the best available for biodiversity assessment of soil ciliates at large (for details, see chapter 3.1.1). The protocol is simple (Fig. 262).

1. Put the material in a Petri dish and spread over the bottom of the dish in at least a 1 cm, better 2 to 3 cm thick layer. As concerns the Namibian samples, sufficient material was available to fill a 2 cm high Petri dish 13 cm across or, rarely, a 3 cm high dish 18 cm in diameter. Basically, a large Petri dish (18 cm) is preferable because it provides more material for preparations.

2. Slightly over-saturate but do **not** flood the sample with distilled water. Water should be added to the sample until 5–20 ml will drain off when the Petri dish is tilted (45°) and the soil gently pressed with a finger. Complete saturation takes up to 12 hours, so check cultures after this time. Never flood the sample, that is make an Aufguss ("infusion") because then only a few common species will develop. Further, the material should have been dry for at least one month.

3. Cover Petri dish and pinch a clip between bottom and lid to enable gas exchange. Generally, care must be taken that samples do not putrefy. This happens rather easily with saline material, soil containing animal excrements or, in "ordinary" samples, if the litter is very easily decomposable. In this case, change the water in the sample and do not cover it for some days so that plenty of air is available; further, slightly under-saturate sample with water. Heavily saline soil (≥ 20‰) should be "washed", if no ciliates develop. Saturate the sample with water, as described above. After two to three days, remove the percolate and saturate again with water. Repeat two to four times, until ciliates begin to develop.

4. A distinct succession occurs in the rewetted samples. Thus, they must be inspected on days 2, 6/7, 13/14, 21/22, and 30. Later inspections usually add only few species, likely because microbiostasis (ciliatostasis; see FOISSNER 1987d) increases and metazoan (rotifers, nematods) and protozoan (mainly heliozoans!) predators often became abundant. For inspection, the Petri dish is tilted some seconds and a rather large drop (~ 0.3 ml) of the drained water ("soil percolate") taken with a Pasteur pipette and inspected for species; several such drops must be investigated from different sites of the Petri dish, until the last drop adds but few species.

2.2.2 Identification of Species, Collection of Material for Preparations, other Culture Methods

Identification: Provided sufficient experience, many ciliate species can be identified from life at low magnification (×100–200). Of course, details must be checked at high magnification (×1000, oil immersion), preferably with interference contrast optics. All "difficult", new, or supposedly new, species must be treated with the silver impregnation techniques described below. Accordingly, our species lists are a mixture of taxa identified in vivo and/or silver preparations. However, we emphasize that all species were seen in silver slides, at least from one site. Thus, seen on a whole, all species were observed in vivo and silver preparations. Identification literature is highly scattered and cited in the reference section and FOISSNER (1998a). Still indispensable are KAHL's monographs and, for colpodids and oxytrichid hypotrichs, the recent reviews by FOISSNER (1993c) and BERGER (1999); for euplotids, peritrichs and suctorians, the reviews by CURDS (1986) and WARREN (1986) are very useful. Keys for limnetic or marine ciliates are almost useless because only about 25% of the species occur both in terrestrial and limnetic habitats.

Collection of Material for Preparations: If a "difficult" species is noted, which happens in more than 70% of the samples, material for preparations must be collected. To obtain many specimens, the Petri dish is tilted (45°) several times for a minute or so and the percolating soil water collected with a Pasteur pipette from several sites of the dish. If only little water (< 10 ml) drains from the sample and/or the species of interest is very rare, it should be sprinkled with 10–15 ml distilled water. This will cause an osmotic shock, detaching or rinsing many specimens from the soil particles and capillaries within about 10 min. Then, the procedure described above is repeated, that is, the Petri dish is tilted several times and the percolating soil water added to the first collection. Finally, the soil sample is again saturated with clean table water (e.g. Eau de Volvic) and stored for the next investigation. Certainly, these procedures strongly change the milieu, and thus a rather different ciliate community may develop, possibly containing further "difficult" species. If so, the whole procedure is repeated, and so on.

Much care must be taken to keep the percolate clean of large (> 2 μm) soil particles, which would disturb the investigation of the preparation, while particles smaller than 2 μm hardly disturb, if not too numerous. To achieve clean material, note the following advice:

1. Usually, the percolating soil water which contains the organisms will be clean because the soil particles soon become stabilized by microbial activities, mainly by fungal hyphae and bacterial mucilage. Thus, extreme care must be taken not to destroy the soil structure developed in the non-flooded Petri dish culture. Accordingly, the Petri dish must be handled gently and, if necessary, distilled water sprinkled softly on the surface. To increase percolation, mild finger pressure on the soil may be applied. Depending on the material sampled, the percolate has a light brown to orange colour (from lignins, humus colloids, etc.), which does not disturb the preparations (but see below).

2. The percolate is now gently shaken and large soil particles allowed to settle for about one minute. Then, the supernatant, which is now ready for preparations, is collected with a Pasteur pipette. Be careful not to lose bottom-dwellers. Occasionally, it may be helpful to sieve the percolate through a plankton net with 50–100 μm mesh-size or to concentrate it by mild centrifugation (max. 2000r/min for a few seconds), especially for preparations

with expensive chemicals (osmium tetroxide in CHATTON-LWOFF silver nitrate impregnation).

Other culture methods: The non-flooded Petri dish cultures, as described above, provided about 90% of the material contained in the monograph. The rest is from a variety of ordinary "limnetic" cultures. First, clone cultures were made in the usual way by transferring individual specimens into various media, preferably Eau de Volvic (French table water), either pure or mixed with soil extract in a ratio of 10:1 and enriched with a crushed and two uncrushed wheat grains to stimulate growth of indigenous food organisms, viz., bacteria and small flagellates; occasionally, selected food items were added, for instance, filamentous cyanobacteria for several nassulids. Second, 2 ml of the percolate (together with all organisms) were mixed with 8 ml Eau de Volvic and enriched with wheat grains, as described above. Of course, such cultures contain a variety of ciliates, and sometimes interesting species develop for a while. Third, a Petri dish was filled with 10–20 µm culture medium plus some wheat grains. Then some grams of soil are added as an inoculate to a small site of the Petri dish, taking care not to distribute it throughout the medium. Such cultures were sometimes helpful for strongly saline material (> 20‰), which is set up with artificial sea-water.

Fourth, if the sample is very saline (> 20‰), it may occur that no ciliates develop. Such samples can be "washed" every third day with fresh table water, which decreases the salt concentration. Frequently, ciliates appear after the third or fourth wash!

2.2.3 Morphological Methods

The methods used for in vivo observation and preparations were the same as described in FOISSNER (1991). Thus, the reader is referred to this paper. Occasionally, other methods were applied; these are mentioned in the respective species descriptions. As concerns protargol impregnation, protocol A (PA) is "FOISSNER's method", while protocol B (PB) is "WILBERT's method".

Scanning electron microscopy of ciliates contained in the percolate was difficult because the fine soil particles adhering to the hairy specimens and /or soil colloids more or less completely precipitated during fixation. Thus, good results were usually obtained only from pure cultures as described above.

2.2.4 Description of Species, Morphometry, and Illustrations

Our study contains only species observed both in vivo and silver preparations, as minimal requirements for a solid description, morphometry, and illustration; light and scanning electron micrographs were prepared whenever possible.

Species descriptions were performed in telegramese style, as is good practice among experienced taxonomists, a fact often overlooked by protozoologists, who prefer prose style, which makes the description unnecessarily long and circumstantial. Furthermore, each of the new or improved taxa is headed by a brief "diagnosis", containing only those features which, in our opinion, separate the species from its nearest relatives, as already emphasized by LINNÉ. A "diagnosis" is not an abbreviated description, as is often assumed, and is thus usually very short.

Usually, our descriptions have a certain order, namely that used in identification: body size and shape; nuclear apparatus; contractile vacuole; cortex and extrusomes; cytoplasm and food; movement; somatic and oral ciliary pattern; occurrence and ecology; comparison with related species. Within the individual items, location of the structure comes first, followed by its shape and size.

Morphometry is indispensable for a good description of a ciliate and was performed on 10–20 randomly selected, well-impregnated specimens. The data is tabulated and thus repeated in the descriptions only if needed for clarity. Most observations were from material as obtained with the non-flooded Petri dish method, that is, not from clone cultures. Thus, we cannot exclude that similar but different species were sometimes confused, although this is unlikely because we excluded specimens which deviated in at least one prominent feature. Certainly, this can generate some bias in the data if used too uncritically. However, we usually excluded only such specimens which had, e.g., a different nuclear structure (likely often postconjugates), a distinctly deviating ciliary pattern (likely often injured, regenerating or malformed specimens), an unusually small size (likely often degenerating, just excysted or divided specimens), or a combination of deviating features. The inclusion of such individuals, which might sometimes belong to another species, would have artificially increased variability.

In vivo measurements of body size were performed at a magnification of ×100–250, while details such as extrusomes and food vacuoles were measured at ×1000, where a measuring unit of the ocular micrometer is 1 μm. Likewise, all measurements of prepared cells were at a magnification of ×1000. Measuring body size in vivo provided only rough values because the cells were moving. We used these data mainly as a kind of control for shrinkage due to the preparation procedures. Thus, the in vivo body size given for a certain species is a composite from a few representative live specimens and the data obtained from the silver slides, assuming a shrinkage of 10–20% in protargol preparations and of 5–10% in silver nitrate slides (DRAGESCO & DRAGESCO-KERNÉIS 1986; own unpubl. observ.). Standard deviation and coefficient of variation were calculated according to statistics textbooks.

Illustrations of live specimens were based on free-hand sketches and/or micrographs and video prints. Generally, our main in vivo illustration of a certain species represents a summary of the observations, that is, shows a "representative" specimen composed on observations of live and prepared cells. Illustrations of prepared cells were made with a camera lucida and show the specimens as they are, smoothed only by removing obvious artifacts. Great care was taken to make these illustrations accurate and beautiful; usually, a "typical" specimen is shown with values near the arithmetic means.

Micrographs are an important supplement to any description, but often difficult to obtain because the cells are moving and/or out of the focal plane. Thus, much patience and skill is needed to produce meaningful micrographs. Even more helpful is scanning electron microscopy because it provides a three-dimensional view of the organism. Unfortunately, good scanning electron micrographs are difficult to obtain from soil ciliates for the reasons explained above. All these problems made it impossible to provide micrographs of all species described.

If not stated otherwise, all figures are orientated with the anterior end of the organism directed to the top of the page. Scale bars are given only in the line drawings because cells shown in the micrographs were often strongly flattened or shrunken (30–50% shrinkage are usual in scanning electron microscope preparations!).

2.3 Species/Subspecies Concept

The species concept, of course, influences the number of species found and/or recognized as undescribed (LUCKOW, 1995, MCDADE, 1995, TURNER, 1999). We usually apply the phylogenetic species concept as defined by NIXON and WHEELER (1990): "A species is the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)". Basically, this is a morphospecies concept which is, according to EHRENDORFER (1984) and FINLAY et al. (1996), as valid as any, and probably more pragmatic than any other; see EHRENDORFER (1984), LUCKOW (1995), MCDADE (1995), and TURNER (1999) for detailed discussion.

We do not consider ourselves as splitters, that is, we classify species as undescribed (new) only if populations can be separated from their nearest relatives by at least one distinct (non-morphometric) morphological feature, such as presence/absence of caudal cirri or rod-shaped vs. fusiform extrusomes, or if quantitative differences, such as body size and/or number of ciliary rows, are really conspicuous ($\geq$ 100%). Furthermore, we must have seen at least 10 individuals and studied the species in vivo and silver preparations, to provide reliable morphometrics, illustrations, and types. Certainly, the present monograph could contain many more new species, if we had included all the taxa/specimens seen only in the silver slides. However, it is our belief that careful live observations are indispensable for a good description. Thus, we rarely describe species seen only in silver slides.

MAYR (1963) defines a subspecies as "an aggregate of local populations of a species inhabiting a geographic subdivision of the range of the species, and differing taxonomically from other populations of the species". This concept, especially geographic isolation has been widely adopted, although there is still a lot of discussion (BÖHME 1978, O'NEILL 1982, ROLÁN-ALVAREZ & ROLÁN 1995). Unfortunately, biogeography of protozoa is still in its infancy, and thus MAYR'S concept hardly can be applied. Nonetheless, subspecies are useful also in protists, when used restrictively and as a simple taxonomic tool.

In the present monograph, we distinguish subspecies according to distinct morphometrical differences in important features (e.g., number of ciliary rows) and/or qualitative (morphological) characters whose taxonomic value is still doubtful or not known. It is the last mentioned feature which makes the subspecies concept so useful: the name can be easily withdrawn if later research proves the features used to be unreliable, and the discoverer does not lose priority to "armchair" taxonomists if the subspecies later gets species rank (INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE 1999). Furthermore, subspecies "collect" the infraspecific variation, that is, data which tend to be lost (ZUSI 1982), and enhance identification of species because of the broader concept; thus subspecies are especially useful for people and disciplines not specifically trained in taxonomy. In spite of the obvious advantages, protozoologists rarely used the subspecies/subgenus concept, although KAHL (1932) established some subgenera and varieties in ciliates and one third of the testate amoebae taxa are "variations" or "forms", most of which must be considered as subspecies according to the ICZN (FOISSNER & KORGANOVA 2000). Further, subspecies are common in extant and fossil foraminifera (BOLTOVSKOY 1954) and fossil tintinnids (BELOKRYS 1997). There is now a tendency to use them also in extant ciliates (SONG & WEI 1998).

A further main factor influencing the number of species recognized as undescribed is the treatment of literature data. Many of the old protozoan species descriptions lack type material and are poor compared with the present standard because the pioneers did not have the

advantages of modern methods. Clearly, there is a tendency to disrespect the efforts of our predecessors and to establish new taxa with new methods. Our approach is to respect and re-interpret previous work and to neotypify species, provided that at least one main feature matches (see also chapter on neotypification). Representative examples for our way of making honest alpha-taxonomy can be found in the section on nassulids in this monograph.

2.4 Type Material and Neotypification

2.4.1 Type Material (Table 1)

All descriptions in this monograph are based on live observations and silver impregnations, which usually yield permanent slides. For the new and the neotypified species, at least 1 holotype and 1 paratype slide have been selected. One or more slides have been selected for the species redescribed. All slides have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria. The slides usually contain several specimens, with about 10 relevant cells marked by a black ink circle on the cover glass (Table 1).

If appropriate, the type slides are accompanied by an equally - sized sheet of paper, which states the species and the kind of types contained (H – holotype specimen, N – neo (holo) type specimen, P – paratype specimen, V – voucher). The specimens which served as a basis for the illustrations are marked by the letter "D", for instance, PD = paratype used for illustration. The holotype specimen (H), of course, has been drawn. Note that some slides contain types of several species, which are distinguished by different colours or letters. Furthermore, several species occurring in Namibia and described in this paper have been found and studied previously in soil samples from other regions of the world. Thus, the type location of some of the new taxa is not in Namibia, that is, not contained in the site descriptions given above. Brief site descriptions for these species and populations are provided in the respective occurrence and ecology sections. The samples were processed like those from Namibia.

2.4.2 Neotypification

We broadly apply neotypification in our monograph. As this poses a major problem (see below), we shall discuss it in detail. Furthermore, we have submitted a manuscript to the Bulletin of Zoological Nomenclature discussing neotypification in protists.

Methods for preparing soft-bodied ciliates with a quality that provides meaningful types to be deposited have only been available for the past three decades. At present, most "modern" ciliate types are deposited in two centres: the Smithsonian Institution in the USA (CORLISS 1972, COLE 1994) and the Museum of Natural History of Upper Austria in Linz (AESCHT 1994). However, more than 90% of all described ciliates lack type material at all, or the material hardly shows the species-specific features, or is difficult to obtain because deposited in private or University collections (see FOISSNER & PFISTER 1997 for an example).

Certainly, the lack of types is one of the most difficult problems in ciliate and protozoan alpha-taxonomy in general. There are innumerable examples of poorly described species, doubtful identifications, and problematic redescriptions. Although my group usually recognizes a thorough redescription as "authoritative" (e.g. FOISSNER 1993c), others do not.

Table 1. Type material of the species described in this monograph and in other papers (FOISSNER 1998b, 2000d, FOISSNER & AGATHA 1999) containing species from Namibia.

Species	Site [a]	Kind of types, number of slides, and kind of preparations (in brackets [b]) deposited				Accession number year 2002
		Holotype	Paratype	Neotype	Voucher	
Actinobolina multinucleata nov. spec.	49	1 (PA)	4 (PA)	–	–	332–334, 338, 339
Afroamphisiella multinucleata nov. spec.	61	1 (PA)	2 (PA)	–	–	111–113
Afrothrix multinucleata nov. spec.	17	1 (PA)	1 (PA)	–	–	255, 256
Amphisiella binucleata multicirrata nov. sspec.	5	1 (PA)	3 (PA)	–	–	419, 420, 423, 424,
Amphisiella binucleata multicirrata nov. sspec.	41	–	–	–	3 (PA)	483, 490, 491
Amphisiella elegans nov. spec.	OS	1 (P)	4 (P)	–	–	594–598
Amphisiella longiseries nov. spec.	4	1 (PA)	5 (PA)	–	–	466–471
Amphisiella longiseries nov. spec.	OS	–	–	–	3 (PA)	472–474
Amphisiella multinucleata nov. spec.	49	1 (P)	2 (P)	–	–	391–393
Amphisiella multinucleata nov. spec.	52	–	–	–	4 (PA)	394–397
Amphisiella multinucleata nov. spec.	OS	–	–	–	2 (PB)	398, 399
Amphisiella namibiensis nov. spec.	54	1 (PB)	4 (PA), 2 (PB)	–	–	5, 8, 108–110, 147, 148
Amphisiella procera nov. spec.	7	1 (PA)	1 (PA)	–	–	380, 381
Amphisiella procera nov. spec.	9	–	–	–	1 (PA)	382
Anatoliocirrus capari nov. spec.	OS	1 (PA)	1 (PA) 11 (PB)	–	–	689–701
Apertospathula armata nov. spec.	OS	1 (PA)	2 (PA)	–	–	599–601
Apertospathula dioplites nov. spec.	30	1 (PA)	3 (PA)	–	–	449–452
Apertospathula inermis nov. spec.	OS	1 (PA)	2 (PA)	–	–	659–661
Apobryophyllum etoschense FOISSNER	60	1 (PA)	3 (PA)	–	–	46–49
Apobryophyllum terricola FOISSNER	49	–	–	–	2 (PA)	354, 359
Apobryophyllum vermiforme nov. spec.	4	1 (PA)	2 (PA)	–	–	475–477
Apocolpodidium etoschense nov. spec.	70	1 (CHL)	5 (CHL, PA, KF)	–	–	77–82
Apocolpodidium etoschense nov. spec.	OS	–	–	–	1 (CHL)	83
Apocolpodidium macrostoma nov. spec.	OS	1 (CHL)	2 (CHL, PA)	–	–	662–664
Apocyclidium obliquum (KAHL)	37	–	–	2 (CHL), 4 (PA)	–	316–321
Apocyclidium obliquum (KAHL)	OS	–	–	–	4 (KF)	322–325
Apoenchelys bamforthi nov. spec.	41	1 (PA)	9 (PA)	–	–	478, 481, 482–489
Apospathidium atypicum (BUITKAMP & WILBERT)	OS	–	–	–	5 (PA)	518–522
Apospathidium terricola nov. spec.	41	1 (PA)	2 (PA)	–	–	478, 481, 482
Apospathidium terricola nov. spec.	5	–	–	–	2 (PA)	479, 480
Apourosomoida halophila nov. spec.	OS	1 (PA)	2 (PA)	–	–	329, 330, 331
Arcuospathidium cultriforme megastoma nov. sspec.	49	1 (PA)	4 (PA)	–	–	346, 353, 355, 359, 361
Arcuospathidium etoschense nov. spec.	69	1 (PA)	2 (PA)	–	–	23–25
Arcuospathidium lorjeae nov. spec.	49	1 (PA)	6 (PA)	–	–	341, 344, 346, 352–355
Arcuospathidium namibiense namibiense nov. spec., n. sspec.	5	1 (PA)	3 (PA)	–	–	417, 429, 431, 432
Arcuospathidium namibiense tristicha nov. sspec.	OS	1 (PA)	2 (PA)	–	–	554–556

(continued)

Species	Site [a]	Kind of types, number of slides, and kind of preparations (in brackets [b]) deposited				Accession number year 2002
		Holotype	Paratype	Neotype	Voucher	
Arcuospathidium novaki nov. spec.	49	1 (PA)	2 (PA)	–	–	338, 350, 358
Arcuospathidium vlassaki FOISSNER	59	1 (PA)	2 (PA)	–	–	26–28
Bakuella granulifera nov. spec.	4	1 (PB)	6 (PB)	–	–	459–465
Bilamellophrya australiensis nov. spec.	OS	1 (PA)	2 (PA)	–	–	705, 708, 709
Bilamellophrya australiensis nov. spec.	OS	–	–	–	1 (PA)	710
Bilamellophrya etoschensis nov. spec.	60	1 (PA)	2 (PA)	–	–	57–59
Bilamellophrya etoschensis nov. spec.	OS	–	–	–	1 (PA)	60
Bilamellophrya hawaiiensis nov. spec.	OS	1 (PA)	2 (PA)	–	–	674–676
Blepharisma bimicronucleatum VILLENEUVE-BRACHON, bluish variant	OS	–	–	–	1 (PA)	528
Bryophyllum lingua multistriatum nov. sspec.	70	1 (PA)	7 (PA)	–	–	34–41
Bryophyllum paucistriatum nov. spec.	OS	1 (PA)	4 (PA)	–	–	523–527
Bryophyllum paucistriatum nov. spec.	56	–	–	–	2 (PA)	183, 183a
Bryophyllum penardi KAHL	OS	–	–	4 (PA)	–	339, 340, 356, 358
Clavoplites australiensis nov. spec.	OS	1 (PA)	5 (PA)	–	–	716–719, 722, 723
Clavoplites edaphicus nov. spec.	OS	1 (PA)	4 (PA)	–	–	716, 720–723
Colpoda cavicola amicronucleata nov. sspec.	55	3 (PA, CHL, F)	7 (PA, CHL, FE)	–	–	156–165
Colpoda cavicola cavicola KAHL	51	–	–	–	4 (CHL)	152–155
Colpoda formisanoi nov. spec.	51	1 (PA)	3 (PA)	–	–	365–368
Colpodidium caudatum WILBERT	3	–	–	–	3 (CHL)	326–328
Colpodidium caudatum WILBERT	OS	–	–	–	2 (PA, CHL)	680, 681
Colpodidium bradburyarum nov. spec.	OS	1 (PA)	2 (CHL)	–	–	677–679
Colpodidium horribile nov. spec.	OS	1 (PB)	2 (PB, CHL)	–	–	532–534
Colpodidium horribile nov. spec.	OS	–	–	–	1 (CHL)	679
Colpodidium horribile nov. spec.	70	–	–	–	9 (KF)	535–543
Colpodidium microstoma nov. spec.	OS	1 (CHL)	2 (PA, KF)	–	–	551–553
Colpodidium trichocystiferum nov. spec.	OS	1 (PA)	1 (PA)	–	–	636, 637
Condylostomides etoschensis nov. spec.	65	1 (PD)	2 (PD)	–	–	170–173
Condylostomides etoschensis nov. spec.	OS	–	–	–	1 (PB)	174
Condylostomides trinucleatus nov. spec.	OS	1 (PA)	1 (PA)	–	–	724, 725
Condylostomides trinucleatus nov. spec.	49	–	–	–	3 (PA)	352, 353, 355
Dileptus anguillula KAHL	OS	–	–	5 (PA)	–	781–785
Dileptus mucronatus PENARD	OS	–	–	–	2 (PA)	568, 569
Dioplitophrya otti nov. spec.	56	1 (PA)	3 (PA)	–	–	54–56, 181
Diplites arenicola nov. spec.	33	1 (PA)	1 (PA)	–	–	258, 259
Diplites telmatobius FOISSNER	29	1 (PA)	1 (PA)	–	–	434, 435
Diplites telmatobius FOISSNER	49	–	–	–	2 (PA)	354, 361
Dragescozoon terricola nov. spec.	OS	1 (CHL)	1 (CHL), 2 (PA)	–	–	544–547
Enchelaria multinucleata nov. spec.	5	1 (PA)	4 (PA)	–	–	418–422
Enchelydium blattereri nov. spec.	OS	1 (PA)	3 (PA)	–	–	705–708

(continued)

Species	Site [a]	Kind of types, number of slides, and kind of preparations (in brackets [b]) deposited				Accession number year 2002
		Holotype	Paratype	Neotype	Voucher	
Enchelys longitricha nov. spec.	OS	1 (PA)	2 (PA)	–	–	607–609
Enchelyodon armatides nov. spec.	48	1 (PA)	2 (PA)	–	–	226–228
Enchelyodon armatides nov. spec.	OS	–	–	–	2 (PA)	687, 688
Enchelyodon armatides nov. spec.	OS	–	–	–	2 (PA)	714, 715
Enchelyodon megastoma nov. spec.	49	1 (PA)	5 (PA)	–	–	347–349, 364, 391, 392
Enchelyodon minutus nov. spec.	73	1 (PA)	2 (PA)	–	–	508–510
Enchelyotricha jesnerae nov. spec.	49	1 (PA)	3 (PA)	–	–	345, 352, 355, 359
Epispathidium polynucleatum nov. spec.	13	1 (PA)	3 (PA)	–	–	281–284
Epispathidium polynucleatum nov. spec.	OS	–	–	–	4 (PA)	285–288
Epitholiolus chilensis (BÜRGER)	26	–	–	2 (PA)	–	272, 273
Erimophrya arenicola nov. spec.	23	1 (PA)	2 (PA)	–	–	243–245
Erimophrya glatzeli nov. spec.	24	1 (PA)	2 (PA)	–	–	246–248
Eschaneustyla lugeri nov. spec.	OS	1 (P)	4 (P)	–	–	738–742
Etoschophrya oscillatoriophaga nov. spec.	67	1 (CHL)	2 (CHL)	–	–	167–169
Etoschothrix terricola nov. spec.	61	1 (PA)	6 (PA)	–	–	140–146
Etoschothrix terricola nov. spec.	57	–	–	–	1 (PA)	22
Euplotopsis incisa nov. spec.	OS	2 (PA, CHL)	1 (PA)	–	–	651–653
Euplotopsis incisa nov. spec.	OS	–	–	–	2 (KF)	654, 655
Exocolpoda augustini (FOISSNER)	39	–	–	–	4 (CHL)	304–307
Frontonia angusta angusta KAHL	OS	–	–	3 (CHL)	–	628–630
Frontonia angusta obovata nov. sspec.	56	1 (CHL)	4 (CHL)	–	–	201–205
Frontonia angusta solea FOISSNER	65	–	–	–	4 (PA, CHL)	206–209
Frontonia depressa (STOKES)	OS	–	–	–	1 (CHL)	631
Frontonia terricola FOISSNER	70	–	–	–	2 (CHL)	199, 200
Frontonia terricola FOISSNER	73	–	–	–	3 (CHL)	511–513
Fuscheria terricola BERGER, FOISSNER & ADAM	49	–	–	–	1 (PA)	375
Gastrostyla mystacea mystacea (STEIN)	OS	–	–	5 (PB)	–	623–627
Gastrostyla mystacea minima HEMBERGER	73	–	–	–	4 (PA, MG)	514–517
Gastrostyla steinii ENGELMANN	OS	–	–	–	11 (PB, MG)	557–567
Gonostomum algicola GELLÉRT	62	–	–	6 (PA)	–	134–139
Gonostomum namibiense nov. spec.	61	1 (PA)	1 (PA)	–	–	121, 122
Gonostomum namibiense nov. spec.	30	–	–	–	2 (PA)	123, 124
Gonostomum namibiense nov. spec.	49	–	–	–	1 (PA)	360
Gonostomum strenuum (ENGELMANN)	49	–	–	4 (PA)	–	357, 362, 389, 390
Hausmanniella patella (KAHL)	15	–	–	–	4 (CHL), 4 (PA)	308–315
Hemisincirra inquieta HEMBERGER	5	–	–	–	6 (PA)	419–421, 423–425
Hemisincirra namibiensis nov. spec.	17	1 (PA)	1 (PA)	–	–	253, 254
Hemisincirra rariseta nov. spec.	5	1 (PA)	2 (PA)	–	–	429–431
Hemiurosoma goertzi nov. spec.	60	1 (PA)	4 (PA)	–	–	102–106
Hemiurosoma terricola nov. spec.	56	1 (PA)	3 (PA)	–	–	127–130

(continued)

Species	Site [a]	Kind of types, number of slides, and kind of preparations (in brackets [b]) deposited				Accession number year 2002
		Holotype	Paratype	Neotype	Voucher	
Hemiurosoma terricola nov. spec.	OS	–	–	–	3 (PA)	131–133
Holosticha brachysticha nov. spec.	OS	1 (PA)	2 (PA)	–	–	754–756
Holophrya salinarum nov. spec.	65	1 (CHL)	1 (CHL)	–	–	206, 209
Ilsiella elegans nov. spec.	OS	1 (CHL)	–	–	–	369
Ilsiella elegans nov. spec.	51	1 (PA)	3 (PA)	–	–	365–368
Kuehneltiella namibiensis nov. spec.	45	1 (CHL)	7 (CHL)	–	–	400–407
Kuklikophrya ougandae (DRAGESCO)	67	–	–	–	3 (PD), 1 (CHL)	169–172
Lamtostyla decorata nov. spec.	31	1 (PA)	3 (PA)	–	–	289–292
Lamtostyla decorata nov. spec.	1	–	–	–	4 (PA)	293–296
Lamtostyla decorata nov. spec.	OS	–	–	–	3 (PA)	297–299
Lamtostyla halophila nov. spec.	18	1 (PA)	1 (PA)	–	–	214, 215
Lamtostyla halophila nov. spec.	69	–	–	–	3 (PA)	216–218
Maryna lichenicola (GELEI)	42	–	–	–	3 (PA)	492–494
Maryna lichenicola (GELEI)	OS	–	–	–	2 (PA)	495, 546
Maryna namibiensis costaricensis nov. sspec.	OS	3 (PB, CHL)	3 (CHL), 2 (PB)	–	–	743–749
Maryna namibiensis namibiensis nov. spec., nov. sspec.	73	2 (PB, CHL)	5 (CHL), 1 (PB)	–	–	496–503
Maryna namibiensis namibiensis nov. spec., nov. sspec.	29	–	–	–	1 (CHL)	504
Maryna ovata (GELEI)	OS	–	–	–	2 (PA)	495, 546
Maryna umbrellata (GELEI)	OS	–	–	3 (CHL), 2 (PB)	–	746, 748–751
Metacineta namibiensis nov. spec.	33	1 (PA)	4 (PA)	–	–	258–262
Metopus contortus (QUENNERSTEDT)	49	–	–	–	3 (PA)	356–358
Metopus gibbus KAHL	OS	–	–	1 (PA)	–	641
Metopus gibbus KAHL	30	–	–	–	4 (PA)	439, 440, 642, 643
Metopus hasei SONDHEIM	29	–	–	–	2 (PA)	434, 435
Metopus hasei SONDHEIM	30	–	–	–	4 (PA)	439–442
Metopus inversus JANKOWSKI	30	–	–	6 (PA)	–	436–440, 444
Metopus minor KAHL	OS	–	–	–	3 (PA)	638–640
Metopus ovalis KAHL	49	–	–	–	1 (PA)	339
Metopus palaeformis KAHL	OS	–	–	3 (PA)	–	576–578
Nassula dragescoi nov. spec.	57	1 (CHL)	2 (CHL)	–	–	65, 68, 650
Nassula dragescoi nov. spec.	OS	–	–	–	1 (PA)	69
Nassula etoschensis nov. spec.	67	1 (CHL)	3 (PA, CHL)	–	–	31, 74–76
Nassula exigua KAHL	OS	–	–	3 (CHL)	–	770–772
Nassula granata nov. spec.	69	1 (PA)	2 (PA)	–	–	70–72
Nassula granata nov. spec.	67	–	–	–	3 (PA, CHL)	31, 63, 73
Nassula longinassa FOISSNER	57	–	–	2 (PA, CHL)	–	66, 67
Nassula parva KAHL	OS			3 (PA)	–	529–531
Nassula tuberculata nov. spec.	OS	F	–	–	–	–
Nassula tuberculata nov. spec.	OS	–	–	–	3 (CHL)	644–646
Nassulides labiatus (KAHL)	OS	–	–	4 (CHL)	–	646–649

(continued)

Species	Site [a]	Kind of types, number of slides, and kind of preparations (in brackets [b]) deposited				Accession number year 2002
		Holotype	Paratype	Neotype	Voucher	
Nassulides labiatus (KAHL)	57	–	–	–	1 (CHL)	650
Naxella lucida (REUTER)	67	–	–	1 (PA), 3 (CHL)	–	31, 61–63
Naxella rosea (TUCOLESCO)	57	–	–	3 (PA, CHL)	–	64–66
Nivaliella plana FOISSNER	OS	–	–	–	3 (PA)	656–658
Nudiamphisiella interrupta nov. spec.	49	1 (PA)	5 (PA)	–	–	343, 351, 370–373
Obliquostoma enchelyodontides nov. spec.	43	1 (PA)	1 (PA)	–	–	413, 414
Obliquostoma namibiense nov. spec.	48	1 (PA)	3 (PA)	–	–	229–232
Odontochlamys alpestris biciliata nov. sspec.	OS	1 (PA)	3 (PA)	–	–	773–776
Odontochlamys alpestris biciliata nov. sspec.	OS	–	–	–	4 (KF)	777–780
Orthoamphisiella breviseries nov. spec.	61	1 (PA)	2 (PA)	–	–	114–116
Ottowphrya dragescoi (FOISSNER)	OS	–	–	–	4 (CHL)	632–635
Oxytricha longa GELEI & SZABADOS	58	–	–	–	2 (PA)	100, 101
Parabryophrya etoschensis nov. spec.	56	1 (PA)	2 (PA)	–	–	181–183
Paraenchelys brachyarmata nov. spec.	OS	1 (PA)	3 (PA)	–	–	766–769
Paraenchelys brachyoplites nov. spec.	43	1 (PA)	3 (PA)	–	–	409–412
Paraenchelys pulchra nov. spec.	54	1 (PA)	3 (PA)	–	–	50–53
Paraenchelys terricola FOISSNER	43	–	–	–	1 (PA)	408
Paragonostomum binucleatum nov. spec.	OS	1 (PA)	4 (PA)	–	–	602–606
Paragonostomum caudatum nov. spec.	OS	1 (PA)	3 (PA)	–	–	733–737
Paragonostomum multinucleatum nov. spec.	11	1 (PA)	1 (PA)	–	–	274, 276
Paragonostomum multinucleatum nov. spec.	OS	–	–	–	4 (PA)	277–280
Paragonostomum rarisetum nov. spec.	5	1 (PA)	4 (PA)	–	–	415, 429–432
Parakahliella binucleata nov. spec.	64	2 (PA)	2 (PA)	–	–	117–120
Parakahliella halophila nov. spec.	OS	1 (PA)	2 (PA)	–	–	665–667
Parakahliella halophila nov. spec.	18	–	–	–	2 (PA)	668, 669
Parakahliella halophila nov. spec.	59	–	–	–	4 (PA)	670–673
Parakahliella namibicola nov. spec.	25	1 (PA)	3 (PA)	–	–	249–252
Periholosticha lanceolata HEMBERGER	OS	–	–	–	2 (PA)	458, 580
Periholosticha lanceolata HEMBERGER	4	–	–	–	2 (PA)	456, 457
Perisincirra longicirrata nov. spec.	OS	1 (PA)	2 (PA)	–	–	548–550
Perisincirra paucicirrata nov. spec.	OS	1 (PA)	3 (PA)	–	–	726–729
Perisincirra paucicirrata nov. spec.	63	–	–	–	3 (PA)	730–732
Phialina minima (KAHL)	OS	–	–	3 (PA)	–	787–789
Phialinides armatus nov. spec.	OS	1 (PA)	4 (PA)	–	–	781–784, 786
Plagiocampa bitricha FOISSNER	OS	1 (PA)	1 (PA)	–	–	687, 688
Plagiocampa namibiensis nov. spec.	30	1 (PA)	1 (PA)	–	–	444, 445
Plagiocampa namibiensis nov. spec.	OS	–	–	–	2 (CHL)	446, 447
Plagiocampa ovata GELEI	51	–	–	–	1 (PA)	365
Plagiocampa pentadactyla nov. spec.	OS	1 (CHL)	1 (CHL)	–	–	446, 447
Plagiocampa pentadactyla nov. spec.	OS	–	–	–	1 (PA)	448

(continued)

Species	Site [a]	Kind of types, number of slides, and kind of preparations (in brackets [b]) deposited				Accession number year 2002
		Holotype	Paratype	Neotype	Voucher	
Plagiocampides halophilus nov. spec.	58	1 (CHL)	2 (CHL, PA)	–	–	210–212
Plagiocampides halophilus nov. spec.	OS	–	–	–	1 (PA)	213
Platyophrya spumacola hexasticha nov. sspec.	5	1 (PA)	4 (PA)	–	–	415–418, 422
Platyophryides latus (KAHL)	OS	–	–	4 (CHL)	–	586–589
Platyophryides latus (KAHL)	71	–	–	–	4 (PA)	590–593
Plesiocaryon terricola nov. spec.	56	2 (PA, CHL)	3 (PA), 1 (CHL)	–	–	175–180
Podophrya halophila KAHL	48	–	–	–	3 (PA)	229, 232, 233
Podophrya tristriata nov. spec.	OS	1 (PA)	2 (PA)	–	–	702–704
Protocyclidium terricola (KAHL)	OS	–	–	2 (CHL), 3 (KF), 2 (PA)	–	610–616
Protocyclidium terricola (KAHL)	OS	–	–	–	2 (CHL), 2 (PA)	617–620
Protocyclidium terricola (KAHL)	66	–	–	–	3 (CHL)	84–86
Protospathidium namibicola nov. spec.	33	1 (PA)	2 (PA)	–	–	257–259
Pseudocohnilembus binucleatus nov. spec.	59	1 (PA)	1 (PA)	–	–	87, 88
Pseudocohnilembus persalinus hexakineta nov. sspec.	61	1 (PA)	3 (PA)	–	–	89–92
Pseudocohnilembus persalinus hexakineta nov. sspec.	14	–	–	–	4 (CHL)	96–99
Pseudocohnilembus persalinus hexakineta nov. sspec.	39	–	–	–	3 (CHL)	93–95
Pseudoholophrya minuta nov. spec.	73	1 (PA)	2 (PA)	–	–	505–507
Pseudoholophrya terricola BERGER et al.	OS	–	–	–	2 (PA)	579, 581
Pseudokreyella etoschensis nov. spec.	54	1 (PA)	7 (PA)	–	–	184–191
Pseudomonilicaryon angustistoma nov. spec.	49	1 (PA)	2 (PA)	–	–	362–364
Pseudomonilicaryon japonicum nov. spec.	OS	1 (PA)	4 (PA)	–	–	682–686
Pseudomonilicaryon massutii (KAHL)	70	–	–	5 (PA)	–	34, 42–45
Pseudouroleptus caudatus caudatus HEMBERGER	OS	–	–	–	3 (PA)	573–575
Pseudouroleptus caudatus namibiensis nov. sspec.	30	1 (PA)	4 (PA)	–	–	449, 452–455
Pseudourostyla franzi FOISSNER	65	–	–	–	1 (PA)	207
Reticulowoodruffia terricola FOISSNER	36	–	–	–	4 (CHL)	300–303
Reticulowoodruffia terricola FOISSNER	39	–	–	–	4 (CHL)	304–307
Rostrophrya fenestrata nov. spec.	11	F	–	–	–	–
Rostrophrya namibiensis maldivensis nov. sspec.	OS	1 (CHL)	3 (CHL)	–	–	582–585
Rostrophrya namibiensis namibiensis nov. spec., nov. sspec.	54	F	F	–	–	–
Rostrophryides africana etoschensis nov. sspec.	67	1 (CHL)	2 (CHL)	–	–	167–169
Semiplatyophrya acrostoma nov. spec.	36	1 (CHL)	2 (CHL)	–	–	300–302
Semispathidium armatum nov. spec.	49	1 (PA)	2 (PA)	–	–	340, 341, 362
Semispathidium enchelyodontides nov. spec.	49	1 (PA)	5 (PA)	–	–	342, 343, 351, 358, 360, 375
Sikorops minor nov. spec.	OS	1 (PA)	2 (PA)	–	–	579–581
Sikorops namibiensis nov. spec.	51	1 (PA)	5 (PA)	–	–	335–337, 366–368
Spathidium aciculare nov. spec.	OS	1 (PA)	4 (PA)	–	–	711–715
Spathidium contractile nov. spec.	49	1 (PA)	4 (PA)	–	–	350, 356–358, 361
Spathidium etoschense nov. spec.	57	1 (PA)	5 (PA)	–	–	17–22
Spathidium extensum KAHL	54	–	–	–	5 (PA)	4–8

(continued)

Species	Site [a]	Kind of types, number of slides, and kind of preparations (in brackets [b]) deposited				Accession number year 2002
		Holotype	Paratype	Neotype	Voucher	
Spathidium lanceoplites nov. spec.	49	1 (PA)	2 (PA)	–	–	342, 351, 358
Spathidium namibicola nov. spec.	23	1 (PA)	6 (PA)	–	–	263–269
Spathidium namibicola nov. spec.	26	–	–	–	2 (PA)	270, 271
Spathidium rusticanum FOISSNER	5	–	–	–	3 (PA)	426–428
Spathidium seppelti etoschense nov. sspec.	60	1 (PA)	1 (PA)	–	–	1, 2
Spathidium turgitorum nov. spec.	54	1 (PA)	8 (PA)	–	–	3–8, 184, 191, 192
Spathidium turgitorum nov. spec.	24	–	–	–	4 (PA)	9–12
Spathidium turgitorum nov. spec.	OS	–	–	–	4 (PA)	13–16
Sterkiella cavicola (KAHL)	OS	–	–	–	8 (MG, PA)	100–108/2000
Supraspathidium armatum nov. spec.	65	1 (PA)	1 (PA)	–	–	29, 30
Supraspathidium armatum nov. spec.	54	–	–	–	2 (PA)	184, 191
Supraspathidium etoschense nov. spec.	67	1 (PA)	2 (PA)	–	–	31–33
Trachelophyllum africanum nov. spec.	OS	1 (PA)	2 (PA)	–	–	570–572
Trachelophyllum africanum nov. spec.	30	–	–	–	1 (PA)	451
Trachelophyllum apiculatum (PERTY)	OS	–	–	2 (PA)	–	764, 765
Trachelophyllum costaricanum nov. spec.	OS	1 (PA)	1 (PA)	–	–	752, 753
Trachelophyllum pannonicum nov. spec.	OS	1 (PA)	1 (PA)	–	–	621, 622
Uroleptus paranotabilis nov. spec.	52	1 (PA)	2 (PA)	–	–	383–385
Uroleptus paranotabilis nov. spec.	OS	–	–	–	3 (PA)	386–388
Urosomoida deserticola nov. spec.	33	1 (PA)	1 (PA)	–	–	257, 258
Urosomoida monostyla nov. spec.	57	1 (PA)	1 (PA)	–	–	125, 126
Urosomoida namibiensis nov. spec.	49	1 (PA)	3 (PA)	–	–	342, 372–374
Urosomoida reticulata nov. spec.	48	1 (PA)	3 (PA)	–	–	219–222
Urosomoida reticulata nov. spec.	OS	–	–	–	3 (PA)	223–225
Vermioxytricha arenicola nov. spec.	24	1(PA)	5 (PA)	–	–	234–239
Vermioxytricha arenicola nov. spec.	OS	–	–	–	3 (PA)	240–242
Vorticella echini KING	55	–	–	–	2 (PA), 2 (KF), 2 (FE)	193–198
Wallackia bujoreani (LEPSI)	59	–	–	–	1 (PA)	107
Wallackia bujoreani (LEPSI)	54	–	–	–	3 (PA, MG)	185, 191, 192
Wallackia elegans nov. spec.	49	1 (PA)	2 (PA)	–	–	343, 375, 376
Wallackia elegans nov. spec.	OS	–	–	–	3 (PA)	377–379
Wolfkosia loeffleri nov. spec.	OS	2 (CHL, KF)	7 (PA, KF)	–	–	617–619, 757–762
Wolfkosia loeffleri nov. spec.	OS	–	–	–	1(CHL)	763
Wolfkosia loeffleri nov. spec.	66	–	–	–	1 (CHL)	86
Woodruffides terricola FOISSNER	55	–	–	3 (CHL)	–	149–151

[a] Site number according to site description in "material and methods". OS – other than Namibian sites (see introduction to "type material").

[b] CHL – silver nitrate after CHATTON-LWOFF, as described in FOISSNER (1991), F – figures, as mentioned in individual species descriptions, FE – FEULGEN stain, KF – silver nitrate after KLEIN-FOISSNER, as described in FOISSNER (1991), MG – morphogenesis, PA – protargol method A, as described in FOISSNER (1991), PB – protargol method B (WILBERT's method), as described in FOISSNER (1991), PD – protargol (DRAGESCO's method).

BERGER (1999), for instance, assigned *Onychodromopsis flexilis* STOKES, 1887, carefully redescribed and neotypified by PETZ & FOISSNER (1996), to *Allotricha*, a genus and species never illustrated or carefully described. Obviously, no consensus can be reached, and ciliate identification and nomenclature remain a matter of choice.

Clearly, many of the existing problems could be solved by types. The present practice of using illustrations as types cannot solve the problem because these cannot be reinvestigated. Thus, neotypification is the only way to overcome these and related problems and to bring stability in ciliate taxonomy and identification. This was emphasized already in 1972 by CORLISS, who established some neotypes for "difficult" ciliates in the sixties. Likewise, MEDIOLI & SCOTT (1985) established neotypes for some testate amoebae. Generally, however, neotypification is very rare for protists. It was only recently that my group commenced using this valuable instrument on a large scale (FOISSNER 1997d, 1999b, FOISSNER & BROZEK 1996, FOISSNER & DRAGESCO 1996, FOISSNER & KREUTZ 1996, PETZ & FOISSNER 1996); several specialists followed (AGATHA & RIEDEL-LORJÉ 1998, PETZ et al. 1995, SONG et al. 2001).

Neotypification is strictly regulated by article 75 of the *Code* (ICZN 1999). Because our neotypes deviate in an important aspect from the *Code* rulings, and protists have several peculiarities (CORLISS 1993), they need a detailed comment. We establish neotypes only if at least one of the following items applies:

(1) No useable type material is available and the identification appears reasonable.

(2) The original description is so incomplete and/or based on so few specimens that any identification becomes arbitrary. Alternatively, such descriptions could be considered as species indeterminata. However, this would greatly increase the number of scientific names because many original descriptions of ciliates are very incomplete, at least from our present point of view. Thus, we prefer to identify our taxa with previous ones, even if these are poorly described, and to redefine them by detailed redescriptions; of course, identification requires matching of at least one main feature.

(3) The species has one or more proposed subjective synonyms, that is, a questionable identity discussed in the literature. This is, in the absence of type material, a "classic" case for neotypification.

(4) If there are several similar species whose identity is threatened by the species to be neotypified.

(5) If there are competing redescriptions.

(6) If the new preparations ("neotype slides") are of a quality allowing the specific features to be clearly recognizable.

Conditions as described above basically pose no problems for neotypification according to the *Code*. However, our neotypes usually do not comply with article 75.3.6., that is, are not from or near the type location. Thus, they might be considered as invalid. However, we defend our approach for the following reasons:

(1) Most ciliates and protists are cosmopolitan, at least at morphospecies level (FINLAY et al. 1996, FOISSNER 1999d).

(2) The existing chaos can be mastered only by types available to everyone. Certainly, the chaos produced by a few probably misidentified neotypes is much smaller than the existing one.

(3) Considering the situation in alpha-taxonomy of ciliates, where only a handful of regularly publishing taxonomists are left worldwide, we cannot wait for neotype material from or near the type location. If so, types will never be established! Furthermore, the chances of rediscovering such minute organisms at a certain location are minimal because they may be in a dormant (cystic) stage most of their lives and cultivation is often not successful.

To sum up, we suggest that neotypes of protists, especially ciliates, should be freed from the type location regulation of the INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE (1999; article 75.3.6.), provided that neotypification is based on a thorough redescription of the organism and useable neotype material has been deposited in an acknowledged repository.

3. RESULTS

3.1 Ecology and Community Analysis

3.1.1 Methodological Problems

Data of the kind we present are highly dependent on the (non-flooded Petri dish) method used to reactivate ciliates from the air-dried samples, that is, to stimulate them to leave the resting cysts and to reproduce to detectable numbers. We highlight this problem, although it was discussed in detail by FOISSNER (1987d, 1997c, 1999d), because it heavily influences data analysis and interpretation. Specifically, it causes undersampling of species which are rare and/or have special demands (FOISSNER 1997c), and explains the phenomenon that 30–40% undescribed species are found in large sample collections, such as the Namibian material, while the individual samples contain only one or two new species (FOISSNER 1999d).

Usually, soil ciliates are not active but encysted, producing a "hidden biodiversity". The resting cysts can survive for years (FOISSNER 1987d), provided they are from specimens living in dry or temperate climates, where soils desiccate from time to time; in humid environments, such as rain forests, the resting cysts are not adapted to survive longer dryness, and thus the non-flooded Petri dish method does not work (FOISSNER 1997d). But even with "optimal" samples, the non-flooded Petri dish method is selective, that is, cannot provide an environment suitable for all kind of ciliates. This becomes evident when the same site is investigated several times over a year (FOISSNER 1999d), or a single sample is manipulated to encourage encysted and more rare forms of ciliates to emerge (ESTEBAN et al. 2000). Figure 4 shows that a single sample from a certain site collects only about one third of the species actually present, that is, the number found in 17 replicates distributed over two years (further examples, see FOISSNER 1987d). Very likely, this applies also to the Namibian samples.

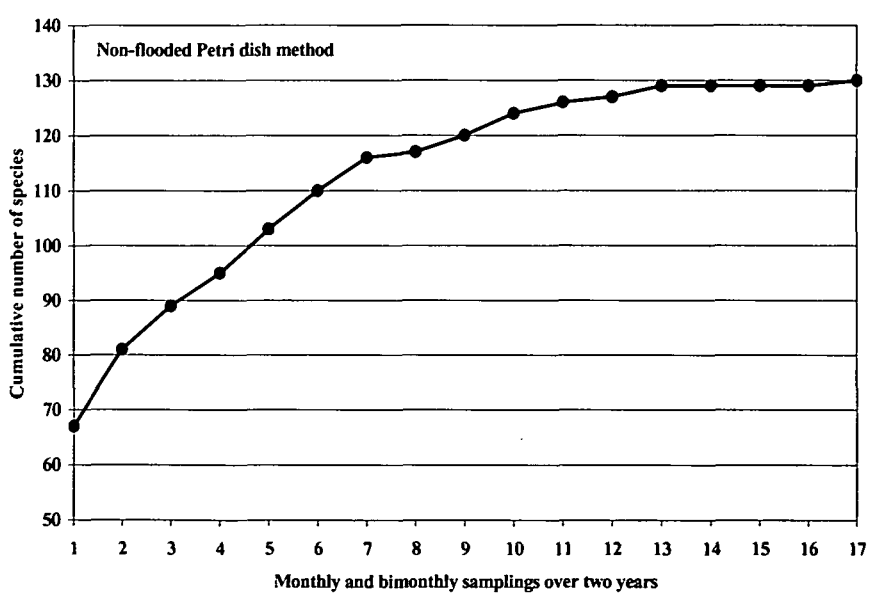


Fig. 1. Cumulative number of species obtained with the non-flooded Petri dish method (FOISSNER 1987d) in 17 monthly and bimonthly samplings from an 100 m^2 area of beech forest soil in Austria. The curve flattens distinctly at sample number 13, indicating that further effort hardly will increase species number significantly. However, direct investigation of fresh samples after rainfalls provided 30 further species. Accordingly, the total number approaches 160 species, which is far from the total number (about 1000) of soil ciliates known. Thus, we do not agree with the hypothesis of FINLAY & ESTEBAN (1998) that "all species of freshwater protozoa could eventually be discovered in one small pond".

Fortunately, we have indications that the situation changes if many samples are analyzed from a not too large area, that is, if the 73 Namibian samples are considered as some sort of replication. To test this, we investigated sites (37) and (56) twice, viz., in 1994 and 2001 (Table 2). Although the species composition and the new species found vary greatly between years (species overlap by only about 50%), almost all known and new species were found at other sites of Namibia in 1994. However, many undescribed species occur at sites not investigated in 1994 (chapter 3.1.7).

Even if a certain ciliate excysts, we can hardly recognize it among the mass of soil particles. To be seen, it must reproduce to a detectable number. And even if this occurrs, there still remains the problem of recognizing it as a distinct taxon among hundreds of individuals from other species, many of which look alike. Only when experience, live observation, and silver impregnation are combined, reliable species lists will emerge.

In sum, there is convincing evidence that the non-flooded Petri dish method is selective, that is, reactivates only a rather small, undefined proportion of the resting cysts present in a sample, and undescribed species or species with specialized demands are undersampled. Thus, the real number of species, described and undescribed, is considerably higher in the samples investigated. Unfortunately, a better method for broad analysis of soil ciliates is not known. On the other hand, FOISSNER discovered about 700 new ciliate species with this simple method, suggesting, inter alia, that a considerable amount of the hidden biodiversity can be revealed by investigating large numbers of samples.

Table 2. Species found at sites (56) and (37) in the years 1996 and 2001. Species marked with a dot were unknown prior to 1980. + = present, – = absent.

Species	Site (56) 1994	Site (56a) 2001	Site (56b) 2001	Site (37) 1994	Site (38) 2001	Site (39) 2001
• *Amphisiella multinucleata* n. sp.	-	-	+	-	-	-
• *Amphisiella elegans* n. sp.	-	-	-	-	-	+
• *Amphisiella magnigranulosa*	+	-	-	-	-	-
Amphisiella terricola	-	+	+	-	-	-
• *Apobryophyllum terricola*	+	-	-	-	-	-
Apocyclidium obliquum	-	-	-	+	-	-
Blepharisma bimicronucleatum	-	+	-	-	-	-
Blepharisma hyalinum	+	+	+	-	-	-
Blepharisma steini	-	+	-	-	-	-
Bryometopus pseudochilodon	+	-	-	-	-	-
• *Bryometopus triquetrus*	+	-	-	-		-
• *Bryophyllum paucistriatum* n. sp.	+	-	-	-	-	-
Cinetochilum margaritaceum	-	-	+	-	-	-
Colpoda aspera	+	+	+	-	-	-
Colpoda cucullus	-	+	+	+	+	-
• *Colpoda edaphoni*	-	-	+	-	-	-
• *Colpoda formisanoi* n. sp.	-	-	+	-	-	-
Colpoda inflata	+	+	+	+	-	+

(continued)

Species	Site (56) 1994	Site (56a) 2001	Site (56b) 2001	Site (37) 1994	Site (38) 2001	Site (39) 2001
Colpoda maupasi	+	+	+	+	+	-
• *Colpoda orientalis*	+	-	-	-	-	-
Colpoda steinii	+	+	+	+	+	+
• *Cyrtohymena citrina*	+	+	-	-	-	-
Dileptus americanus	-	+	-	-	-	-
• *Dioplitophrya otti* n. sp.	+	-	-	-	-	-
Drepanomonas sphagni	+	-	-	-	-	-
• *Enchelyodon nodosus*	+	-	-	-	-	-
Epispathidium ascendens	-	+	-	-	-	-
• *Exocolpoda augustini*	+	-	-	+	-	+
• *Frontonia angusta obovata* n. ssp.	+	-	-	-	-	-
• *Fuscheria terricola*	+	-	-	-	-	+
Gonostomum affine	+	+	+	-	+	-
Gonostomum algicola	-	-	+	-	-	-
• *Grossglockneria acuta*	+	+	+	-	-	-
Hausmanniella discoidea	+	-	-	-		-
Hausmanniella patella	-	+	-	+	-	-
• *Hemisincirra gellerti verrucosa*	-	-	+	-	-	-
• *Hemisincirra inquieta*	-	+	+	-	-	-
• *Hemiurosoma goertzi* n. sp.	+	-	-	-	-	-
• *Hemiurosoma terricola* n. sp.	+	-	-	-	-	-
• *Holosticha sylvatica*	-	-	+	-	-	-
• *Holostichides terricola*	+	+	+	-	-	-
Homalogastra setosa	-	+	+	-	-	+
• *Idiocolpoda pelobia*	+	-	+	-	-	-
• *Ilsiella palustris*	+	-	-	-	-	-
Kahlilembus attenuatus	-	-	+	-	-	-
• *Keronopsis dieckmanni*	+	+	+	-	-	-
• *Lamtostyla australis*	+	+	+	-		-
• *Lamtostyla decorata* n. sp.	-	+	-	-	-	-
• *Lamtostyla islandica*	-	+	+	-	-	-
• *Lamtostyla kirkensis*	-	-	-	-	+	-
Leptopharynx costatus	+	+	+	-	-	-
• *Maryna antarctica*	+	-	-	-	-	-
Metopus hasei	+	-	-	-	-	-
Metopus palaeformis	+	-	-	-	-	-
• *Mykophagophrys terricola*	-	+	-	-	-	-
• *Nassula dragescoi* n. sp.	+	+	-	-	-	-
Nassula parva	-	+	+	-	-	-
• *Nivaliella plana*	+	+	+	-	+	+
• *Odontochlamys alpestris bitricha* n. ssp.	-	-	+	-	-	-
• *Ottophrya dragescoi*	+	-	-	-	+	-
• *Parabryophrya etoschensis* n. sp.	+	-	-	-	-	-
• *Paraenchelys terricola*	+	-	-	-	-	-
• *Paragonostomum binucleatum* n. sp.	+	-	-	-	-	-
• *Paragonostomum multinucleatum* n. sp.	-	-	-	+	-	-
• *Paragonostomum rarisetum* n. sp.	-	-	+	-	-	-
• *Periholosticha lanceolata*	-	+	+	-	-	-
• *Plagiocampa difficilis*	-	+	+	-	-	-

(continued)

Species	Site (56) 1994	Site (56a) 2001	Site (56b) 2001	Site (37) 1994	Site (38) 2001	Site (39) 2001
Plagiocampa rouxi	+	-	-	-	-	-
• *Platyophrya macrostoma*	-	-	+	-	-	-
• *Platyophrya paoletti*	+	-	-	-	-	-
• *Platyophrya similis*	-	+	-	-	-	-
Platyophrya spumacola	+	+	+	-	-	-
Platyophrya vorax	-	+	-	-	-	-
Plesiocaryon elongatum	+	+	+	+	+	+
Plesiocaryon terricola	+	+	-	-	-	-
Protocyclidium muscicola	+	+	+	-	-	-
Protocyclidium terricola	-	+	+	-	-	-
• *Protospathidium terricola*	-	+	+	-	-	-
• *Pseudochilodonopsis mutabilis*	+	-	-	-	-	-
• *Pseudocohnilembus persalinus hexakineta* n. ssp.	-	-	-	-	+	+
• *Pseudocyrtolophosis alpestris*	+	+	+	-	-	-
• *Pseudoholophrya terricola*	+	-	+	-	-	-
Pseudomicrothorax agilis	+	-	-	-	-	-
Pseudoplatyophrya nana	+	+	+	+	+	-
• *Pseudoplatyophrya saltans*	-	+	-	-	-	-
• *Reticulowoodruffia australis*	-	-	-	-	-	+
Sathrophilus muscorum	+	+	+	-		-
• *Semiplatyophrya acrostoma* n. sp.	-	-	-	+	-	+
• *Sikorops minor* n. sp.	+	-	-	-	-	-
• *Sikorops namibiensis* n. sp.	-	-	+	-	-	-
• *Sorogena stoianovitchae*	-	+	+	-	-	-
• *Spathidium longicaudatum*	-	+	+	-	-	-
Spathidium procerum	+	+	+	-	-	-
• *Spathidium rusticanum*	-	-	+	-	-	-
• *Sphaerophrya terricola*	-	+	-	-	-	-
Sterkiella histriomuscorum	-	-	+	-	-	-
• *Tachysoma humicola longiseta*	-	+	-	-	-	-
• *Tectohymena terricola*	+	-	-	-	-	-
• *Terricirra viridis*	-	-	+	-	-	-
• *Trihymena terricola*	-	+	-	-	-	-
• *Uroleptus notabilis*	-	+	-	-	-	-
• *Uroleptus paranotabilis*	-	+	-	-	-	-
• *Urosomoida agiliformis*	-	-	+	-	-	-
Urosomoida agilis	+	+	+	-	-	-
• *Vorticella astyliformis*	+	+	-	-	-	-
Woodruffia rostrata	-	-	-	+	-	-
• *Woodruffides terricola*	-	+	-	-	-	-
Number of species	56	52	50	12	10	11
Unidentified species	5	1	1	1	0	0

3.1.2 Species Lists and Similarity (Cluster) Analysis of Sites

Tables 3 and 4 provide an overview of the ciliate species contained in the present monograph and show several community parameters (frequency, geographic distribution, etc.); see table headings for more detailed information. Additionally, the species occurring in the Etosha region and the dunes of the Namib Desert are separately listed in tables 5 and 6 to facilitate comparisons and calculations. We emphasize that the lists have been prepared very carefully, that is, contain only species identified both in vivo and silver preparations, as explained in chapter 2.2.2.

Table 3. Taxonomical and ecological summary of the species (i) found in Namibian and other soil samples and (ii) described or redescribed in this monograph. The list contains 388 taxa, of which 69 are redescribed and 143 are new species. New taxa marked by an asterisk (*) were not found in Namibia. See table 4 for the species found in the 73 Namibian samples, and FOISSNER (1998a) for a world list of soil ciliates.

Species	Taxonomic group[a]	Food[b]	Geographical distribution[c] H	P	A	N	Ar	Degree of autochthonism[d]	Main work done by[e]
Acaryophrya collaris (KAHL, 1926) DINGFELDER, 1962	GY	C	+	+	-	-	-	*	-
Actinobolina multinucleata n. sp.	GY	C	-	+	-	-	-	*	A
Afroamphisiella multinucleata n. sp.	HY	B	-	+	-	-	-	**	B
Afrothrix multinucleata n. sp.	HY	B,F	-	+	-	-	-	***	B
Amphisiella binucleata binucleata (HEMBERGER, 1985) FOISSNER, 1988	HY	F?	+	-	-	-	-	**	F
Amphisiella binucleata multicirrata n. ssp.	HY	B,C,F,G,N	-	+	-	-	-	**	F
Amphisiella elegans n. sp.	HY	C,N	+	+	-	-	-	***	F
Amphisiella longiseries n. sp.	HY	C,B	+	+	-	-	-	**	B
Amphisiella magnigranulosa FOISSNER, 1988	HY	C,G,H	+	+	+	+	-	***	F
Amphisiella multinucleata n. sp.	HY	C,F	-	+	-	+	-	***	B
Amphisiella namibiensis n. sp.	HY	C	+	+	-	-	-	**	A
Amphisiella polycirrata BERGER & FOISSNER, 1989	HY	C,F	-	+	-	+	-	***	F
Amphisiella procera n. sp.	HY	B	-	+	-	-	-	***	B
Amphisiella terricola GELLÉRT, 1955	HY	C	+	+	+	+	-	***	-
Amphisiella vitiphila (FOISSNER, 1987) FOISSNER, 1988	HY	C,F	-	+	-	+	-	**	-
Anatoliocirrus capari n. sp.	HY	B,C,N	+	+	-	+	-	**	see text
Apertospathula armata n. sp.	GY	?	?	+	-	-	-	**	F
Apertospathula dioplites n. sp.	GY	C	-	+	-	-	-	**	F
Apertospathula inermis n. sp.	GY	?	+	+	+	-	-	*	F
Apobryophyllum etoschense FOISSNER, 1998	GY	C	-	+	-	-	-	***	F
Apobryophyllum terricola FOISSNER, 1998	GY	C?	-	+	-	-	-	***	F
Apobryophyllum vermiforme n. sp.	GY	C?	-	+	-	-	-	**	F
Apocolpodidium etoschense n. sp.	NA	F?	+	+	-	-	-	**	A
Apocolpodidium macrostoma n. sp. (*)	NA	?	+	-	-	-	-	**	A
Apocyclidium obliquum (KAHL, 1926) n. comb.	HM	B	+	+	-	-	-	*	A
Apoenchelys bamforthi n. sp.	GY	C,N	-	+	-	-	-	**	F
Apospathidium atypicum (BUITKAMP & WILBERT, 1974) n. comb.	GY	C,N	+	+	+	+	-	***	F
Apospathidium terricola n. sp.	GY	C?	-	+	-	-	-	***	F
Apourosomoida halophila n. sp.	HY	B	-	+	-	-	-	**	F
Arcuospathidium cultriforme lionotiforme (KAHL, 1930) FOISSNER, 1984	GY	C	+	+	+	+	-	***	-
Arcuospathidium cultriforme megastoma n. ssp.	GY	C	-	+	-	-	-	**	F
Arcuospathidium etoschense n. sp.	GY	C?	-	+	-	-	-	***	F
Arcuospathidium lorjeae n. sp.	GY	C?	-	+	-	-	-	**	A
Arcuospathidium multinucleatum FOISSNER, 1999	GY	C	-	+	+	+	-	***	-
Arcuospathidium muscorum (DRAGESCO & DRAGESCO-KERNÉIS, 1979) FOISSNER, 1984	GY	C,H	+	+	+	+	-	***	-
Arcuospathidium namibiense namibiense n. sp. n. ssp.	GY	B	-	+	-	-	-	***	F

(continued)

Species	Taxonomic group[a]	Food[b]	Geographical distribution[c] H	P	A	N	Ar	Degree of autochthonism[d]	Main work done by[e]
Arcuospathidium namibiense tristicha n. ssp.	GY	C	-	+	-	+	-	***	F
Arcuospathidium novaki n. sp.	GY	C	-	+	-	-	-	**	F
Arcuospathidium vlassaki FOISSNER, 2000	GY	C	-	+	-	-	-	***	-
Bakuella granulifera n. sp.	HY	C,D,H,R,T	-	+	-	-	-	**	B
Balantidioides dragescoi FOISSNER, ADAM & FOISSNER, 1982	HE	C	+	+	+	-	-	***	-
Bilamellophrya australiensis n. sp. (*)	GY	C?	-	-	+	-	-	**	F
Bilamellophrya etoschensis n. sp.	GY	C?	-	+	-	+	-	**	F
Bilamellophrya hawaiiensis n. sp. (*)	GY	C,F	-	-	+	-	-	**	F
Birojimia muscorum (KAHL, 1932) BERGER & FOISSNER, 1989	HY	C,F,H,S	+	+	+	+	+	**	F
Blepharisma bimicronucleatum VILLENEUVE-BRACHON, 1940	HE	B	+	+	+	+	+	*	F
Blepharisma hyalinum PERTY, 1849	HE	B,H	+	+	+	+	+	*	-
Blepharisma steini KAHL, 1932	HE	B	+	+	+	+	+	*	-
Bresslaua insidiatrix CLAFF, DEWEY & KIDDER, 1941	CO	C,F	+	+	-	-	-	**	-
Bresslaua vorax KAHL, 1931	CO	B,C,F,G,H	+	+	+	+	-	**	-
Bryometopus atypicus FOISSNER, 1980	CO	B,F,G	+	+	+	+	-	*	-
Bryometopus pseudochilodon KAHL, 1932	CO	B,G	+	+	+	+	+	**	-
Bryometopus triquetrus FOISSNER, 1993	CO	B,E,F	+	+	+	+	-	**	-
Bryophyllum lingua multistriatum n. ssp.	GY	C?R	-	+	-	-	-	***	F
Bryophyllum loxophylliforme KAHL, 1931	GY	C,E,H,R	+	+	+	+	+	***	-
Bryophyllum paucistriatum n. sp.	GY	C,F	+	+	-	-	-	***	F
Bryophyllum penardi KAHL, 1931	GY	C,F,R	+	+	-	-	-	*	F
Bursaria truncatella MÜLLER, 1773	CO	C,D,F,G,R,T	+	+	+	+	-	*	-
Chilodonella uncinata (EHRENBERG, 1838) STRAND, 1928	CY	B	+	+	+	+	-	*	-
Cinetochilum margaritaceum (EHRENBERG, 1830) PERTY, 1852	HM	B,D,G	+	+	+	+	-	*	-
Circinella filiformis (FOISSNER, 1982) FOISSNER, 1994	HY	B	+	+	+	-	-	***	-
Clavoplites australiensis n. sp.	GY	C	-	+	+	-	-	**	F
Clavoplites edaphicus n. sp.	GY	C	?	+	+	-	-	**	F
Clavoplites terrenum (FOISSNER, 1984) n. comb.	GY	C	+	+	+	+	-	**	-
Colpoda aspera Kahl, 1926	CO	B	+	+	+	+	+	**	-
Colpoda cavicola amicronucleata n. ssp.	CO	B,H	-	+	-	-	-	***	F
Colpoda cavicola cavicola KAHL, 1935	CO	B,G,H	+	+	-	+	-	***	F
Colpoda cucullus (MÜLLER, 1773) GMELIN, 1790	CO	B,F,G	+	+	+	+	+	*	-
Colpoda ecaudata (LIEBMANN, 1936) FOISSNER, BLATTERER, BERGER & KOHMANN, 1991	CO	B	+	+	+	+	+	*	-
Colpoda edaphoni FOISSNER, 1980	CO	B	+	+	+	+	-	***	-
Colpoda elliotti BRADBURY & OUTKA, 1967	CO	B	+	+	+	+	-	***	-
Colpoda formisanoi n. sp.	CO	B	+	+	-	-	-	***	F
Colpoda henneguyi FABRE-DOMERGUE, 1889	CO	B,H	+	+	+	+	+	**	-
Colpoda inflata (STOKES, 1884) KAHL, 1931	CO	B,F	+	+	+	+	+	*	-
Colpoda lucida GREEFF, 1888	CO	B	+	+	+	+	+	**	-
Colpoda magna (GRUBER, 1879) LYNN, 1978	CO	B,C,F,G	+	+	+	+	-	*	-
Colpoda maupasi ENRIQUES, 1908	CO	B	+	+	+	+	+	**	-
Colpoda minima (ALEKPEROV, 1985) FOISSNER, 1993	CO	B	+	+	+	+	-	*	-
Colpoda orientalis FOISSNER, 1993	CO	B	+	+	-	+	-	**	-
Colpoda steinii MAUPAS, 1883	CO	B,E,G,H	+	+	+	+	+	*	-
Colpoda variabilis FOISSNER, 1980	CO	B,G	+	+	-	+	+	*	-
Colpodidium bradburyarum n. sp. (*)	NA	B	+	-	-	-	-	**	A
Colpodidium caudatum WILBERT, 1982	NA	B	+	+	+	+	-	***	A
Colpodidium horribile n. sp.	NA	B	+	+	-	-	-	**	A
Colpodidium microstoma n. sp. (*)	NA	F?	-	+	+	-	-	**	A
Colpodidium trichocystiferum n. sp.	NA	B	+	+	-	-	-	**	A
Condylostomides etoschensis n. sp.	HE	C,F,H,T	-	+	-	-	-	*	F
Condylostomides trinucleatus n. sp.	HE	C,F,G,H	-	+	+	-	-	*	F
Coriplites terricola FOISSNER, 1988	GY	C,F	+	+	+	+	-	**	-
Cyrtohymena candens (KAHL, 1932) FOISSNER, 1989	HY	B,C,F,N	+	+	+	+	+	**	-
Cyrtohymena citrina (BERGER & FOISSNER, 1987) FOISSNER, 1989	HY	C,D,H,T	+	+	+	+	-	**	-
Cyrtohymena quadrinucleata (DRAGESCO & NJINÉ, 1971) FOISSNER, 1989	HY	C	+	+	+	+	+	*	-
Cyrtolophosis mucicola STOKES, 1885	CO	B	+	+	+	+	+	*	-
Deviata bacilliformis (GELEI, 1954) EIGNER, 1995	HY	B,G	+	+	+	-	-	*	-
Dileptus americanus KAHL, 1931	GY	C,F	+	+	+	-	-	**	-

(continued)

Species	Taxonomic group [a]	Food [b]	Geographical distribution [c] H	P	A	N	Ar	Degree of autochthonism [d]	Main work done by [e]
Dileptus armatus FOISSNER & SCHADE, 2000 in FOISSNER (2000)	GY	C,T	+	+	-	-	-	**	-
Dileptus breviproboscis FOISSNER, 1981	GY	?	+	+	-	+	-	***	F
Dileptus mucronatus PENARD, 1922	GY	C	+	+	+	-	-	*	F
Dileptus similis FOISSNER, 1995	GY	C	-	+	-	+	-	**	-
Dileptus terrenus FOISSNER, 1981	GY	C	+	+	-	+	-	**	-
Dioplitophrya otti n. sp.	GY	C?	-	+	-	-	-	**	F
Diplites arenicola n. sp.	GY	C,F	-	+	-	-	-	**	F
Diplites telmatobius FOISSNER, 1998	GY	C	-	+	-	-	-	**	F
Dragescozoon terricola n. sp. (*)	CO	B	-	+	-	-	-	***	F
Drepanomonas exigua bidentata FOISSNER, 1999	NA	B?	+	+	+	-	-	***	-
Drepanomonas muscicola FOISSNER, 1987	NA	B	+	+	+	+	+	**	-
Drepanomonas pauciciliata FOISSNER, 1987	NA	B	+	+	+	+	+	**	-
Drepanomonas revoluta PENARD, 1922	NA	B,F	+	+	+	+	+	*	-
Drepanomonas sphagni KAHL, 1931	NA	B	+	+	+	+	+	**	-
Enchelaria multinucleata n. sp.	GY	C?	-	+	-	-	-	**	F
Enchelydium amphora (KAHL, 1926) KAHL, 1930	GY	?	-	+	-	-	-	*	-
Enchelydium blattereri n. sp. (*)	GY	C,F?H?	-	-	+	-	-	**	F
Enchelyodon armatides n. sp.	GY	C,F	+	+	+	+	-	**	F
Enchelyodon kenyaensis n. sp. (*)	GY	C?	-	+	-	-	-	**	F
Enchelyodon longinucleatus FOISSNER, 1984	GY	C?	+	+	+	+	-	***	-
Enchelyodon megastoma n. sp.	GY	B,F	-	+	-	-	-	*	F
Enchelyodon minutus n. sp.	GY	C?F?	-	+	-	-	-	**	F
Enchelyodon nodosus BERGER, FOISSNER & ADAM, 1984	GY	C?	+	+	-	-	-	**	-
Enchelyodon terrenus FOISSNER, 1984	GY	C?	+	+	-	-	-	***	-
Enchelyotricha jesnerae n. sp.	GY	C	-	+	-	-	-	**	F
Enchelys geleii (FOISSNER, 1981) FOISSNER, 2000	GY	C,F,N	+	+	-	+	-	***	-
Enchelys longitricha n. sp.	GY	C?	+	+	-	-	-	***	F
Enchelys multinucleata (DRAGESCO & DRAGESCO-KERNÉIS, 1979) BERGER, FOISSNER & ADAM, 1984	GY	C	+	+	+	+	-	***	-
Enchelys polynucleata (FOISSNER, 1984) n. comb.	GY	C	+	+	+	+	+	***	-
Epispathidium amphoriforme (GREEFF, 1888) FOISSNER, 1984	GY	C	+	+	+	+	-	**	-
Epispathidium ascendens (WENZEL, 1955) FOISSNER, 1987	GY	C	+	+	+	+	+	**	-
Epispathidium polynucleatum n. sp.	GY	C	-	+	+	+	-	**	F
Epispathidium terricola FOISSNER, 1987	GY	C	+	+	+	+	+	**	-
Epistylis alpestris FOISSNER, 1978	PE	B	+	+	+	+	-	*	F
Epitholiolus chilensis (BÜRGER, 1906) nov. comb.	GY	C	-	+	-	-	-	*	F
Erimophrya arenicola n. sp.	HY	B,F	-	+	-	-	-	***	B, F
Erimophrya glatzeli n. sp.	HY	B,F	-	+	-	-	-	***	B, F
Eschaneustyla lugeri n. sp. (*)	HY	B,F,H,S,T	-	-	+	-	-	**	B
Eschaneustyla terricola FOISSNER, 1982	HY	C,D,G,H	+	+	-	+	-	**	F
Etoschophrya oscillatoriophaga n. sp.	CO	E	-	+	-	-	-	**	F
Etoschothrix terricola n. sp.	HY	C	-	+	-	-	-	**	F
Euplotopsis incisa n. sp.	HY	B	+	+	-	+	-	***	F
Euplotopsis muscicola (KAHL, 1932) BORROR & HILL, 1995	HY	B,E	+	+	+	+	-	**	-
Euplotopsis muscicola alatus (KAHL, 1932) nov. comb.	HY	?	+	+	-	-	-	***	-
Exocolpoda augustini (FOISSNER, 1987) n. comb.	CO	B	+	+	+	+	-	***	F
Frontonia angusta angusta KAHL, 1931	HM	D,E,F,G,H,R	SNN						A
Frontonia angusta obovata n. ssp.	HM	D,G	-	+	-	-	-	**	A
Frontonia angusta solea FOISSNER, 1987	HM	D,E,T	+	+	-	-	-	**	A
Frontonia depressa (STOKES, 1886) KAHL, 1931	HM	C,G,H,N	+	+	+	+	+	*	A
Frontonia terricola FOISSNER, 1987	HM	C	+	+	-	-	-	***	A
Furgasonia theresae (FABRE-DOMERGUE, 1889) n. comb.	NA	B	-	+	-	-	-	*	F
Fuscheria lacustris SONG & WILBERT, 1989	GY	C?	+	+	+	-	+	*	-
Fuscheria nodosa FOISSNER, 1983	GY	C	-	+	+	-	-	*	-
Fuscheria terricola BERGER, FOISSNER & ADAM, 1983	GY	C	+	+	+	+	+	***	F
Gastrostyla bavariensis n. sp. (*)	HY	B,D,G	-	-	-	+	-	*	B, F
Gastrostyla mystacea minima HEMBERGER, 1985	HY	B,D,G	-	+	-	+	-	*	B
Gastrostyla mystacea mystacea (STEIN, 1859) STERKI, 1878	HY	C,G	SNN						B, F
Gastrostyla steinii ENGELMANN, 1862	HY	C,F,B,D,G	+	+	+	+	-	*	B
Gonostomum affine (STEIN, 1859) STERKI, 1878	HY	B,F,S	+	+	+	+	+	*	-

(continued)

Species	Taxonomic group[a]	Food[b]	Geographical distribution[c] H	P	A	N	Ar	Degree of autochthonism[d]	Main work done by[e]
Gonostomum algicola GELLÉRT, 1942	HY	B	+	+	-	-	-	***	A
Gonostomum kuehnelti FOISSNER, 1987	HY	B,F	+	+	+	+	+	***	-
Gonostomum namibiense n. sp.	HY	B	+	+	-	-	-	**	B
Gonostomum strenuum (ENGELMANN, 1862) STERKI, 1878	HY	B,G	+	+	+	-	-	**	B
Grossglockneria acuta FOISSNER, 1980	CO	H	+	+	+	+	+	***	-
Grossglockneria hyalina FOISSNER, 1985	CO	H	+	+	+	+	-	***	-
Halteria grandinella (MÜLLER, 1773) DUJARDIN, 1841	OL	B,F,G	+	+	+	+	+	*	-
Hausmanniella discoidea (GELLÉRT, 1956) FOISSNER, 1984	CO	B,C,G,H	+	+	+	+	-	***	-
Hausmanniella patella (KAHL, 1931) FOISSNER, 1984	CO	C,G,H	+	+	+	+	-	***	F
Hemiamphisiella granulifera (FOISSNER, 1987) FOISSNER, 1988	HY	F,H,N	+	+	+	-	-	**	-
Hemiamphisiella terricola FOISSNER, 1988	HY	C,D,F,H	+	+	+	+	-	**	-
Hemiamphisiella wilberti (FOISSNER, 1982) FOISSNER, 1988	HY	T	+	+	+	-	-	**	-
Hemisincirra gellerti verrucosa FOISSNER & SCHADE, 2000 in FOISSNER (2000)	HY	B	+	+	+	+	-	***	-
Hemisincirra inquieta HEMBERGER, 1985	HY	B,F	+	+	+	+	-	***	F
Hemisincirra namibiensis n. sp.	HY	?	-	+	-	-	-	**	B
Hemisincirra rariseta n. sp.	HY	B,H	-	+	-	-	-	***	F
Hemiurosoma goertzi n. sp.	HY	B,C,H	-	+	-	-	-	**	B
Hemiurosoma terricola n. sp.	HY	B,F?	+	+	-	+	-	***	F
Holophrya salinarum n. sp.	GY	?	-	+	-	-	-	*	F
Holosticha australis BLATTERER & FOISSNER, 1988	HY	C,T	+	+	+	+	-	**	-
Holosticha brachysticha n. sp.	HY	B	-	+	-	+	-	**	B
Holosticha stueberi FOISSNER, 1987	HY	C,F,H,N	+	+	+	-	-	**	-
Holosticha tetracirrata BUITKAMP & WILBERT, 1974	HY	B,C,D,G,H	+	+	+	+	+	**	-
Holostichides terricola FOISSNER, 1988	HY	B,H,S	+	+	+	+	-	***	-
Homalogastra setosa KAHL, 1926	HM	B	+	+	+	+	+	*	-
Idiocolpoda pelobia FOISSNER, 1993	CO	B	-	+	+	-	-	**	-
Ilsiella elegans n. sp.	CO	B	+	+	+	-	-	***	F
Ilsiella palustris FOISSNER, 1993	CO	B	+	+	+	-	-	**	-
Kahlilembus attenuatus (SMITH, 1897) FOISSNER, BERGER & KOHMANN, 1994	HM	B	+	+	+	+	-	*	-
Keronopsis dieckmanni FOISSNER, 1998	HY	C,F	-	+	-	-	-	**	-
Kuehneltiella namibiensis n. sp.	CO	C,R	-	+	-	-	-	***	F
Kuklikophrya ougandae (DRAGESCO, 1972) FOISSNER, 1993	CO	E	+	+	-	+	-	*	F
Lamtostyla australis (BLATTERER & FOISSNER, 1988) PETZ & FOISSNER, 1996	HY	B,C,F,G,H	+	+	+	+	-	***	-
Lamtostyla decorata n. sp.	HY	B,C,F	+	+	+	-	-	**	B, F
Lamtostyla edaphoni BERGER & FOISSNER, 1987	HY	B	+	+	+	+	+	***	-
Lamtostyla halophila n. sp.	HY	B	-	+	-	-	-	**	F
Lamtostyla hyalina (BERGER, FOIS. & ADAM, 1984) BERGER & FOISSNER, 1987	HY	?	+	+	-	+	+	***	-
Lamtostyla islandica BERGER & FOISSNER, 1988	HY	B,F	+	+	+	+	+	***	-
Lamtostyla kirkeniensis BERGER & FOISSNER, 1988	HY	B,C,F,H	+	+	+	-	-	***	-
Leptopharynx costatus MERMOD, 1914	NA	B,F	+	+	+	+	+	*	-
Litonotus muscorum (KAHL, 1931) BLATTERER & FOISSNER, 1988	GY	C	+	+	+	+	-	***	-
Maryna antarctica FOISSNER, 1993	CO	B	+	+	-	-	+	**	-
Maryna atra (GELEI, 1950) FOISSNER, 1993	CO	B	+	+	-	-	-	*	-
Maryna lichenicola (GELEI, 1950) FOISSNER, 1993	CO	B	+	+	-	-	-	**	F
Maryna minima (GELEI, 1950) FOISSNER, 1993	CO	B	+	+	-	-	-	*	F
Maryna namibiensis costaricensis n. ssp. (*)	CO	B,F	-	-	-	+	-	*	F
Maryna namibiensis namibiensis n. sp., n. ssp.	CO	B	-	+	-	-	-	*	F
Maryna ovata (GELEI, 1950) FOISSNER, 1993	CO	B	+	+	-	+	-	*	-
Maryna umbrellata (GELEI, 1950) FOISSNER, 1993	CO	B	+	+	+	+	-	*	F
Meseres corlissi PETZ & FOISSNER, 1992	OL	G	-	+	-	-	-	*	-
Metacineta namibiensis n. sp.	SU	C,F	-	+	-	-	-	**	A
Metopus contortus (QUENNERSTEDT, 1867) KAHL, 1932	ME	B	-	+	-	-	-	*	F
Metopus gibbus KAHL, 1927	ME	B	+	+	-	+	-	*	A
Metopus hasei SONDHEIM, 1929	ME	B	+	+	+	+	-	**	-
Metopus inversus (JANKOWSKI, 1964) FOISSNER & AGATHA, 1999	ME	B	-	+	-	-	-	*	-
Metopus minor KAHL, 1927	ME	B	+	+	-	+	-	*	F
Metopus ovalis KAHL, 1927	ME	B	-	+	-	+	-	*	-
Metopus palaeformis KAHL, 1927	ME	B	+	+	-	+	-	*	F
Metopus setosus KAHL, 1927	ME	B	-	+	-	+	-	*	-
Microdiaphanosoma arcuatum (GRANDORI & GRANDORI, 1934) WENZEL, 1953	CO	B	+	+	+	+	+	***	-

(continued)

Species	Taxonomic group[a]	Food[b]	Geographical distribution[c] H	P	A	N	Ar	Degree of autochthonism[d]	Main work done by[e]
Mykophagophrys terricola (FOISSNER, 1985) FOISSNER, 1995	CO	H	+	+	+	+	+	***	-
Nassula dragescoi n. sp.	NA	E	-	+	-	-	-	*	A
Nassula etoschensis n. sp.	NA	E	-	+	-	-	-	**	A
Nassula exigua KAHL, 1931 (*)	NA	E	+	-	-	+	-	***	A
Nassula granata n. sp.	NA	E	-	+	-	-	-	**	A
Nassula longinassa FOISSNER, 1980	NA	E	+	+	-	-	-	*	A
Nassula parva KAHL, 1928	NA	E	+	+	-	-	-	*	A
Nassula tuberculata n. sp.	NA	E	+	+	-	-	+	**	A
Nassulides labiatus (KAHL, 1933) n. comb.	NA	E	+	+	-	-	-	*	A
Nassulides pictus (GREEFF, 1888) n. comb.	NA	E	+	+	-	-	-	*	-
Naxella lucida (REUTER, 1961) n. comb.	NA	E	+	+	-	-	-	*	A
Naxella rosea (TUCOLESCO, 1962) n. comb.	NA	E	-	+	-	-	-	*	A
Nivaliella plana FOISSNER, 1980	CO	H	+	+	+	+	+	***	F
Notoxoma parabryophryides FOISSNER, 1993	CO	B	+	+	+	+	-	***	-
Nudiamphisiella interrupta n. sp.	HY	B	-	+	-	+	-	**	B
Obliquostoma enchelyodontides n. sp.	GY	C?	-	+	-	-	-	**	F
Obliquostoma namibiense n. sp.	GY	C?	-	+	-	-	-	**	F
Odontochlamys alpestris alpestris FOISSNER, 1981	CY	B,F	+	+	+	+	-	*	A
Odontochlamys alpestris biciliata n. ssp.	CY	B	-	+	-	+	-	**	A
Odontochlamys convexa (KAHL, 1931) BLATTERER & FOISSNER, 1992	CY	B?	+	+	+	+	-	***	-
Opercularia curvicaule (PENARD, 1922) FOISSNER, 1998	PE	B	+	+	+	+	+	**	-
Orthoamphisiella breviseries n. sp.	HY	B	+	+	-	-	-	**	B
Ottowphrya dragescoi (FOISSNER, 1987) n. comb.	CO	C	+	+	+	-	-	***	F
Oxytricha africana FOISSNER, 1999	HY	F,T	-	+	+	-	-	**	-
Oxytricha elegans FOISSNER, 1999	HY	B,F	-	+	-	-	-	**	-
Oxytricha granulifera FOISSNER & ADAM, 1983	HY	B,F,H	+	+	+	+	+	**	-
Oxytricha granulifera quadricirrata BLATTERER & FOISSNER, 1988	HY	B,F,H	-	+	+	+	-	**	-
Oxytricha lanceolata SHIBUYA, 1930	HY	B,F,G	+	+	+	+	+	**	-
Oxytricha longa GELEI & SZABADOS, 1950	HY	B,F	+	+	-	-	-	*	B
Oxytricha longigranulosa BERGER & FOISSNER, 1989	HY	C,F,H	+	+	+	+	+	**	-
Oxytricha opisthomuscorum FOIS., BLATTERER, BERGER & KOHMANN, 1991	HY	B,F,G	+	+	-	+	+	**	-
Oxytricha siseris VUXANOVICI, 1963	HY	B?	+	+	+	+	-	*	-
Parabryophrya etoschensis n. sp.	CO	B	-	+	-	-	-	***	F
Paracineta lauterborni SONDHEIM, 1929	SU	C	+	+	+	+	-	**	-
Paraenchelys brachyarmata n. sp.	GY	C?	-	+	-	+	-	**	F
Paraenchelys brachyoplites n. sp.	GY	B,C?	+	+	-	-	-	**	F
Paraenchelys pulchra n. sp.	GY	C?	-	+	-	-	-	**	F
Paraenchelys terricola FOISSNER, 1984	GY	C	+	+	+	+	+	***	F
Paraenchelys wenzeli FOISSNER, 1984	GY	C?	+	+	+	+	-	***	-
Parafurgasonia protectissima (PENARD, 1922) FOISSNER, 1999	NA	B?	+	+	+	+	-	**	-
Parafurgasonia sorex (PENARD, 1922) FOISSNER & ADAM, 1981	NA	G,H?N	+	+	+	+	-	***	-
Parafurgasonia terricola FOISSNER, 1999	NA	B?	+	+	-	+	-	***	-
Paragastrostyla lanceolata HEMBERGER, 1985	HY	B?	-	+	-	+	-	**	F
Paragonostomum binucleatum n. sp.	HY	B	+	+	-	-	-	***	B
Paragonostomum caudatum n. sp.	HY	B	+	+	+	-	-	***	B
Paragonostomum multinucleatum n. sp.	HY	B,G	+	+	-	-	-	***	B
Paragonostomum rarisetum n. sp.	HY	B	-	+	-	-	-	***	F
Paraholosticha muscicola KAHL, 1932	HY	C,F,G,H	+	+	-	-	+	**	-
Parakahliella binucleata n. sp.	HY	B,C,E,F,N	-	+	-	-	-	***	B
Parakahliella halophila n. sp.	HY	B,C,F,H	+	+	-	-	-	**	F
Parakahliella namibicola n. sp.	HY	F,N	-	+	-	-	-	***	F
Pedohymena australiensis FOISSNER, 1995	NA	B	-	+	+	+	-	***	-
Periholosticha lanceolata HEMBERGER, 1985	HY	B?	-	+	-	+	-	***	F
Perisincirra longicirrata n. sp.	HY	F	-	+	-	-	-	**	B
Perisincirra paucicirrata n. sp.	HY	H	-	+	+	-	-	**	B
Phialina binucleata BERGER, FOISSNER & ADAM, 1984	GY	C	+	+	+	+	-	**	-
Phialina minima (KAHL, 1927) n. comb.	GY	C?	-	+	-	-	-	*	F
Phialinides armatus n. sp. (*)	GY	C?	-	-	-	+	-	**	F
Phialinides australis FOISSNER, 1988	GY	C	-	+	+	+	-	**	-
Plagiocampa bitricha FOISSNER, 1999	PR	N	+	+	+	-	-	**	-

(continued)

Species	Taxonomic group[a]	Food[b]	Geographical distribution[c]					Degree of autochthonism[d]	Main work done by[e]
			H	P	A	N	Ar		
Plagiocampa difficilis FOISSNER, 1981	PR	B,F	+	+	+	-	+	**	-
Plagiocampa namibiensis n. sp.	PR	C?	-	+	-	-	-	**	F
Plagiocampa ovata GELEI, 1954	PR	C,F	+	+	+	-	-	*	F
Plagiocampa pentadactyla n. sp.	PR	C?F?	+	+	-	+	-	**	F
Plagiocampa rouxi KAHL, 1926	PR	B,G	+	+	+	+	-	*	-
Plagiocampides halophilus n. sp.	PR	C,E	-	+	-	+	-	*	A, F
Platyophrya binucleata FOISSNER, 1987	CO	H	+	+	-	-	-	***	-
Platyophrya macrostoma FOISSNER, 1980	CO	B	+	+	+	+	+	***	-
Platyophrya paoletti FOISSNER, 1997	CO	B	-	+	-	+	-	***	-
Platyophrya spumacola hexasticha nov. ssp.	CO	F	-	+	-	-	-	**	F
Platyophrya spumacola spumacola KAHL, 1927	CO	B,C,E,F,G,H,R,T	+	+	+	+	+	**	F
Platyophrya vorax KAHL, 1926	CO	B,F,G,H	+	+	+	+	+	*	-
Platyophryides latus (KAHL, 1930) FOISSNER, 1987	CO	C,G,H	+	+	-	+	+	***	F
Plesiocaryon elongatum (SCHEWIAKOFF, 1892) n. comb.	CO	B	+	+	+	+	+	*	F
Plesiocaryon terricola n. sp.	CO	B	+	+	+	+	-	***	F
Pleuroplites australis FOISSNER, 1988	GY	C,F	+	+	+	+	+	***	-
Pleuroplitoides smithi FOISSNER, 1996	GY	C	+	+	+	+	+	***	-
Podophrya halophila KAHL, 1934	SU	C	-	+	+	+	-	*	A
Podophrya tristriata n. sp. (*)	SU	C?F	+	-	+	-	-	**	A
Protocyclidium muscicola (KAHL, 1931) n. comb.	HM	B	+	+	+	+	+	**	-
Protocyclidium terricola (KAHL, 1931) n. comb.	HM	B,G	+	+	+	+	-	**	A
Protospathidium namibicola n. sp.	GY	C	-	+	-	-	-	***	F
Protospathidium serpens (KAHL, 1930) FOISSNER, 1981	GY	C?	+	+	+	+	+	**	-
Protospathidium vermiforme n. sp. (*)	GY	C?	+	-	-	-	-	***	F
Pseudochilodonopsis mutabilis FOISSNER, 1981	CY	B	+	+	+	+	+	**	-
Pseudocohnilembus binucleatus n. sp.	HM	B	-	+	-	-	-	**	F
Pseudocohnilembus persalinus hexakineta n. ssp.	HM	B	-	+	-	-	-	*	F
Pseudocohnilembus persalinus persalinus EVANS & THOMPSON, 1984	HM	B	+	+	-	-	-	*	-
Pseudocyrtolophosis alpestris FOISSNER, 1980	CO	B	+	+	+	+	+	**	-
Pseudoholophrya minuta n. sp.	GY	C?	-	+	-	-	-	**	F
Pseudoholophrya terricola BERGER, FOISSNER & ADAM, 1984	GY	C	+	+	+	+	+	***	F
Pseudokreyella australis FOISSNER, 1993	CO	B	+	+	+	-	-	***	-
Pseudokreyella etoschensis n. sp.	CO	B	-	+	-	-	-	***	F
Pseudomicrothorax agilis MERMOD, 1914	NA	B,E,G	-	+	-	+	-	*	-
Pseudomicrothorax dubius (MAUPAS, 1883) PENARD, 1922	NA	B,E	-	+	-	-	-	*	-
Pseudomonilicaryon angustistoma n. sp.	GY	C	-	+	-	+	-	**	F
Pseudomonilicaryon japonicum n. sp. (*)	GY	C,R	+	-	-	-	-	**	A
Pseudomonilicaryon massutii (KAHL, 1933) n. comb.	GY	C	-	+	-	-	-	*	A
Pseudoplatyophrya nana (KAHL, 1926) FOISSNER, 1980	CO	H	+	+	+	+	+	***	-
Pseudoplatyophrya saltans FOISSNER, 1988	CO	H	+	+	+	+	+	***	-
Pseudouroleptus caudatus caudatus HEMBERGER, 1985	HY	C,D,E,F,N,T	-	+	-	+	-	*	F
Pseudouroleptus caudatus namibiensis n. ssp.	HY	C,D,E,F,N,T	-	+	-	-	-	*	F
Pseudouroleptus procerus BERGER & FOISSNER, 1987	HY	C,F,G,N	+	+	-	-	-	***	-
Pseudourostyla franzi FOISSNER, 1987	HY	C,H,N,T	-	+	+	+	-	**	-
Pseudovorticella sphagni FOISSNER & SCHIFFMANN, 1974	PE	B	+	+	+	+	-	*	-
Reticulowoodruffia terricola FOISSNER, 1993	CO	B	+	+	-	-	-	***	F
Rostrophrya fenestrata n. sp.	CO	?	+	+	-	-	-	**	F
Rostrophrya namibiensis maldivensis n. ssp.	CO	?	-	+	-	-	-	**	F
Rostrophrya namibiensis namibiensis n. sp. n. ssp.	CO	B,E,H	-	+	-	-	-	**	F
Rostrophryides africana africana FOISSNER, 1987	CO	?	+	+	-	+	-	***	F
Rostrophryides africana etoschensis n. ssp.	CO	C?E	-	+	-	-	-	**	F
Sagittaria hyalina FOISSNER, CZAPIK & WIACKOWSKI, 1981	CO	B	+	+	+	+	-	*	-
Sathrophilus muscorum (KAHL, 1931) CORLISS, 1960	HM	B	+	+	+	+	+	**	-
Semiplatyophrya acrostoma n. sp.	CO	B?	-	+	-	-	-	***	F
Semiplatyophrya foissneri WILBERT & KAHAN, 1986	CO	B	+	+	+	-	-	***	-
Semispathidium armatum n. sp.	GY	C?	-	+	-	-	-	**	F
Semispathidium enchelyodontides n. sp.	GY	C,F	-	+	-	-	-	**	F
Sikorops minor n. sp.	GY	C?F	+	+	-	-	-	***	F
Sikorops namibiensis n. sp.	GY	C,F	-	+	+	+	-	**	F
Sorogena stoianovitchae BRADBURY & OLIVE, 1980	CO	C	+	+	+	+	-	***	-

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Species	Taxonomic group[a]	Food[b]	Geographical distribution[c] H	P	A	N	Ar	Degree of autochthonism[d]	Main work done by[e]
Spathidium aciculare n. sp.	GY	C	-	+	+	-	-	**	F
Spathidium anguilla VUXANOVICI, 1962	GY	C?	+	+	+	+	-	*	-
Spathidium bavariense KAHL, 1930	GY	C	+	+	+	+	-	**	-
Spathidium claviforme KAHL, 1930	GY	C	+	+	+	+	-	**	-
Spathidium contractile n. sp.	GY	C	-	+	-	-	-	**	F
Spathidium etoschense n. sp.	GY	?	-	+	-	-	-	**	F
Spathidium extensum KAHL, 1933	GY	C	-	+	-	-	-	**	F
Spathidium lanceoplites n. sp.	GY	C?	-	+	-	-	-	**	F
Spathidium namibicola n. sp.	GY	C,F	-	+	-	-	-	***	A
Spathidium procerum KAHL, 1930	GY	C?	+	+	+	+	-	**	-
Spathidium rusticanum FOISSNER, 1981	GY	C?	+	+	-	-	-	***	F
Spathidium seppelti etoschense n. ssp.	GY	C	-	+	-	-	-	**	F
Spathidium spathula (MÜLLER, 1773) MOODY, 1912	GY	C	+	+	+	+	-	*	-
Spathidium turgitorum n. sp.	GY	F	?	+	-	-	-	**	F
Sphaerophrya terricola FOISSNER, 1986	SU	C	+	+	+	+	+	**	-
Stammeridium kahli (WENZEL, 1953) WENZEL, 1969	NA	B	+	+	+	+	-	***	-
Sterkiella cavicola (KAHL, 1935) FOISSNER, BLATTERER, BERGER & KOHMANN, 1991	HY	C,N	+	+	+	+	-	***	F
Sterkiella histriomuscorum (FOISSNER, BLATTERER, BERGER & KOH MANN, 1991) FOISSNER, BLATTERER, BERGER & KOHMANN, 1991	HY	B,C,F,N	+	+	+	+	+	*	-
Supraspathidium armatum n. sp.	GY	C	-	+	-	-	-	**	F
Supraspathidium etoschense n. sp.	GY	C	-	+	-	-	-	**	F
Tachysoma granulifera BERGER & FOISSNER, 1987	HY	F,G,H,N	+	+	+	-	-	***	-
Tachysoma humicola humicola GELLÉRT, 1957	HY	B,T	+	+	+	+	-	***	-
Tectohymena terricola FOISSNER, 1993	CO	B	+	+	-	-	-	***	-
Terricirra livida (BERGER & FOISSNER, 1987) BERGER & FOISSNER, 1989	HY	B	+	+	+	-	-	***	-
Terricirra matsusakai BERGER & FOISSNER, 1989	HY	B	+	+	+	+	-	***	F
Tetrahymena rostrata (KAHL, 1926) CORLISS, 1952	HM	B,G	+	+	+	+	-	**	-
Trachelophyllum africanum n. sp.	GY	C,F	-	+	-	+	-	**	F
Trachelophyllum apiculatum (PERTY, 1852) CLAPARÈDE & LACHMANN, 1859	GY	C,F?	+	+	+	+	-	*	F
Trachelophyllum costaricanum n. sp. (*)	GY	C	?	?	-	+	-	**	F
Trachelophyllum pannonicum n. sp. (*)	GY	C	+	-	-	-	-	**	F
Trihymena terricola FOISSNER, 1988	CO	B?	+	+	+	+	-	***	-
Uroleptus notabilis (FOISSNER, 1982) FOISSNER, 1998	HY	F,H,T	+	+	+	+	-	**	-
Uroleptus paranotabilis n. sp.	HY	?	-	+	-	-	+	**	B, F
Urosoma emarginata (STOKES, 1885) BERGER, 1999	HY	B	+	+	-	-	-	*	-
Urosoma karinae FOISSNER, 1987	HY	B?F	+	+	+	-	-	**	-
Urosomoida agiliformis FOISSNER, 1982	HY	B,C,	+	+	+	+	-	**	F
Urosomoida agilis (ENGELMANN, 1862) HEMBERGER, 1985	HY	B,D,N,S,T	+	+	+	+	-	*	-
Urosomoida antarctica FOISSNER, 1996	HY	B,F?N?	-	+	-	-	+	**	-
Urosomoida deserticola n. sp.	HY	B,F	-	+	-	-	-	***	F
Urosomoida monostyla n. sp.	HY	B,F	-	+	-	-	-	**	F
Urosomoida namibiensis n. sp.	HY	B?	-	+	-	-	-	**	B
Urosomoida reticulata n. sp.	HY	C,H,T	-	+	-	+	-	*	B
Vermioxytricha arenicola n. sp.	HY	B,H,S	+	+	-	-	-	***	B
Vermioxytricha muelleri (FOISSNER, 1986) nov. comb.	HY	B	+	+	-	-	-	***	-
Vorticella astyliformis FOISSNER, 1981	PE	B,S	+	+	+	+	+	***	-
Vorticella echini KING, 1931	PE	B	+	+	-	-	-	**	A
Vorticella infusionum DUJARDIN, 1841	PE	B	+	+	+	-	+	*	-
Wallackia bujoreani (LEPSI, 1951) BERGER & FOISSNER, 1989	HY	B	+	+	-	-	-	***	F
Wallackia elegans n. sp.	HY	B	-	+	-	-	-	***	B
Wolfkosia loeffleri n. sp.	NA	B?	-	+	-	+	-	*	F
Woodruffia australis FOISSNER, 1993	CO	B	-	+	+	+	-	***	F
Woodruffia rostrata KAHL, 1931	CO	C	+	+	+	-	-	*	-
Woodruffides metabolicus (JOHNSON & LARSON, 1938) FOISSNER, 1987	CO	C	+	+	+	+	-	**	F
Woodruffides terricola FOISSNER, 1987	CO	C,F,N	+	+	+	+	-	***	F

[a] Classification mainly after CORLISS (1979), that of colpodids after FOISSNER (1993). CO – colpodid, CY – cyrtophorid, GY – gymnostomatid (haptorid), HE – heterotrich, HM – hymenostome, HY – hypotrich, ME – metopid, NA – nassulid, OL – oligotrich, PE – peritrich, PR – prostomatid, SU – suctorian.

[b] Food items were determined mainly by examination of the food vacuoles. B – bacteria, C – ciliates, D – diatoms, E – blue green algae (cyanobacteria), F – colourless flagellates, G – green algae, including autotrophic flagellates, H – hyphae and/or spores of fungi and yeasts, N – naked amoebae, R – rotifers and/or nematodes, S – inorganic and organic soil particles ("detritus"), T – testate amoebae.

[c] This compilation contains only **reliable** records from terrestrial habitats globally. Thus, unsubstantiated records (for instance, *Metopus palaeformis* by ESTEBAN et al. 1995 from volcanic soil on the Canary Islands) and true limnetic or marine records are **not** included (for instance, *Metopus contortus* discovered in a marine habitat in Sweden). Occasionally, this may be a little bit arbitrarily, for instance, with samples from river banks, dry road puddles, or the Etosha Pan, which is sometimes flooded. See also next footnote. Classification of biogeographic regions. H – Holarctis (North America, Greenland, Eurasia with Iceland, Canary Islands, Korea, Japan, and north Africa), P – Palaeotropis (Africa south of Sahara desert, Madagascar, India, southwest Asia), A – Australis (mainly Australia), N – Neotropis (Central and South America), Ar – Archinotis (Antarctica and Islands in the southern oceans), SNN – reliable soil records not known.

[d] * low, reliably recorded also from freshwater habitats; ** probably strong; includes most of the new species and many inhabitants found in mosses and in mud and soil samples from astatic (ephemeral) puddles; *** probably found exclusively in true terrestrial habitats (litter, soil, humus under and in moss etc.). Only species with specific food requirements or very characteristic morphological adaptations have been classified to this level; furthermore, species belonging to genera known from soil only, were usually also classified to this level.

[e] Species described by A – Sabine AGATHA, B – Helmut BERGER, F – Wilhelm FOISSNER.

Table 4. Distribution and frequency (%) of the 365 identified ciliate taxa found in 73 samples from terrestrial habitats of Namibia. The 128 new taxa found in these samples are marked by "n. sp.", "n. ssp." or, if described in earlier papers, "(n. sp.)". For authorship and date of other species, see table 1. Presence is indicated by "1", absence by "–".

Sp. No.	Species	Sites / Samples 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1	*Acaryophrya collaris*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2	*Actinobolina multinucleata* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
3	*Afroamphisiella multinucleata* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
4	*Afrothrix multinucleata* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
5	*Amphisiella binucleata multicirrata* n. ssp.	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
6	*Amphisiella elegans* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
7	*Amphisiella longiseries* n. sp.	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
8	*Amphisiella magnigranulosa*	–	1	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	1	–	–	1	1
9	*Amphisiella multinucleata* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
10	*Amphisiella namibiensis* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
11	*Amphisiella polycirrata*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
12	*Amphisiella procera* n. sp.	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
13	*Amphisiella terricola*	–	1	–	–	–	–	–	–	1	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–
14	*Amphisiella vitiphila*	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
15	*Anatoliocirrus capari* n. sp.	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
16	*Apertospathula armata* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
17	*Apertospathula dioplites* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
18	*Apertospathula inermis* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
19	*Apobryophyllum etoschense* (n. sp.)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
20	*Apobryophyllum terricola*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
21	*Apobryophyllum vermiforme* n. sp.	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
22	*Apocolpodidium etoschense* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
23	*Apocyclidium obliquum* n. comb.	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
24	*Apoenchelys bamforthi* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
25	*Apospathidium atypicum* n. comb.	1	1	–	–	–	–	–	1	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–
26	*Apospathidium terricola* n. sp.	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
27	*Apourosomoida halophila* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
28	*Arcuospathidium cultriforme lionotiforme*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
29	*Arcuospathidium cultriforme megastoma* n. ssp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
30	*Arcuospathidium etoschense* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
31	*Arcuospathidium lorjeae* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
32	*Arcuospathidium multinucleatum*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
33	*Arcuospathidium muscorum*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
34	*Arcuospathidium namibiense namibiense* n. sp. n. ssp.	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
35	*Arcuospathidium namibiense tristicha* n. ssp.	–	–	–	1	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
36	*Arcuospathidium novaki* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
37	*Arcuospathidium vlassaki* (n. sp.)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
38	*Bakuella granulifera* n. sp.	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
39	*Balantidioides dragescoi*	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
40	*Bilamellophrya etoschensis* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
41	*Birojimia muscorum*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
42	*Blepharisma bimicronucleatum*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
43	*Blepharisma hyalinum*	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
44	*Blepharisma steini*	1	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
45	*Bresslaua insidiatrix*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
46	*Bresslaua vorax*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
47	*Bryometopus atypicus*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
48	*Bryometopus pseudochilodon*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
49	*Bryometopus triquetrus*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
50	*Bryophyllum lingua multistriatum* n. ssp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
51	*Bryophyllum loxophylliforme*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
52	*Bryophyllum paucistriatum* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
53	*Bryophyllum penardi*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
54	*Bursaria truncatella*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
55	*Chilodonella uncinata*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
56	*Cinetochilum margaritaceum*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
57	*Circinella filiformis*	1	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–
58	*Clavoplites australiensis* n. sp.	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
59	*Clavoplites edaphicus* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–

Table 4 continued

Sp. No.	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	%
	Sites / Samples																																											
1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	2,7
2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1,4
4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
5	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
6	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8,2
7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
8	–	–	–	–	–	–	–	–	–	–	1	1	1	–	–	1	–	1	–	1	1	–	–	–	–	1	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	23,3
9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	4,1
11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
12	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
13	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12,3
14	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
16	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
17	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
18	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	2,7
19	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	4,1
20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
21	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
22	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1,4
23	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6,8
24	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
25	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8,2
26	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
27	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1,4
28	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
29	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	2,7
31	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
32	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	5,5
33	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	9,6
34	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
35	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5,5
36	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
37	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
38	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	4,1
39	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4,1
40	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	2,7
41	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
42	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
43	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	1	–	1	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	13,7
44	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8,2
45	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	2,7
46	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
47	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1,4
48	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	5,5
49	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
50	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1,4
51	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5,5
52	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4,1
53	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
54	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1,4
55	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
56	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	5,5
57	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11,0
58	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
59	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	2,7

Sp. No.	Species	Sites / Samples 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
60	*Clavoplites terrenum* n. comb.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
61	*Colpoda aspera*	–	1	1	–	1	1	–	–	1	–	–	1	1	–	1	–	–	–	–	–	–	–	–	1	1	–	–	1	–	–
62	*Colpoda cavicola amicronucleata* n. ssp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
63	*Colpoda cavicola cavicola*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
64	*Colpoda cucullus*	1	1	1	1	1	1	1	1	1	–	–	1	–	–	1	1	1	–	–	–	1	1	1	–	–	–	1	1	1	1
65	*Colpoda ecaudata*	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	1	–	1	–	1	–	–	–	–	–	1	–	–	–
66	*Colpoda edaphoni*	–	–	–	–	1	–	–	–	1	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1
67	*Colpoda elliotti*	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	1
68	*Colpoda formisanoi* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
69	*Colpoda henneguyi*	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
70	*Colpoda inflata*	1	1	1	1	1	1	–	–	1	–	1	1	1	–	1	1	1	–	–	1	–	1	1	1	–	1	1	1	–	1
71	*Colpoda lucida*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
72	*Colpoda magna*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
73	*Colpoda maupasi*	1	1	1	1	1	1	1	1	1	–	1	1	1	–	1	1	1	–	–	1	–	1	1	1	–	1	1	1	1	1
74	*Colpoda minima*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
75	*Colpoda orientalis*	–	–	1	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
76	*Colpoda steinii*	1	1	1	1	1	1	1	1	–	–	1	1	–	1	1	1	1	–	1	1	1	1	1	1	–	1	1	1	1	1
77	*Colpoda variabilis*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
78	*Colpodidium caudatum*	–	–	1	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
79	*Colpodidium horribile* n. sp.	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
80	*Colpodidium trichocystiferum* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
81	*Condylostomides etoschensis* n. sp.	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
82	*Condylostomides trinucleatus* n. sp.	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
83	*Coriplites terricola*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
84	*Cyrtohymena candens*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
85	*Cyrtohymena citrina*	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
86	*Cyrtohymena quadrinucleata*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
87	*Cyrtolophosis mucicola*	–	–	1	1	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	1	–	–	1	1
88	*Deviata bacilliformis*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
89	*Dileptus americanus*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
90	*Dileptus armatus*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
91	*Dileptus breviproboscis*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
92	*Dileptus mucronatus*	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
93	*Dileptus similis*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
94	*Dileptus terrenus*	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–
95	*Dioplitophrya otti* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
96	*Diplites arenicola* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
97	*Diplites telmatobius* (n. sp.)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
98	*Drepanomonas exigua bidentata*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
99	*Drepanomonas muscicola*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
100	*Drepanomonas pauciciliata*	1	1	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–
101	*Drepanomonas revoluta*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
102	*Drepanomonas sphagni*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
103	*Enchelaria multinucleata* n. sp.	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
104	*Enchelydium amphora*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
105	*Enchelyodon armatides* n. sp.	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
106	*Enchelyodon longinucleatus*	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
107	*Enchelyodon megastoma* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
108	*Enchelyodon minutus* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
109	*Enchelyodon nodosus*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
110	*Enchelyodon terrenus*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
111	*Enchelyotricha jesnerae* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
112	*Enchelys geleii*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
113	*Enchelys longitricha* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
114	*Enchelys multinucleata*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
115	*Enchelys polynucleata* n. comb.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
116	*Epispathidium amphoriforme*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
117	*Epispathidium ascendens*	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	1
118	*Epispathidium polynucleatum* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
119	*Epispathidium terricola*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
120	*Epistylis alpestris*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
121	*Epitholiolus chilensis* n. comb.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
122	*Erimophrya arenicola* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–

Sp. No.	Sites / Samples 31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	%
60	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
61	–	–	–	–	–	–	–	–	–	1	–	–	1	1	1	1	–	1	1	–	1	1	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	1	1	–	–	32,9
62	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
63	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
64	1	1	–	1	1	–	1	1	–	1	1	1	1	1	1	1	1	1	1	1	1	1	–	1	1	–	1	–	–	1	–	1	1	1	–	1	1	–	–	1	–	–	–	67,1
65	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	1	–	1	–	–	–	–	–	–	–	–	–	–	15,1
66	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8,2
67	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11,0
68	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
69	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	1	–	1	–	–	–	1	–	–	1	–	–	–	–	1	1	–	–	–	–	–	–	1	–	–	–	16,4
70	1	1	1	1	1	1	1	–	1	1	1	1	1	1	1	1	1	1	1	1	1	1	–	1	1	1	1	–	–	1	–	1	–	1	–	–	–	–	–	1	–	1	1	71,2
71	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	6,8
72	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	4,1
73	1	1	1	1	1	1	1	1	–	1	1	1	1	1	1	1	1	1	1	1	1	1	–	1	1	1	1	–	–	1	–	1	1	1	–	1	–	–	–	1	1	1	1	79,5
74	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	6,8
75	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	1	1	1	–	–	–	–	1	–	–	–	13,7
76	1	1	1	1	1	–	1	1	1	1	1	1	1	1	1	1	1	–	1	1	1	1	–	1	1	1	–	–	–	1	–	1	1	1	–	–	1	–	–	–	1	1	1	76,7
77	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	4,1
78	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	1	–	–	–	–	–	1	1	–	–	–	–	1	–	–	1	16,4
79	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	5,5
80	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
81	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	1	–	–	–	5,5
82	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
83	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
84	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
85	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5,5
86	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	8,2
87	–	–	–	–	–	–	–	–	–	1	1	1	1	–	–	–	–	–	1	1	1	–	1	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	1	–	–	–	26,0
88	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	2,7
89	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
90	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
91	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
92	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
93	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
94	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	9,6
95	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
96	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
97	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	4,1
98	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
99	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
100	–	–	1	–	–	–	–	–	–	1	–	–	1	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	15,1
101	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	9,6
102	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	11,0
103	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
104	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
105	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6,8
106	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9,6
107	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
108	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1,4
109	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	2,7
110	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
111	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
112	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
113	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
114	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1,4
115	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
116	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
117	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	9,6
118	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	4,1
119	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
120	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	4,1
121	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
122	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7

Sp. No.	Species	Sites / Samples 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
123	*Erimophrya glatzeli* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
124	*Eschaneustyla terricola*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
125	*Etoschophrya oscillatoriophaga* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
126	*Etoschothrix terricola* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
127	*Euplotopsis incisa* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
128	*Euplotopsis muscicola*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	
129	*Euplotopsis muscicola alatus*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
130	*Exocolpoda augustini* n. comb.	–	1	–	1	1	–	–	1	1	–	1	1	–	–	1	1	1	–	–	1	–	–	1	1	–	1	1	1	–	–
131	*Frontonia angusta obovata* n. ssp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
132	*Frontonia angusta solea*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
133	*Frontonia depressa*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
134	*Frontonia terricola*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	
135	*Furgasonia theresae*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
136	*Fuscheria lacustris*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
137	*Fuscheria nodosa*	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
138	*Fuscheria terricola*	1	–	1	1	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1
139	*Gastrostyla mystacea minima*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
140	*Gastrostyla steinii*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
141	*Gonostomum affine*	1	1	1	1	1	1	–	1	1	–	–	1	–	–	1	1	1	1	–	–	–	–	–	1	–	1	1	1	–	1
142	*Gonostomum algicola*	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
143	*Gonostomum kuehnelti*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
144	*Gonostomum namibiense* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
145	*Gonostomum strenuum*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
146	*Grossglockneria acuta*	–	–	–	1	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	1	–	–	–	–	1	1	–
147	*Grossglockneria hyalina*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
148	*Halteria grandinella*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
149	*Hausmanniella discoidea*	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–
150	*Hausmanniella patella*	–	1	–	–	–	–	–	1	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–
151	*Hemiamphisiella granulifera*	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
152	*Hemiamphisiella terricola*	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	
153	*Hemiamphisiella wilberti*	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
154	*Hemisincirra gellerti verrucosa*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	
155	*Hemisincirra inquieta*	1	–	1	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	1	1	–	–
156	*Hemisincirra namibiensis* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
157	*Hemisincirra rariseta* n. sp.	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
158	*Hemiurosoma goertzi* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
159	*Hemiurosoma terricola* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	
160	*Holophrya salinarum* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
161	*Holosticha australis*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
162	*Holosticha brachysticha* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
163	*Holosticha stueberi*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
164	*Holosticha tetracirrata*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
165	*Holostichides terricola*	1	1	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	
166	*Homalogastra setosa*	1	–	–	1	–	–	–	1	–	–	1	1	–	–	–	–	–	1	–	–	–	–	1	1	–	–	1	–	1	1
167	*Idiocolpoda pelobia*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
168	*Ilsiella elegans* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
169	*Ilsiella palustris*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
170	*Kahlilembus attenuatus*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
171	*Keronopsis dieckmanni*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
172	*Kuehneltiella namibiensis* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
173	*Kuklikophrya ougandae*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
174	*Lamtostyla australis*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	1	1	–	1	1	1	–	–
175	*Lamtostyla decorata* n. sp.	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
176	*Lamtostyla edaphoni*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
177	*Lamtostyla halophila* n. sp.	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
178	*Lamtostyla hyalina*	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
179	*Lamtostyla islandica*	–	1	–	–	1	1	–	–	1	–	–	1	1	–	1	1	–	–	–	–	–	1	–	1	–	–	–	1	–	–
180	*Lamtostyla kirkeniensis*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
181	*Leptopharynx costatus*	1	1	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1
182	*Litonotus muscorum*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
183	*Maryna antarctica*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
184	*Maryna atra*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	
185	*Maryna lichenicola*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Sp. No.	Sites / Samples 31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	%
123	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
124	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
125	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	2,7
126	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	2,7
127	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
128	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	1	–	–	–	1	–	–	–	–	11,0
129	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
130	1	1	1	1	1	1	1	–	1	–	1	1	–	–	–	–	–	–	1	1	1	–	–	1	–	1	1	–	–	–	–	1	–	1	–	–	–	–	1	–	1	–	–	49,3
131	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	2,7
132	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1,4
133	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1,4
134	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	1	6,8
135	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1,4
136	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
137	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	1	5,5
138	1	–	–	–	–	–	–	–	1	1	1	–	1	–	–	–	–	1	1	1	–	1	1	1	–	1	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	28,8
139	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2,7
140	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
141	1	–	1	1	–	–	–	1	–	1	1	1	1	1	1	–	1	1	1	1	1	1	1	1	–	1	1	–	–	1	–	1	1	1	1	–	–	–	–	1	–	1	–	61,6
142	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	1	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	9,6
143	–	–	–	–	–	–	–	–	–	1	1	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5,5
144	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	6,8
145	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
146	–	–	1	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	16,4
147	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	5,5
148	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	1	–	–	1	–	1	–	1	–	1	–	–	1	–	–	1	16,4
149	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	1	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	13,7
150	–	1	–	1	1	–	1	–	–	–	–	1	–	–	–	–	1	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	19,2
151	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	4,1
152	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	6,8
153	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
154	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	5,5
155	–	–	1	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	1	–	–	–	–	–	–	–	19,2
156	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
157	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
158	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	5,5
159	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4,1
160	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1,4
161	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
162	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
163	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	2,7
164	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	2,7
165	–	–	1	–	–	–	–	–	–	1	1	1	1	–	–	1	–	1	–	–	–	–	–	1	–	1	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	23,3
166	1	1	1	–	–	–	–	–	1	–	1	–	1	–	–	–	–	1	1	1	–	1	1	1	–	–	1	1	–	1	–	1	1	1	1	1	1	–	1	1	1	–	–	47,9
167	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	4,1
168	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
169	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
170	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	6,8
171	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
172	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
173	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	4,1
174	1	1	1	1	1	–	–	–	–	–	–	–	–	–	1	1	1	–	1	–	1	1	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	28,8
175	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5,5
176	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	4,1
177	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	1	–	–	8,2
178	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
179	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	21,9
180	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	6,8
181	–	–	1	–	–	–	–	–	–	1	1	1	1	1	1	1	–	1	1	1	1	1	–	1	–	1	–	–	–	1	1	1	1	–	1	–	–	–	–	1	–	1	–	38,4
182	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	2,7
183	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
184	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
185	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4

Sp. No.	Species	Sites / Samples 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
186	*Maryna minima*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
187	*Maryna namibiensis namibiensis* n. sp. n. ssp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
188	*Maryna ovata*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
189	*Maryna umbrellata*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
190	*Meseres corlissi*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
191	*Metacineta namibiensis* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
192	*Metopus contortus*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
193	*Metopus gibbus*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
194	*Metopus hasei*	–	–	–	1	–	–	–	1	1	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	1	1
195	*Metopus inversus*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
196	*Metopus minor*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
197	*Metopus ovalis*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
198	*Metopus palaeformis*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
199	*Metopus setosus*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
200	*Microdiaphanosoma arcuatum*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
201	*Mykophagophrys terricola*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
202	*Nassula dragescoi* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
203	*Nassula etoschensis* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
204	*Nassula granata* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
205	*Nassula longinassa*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
206	*Nassula parva*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
207	*Nassula tuberculata* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
208	*Nassulides labiatus* n. comb.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
209	*Nassulides pictus* n. comb.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
210	*Naxella lucida* n. comb.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
211	*Naxella rosea* n. comb.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
212	*Nivaliella plana*	1	1	–	1	1	1	–	1	1	–	–	1	1	–	1	1	1	–	–	1	–	–	1	1	–	1	1	1	1	1
213	*Notoxoma parabryophryides*	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
214	*Nudiamphisiella interrupta* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
215	*Obliquostoma enchelyodontides* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
216	*Obliquostoma namibiense* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
217	*Odontochlamys alpestris biciliata* n. ssp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
218	*Odontochlamys convexa*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
219	*Opercularia curvicaule*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
220	*Orthoamphisiella breviseries* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
221	*Ottowphrya dragescoi* n. comb.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
222	*Oxytricha africana*	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
223	*Oxytricha elegans*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
224	*Oxytricha granulifera*	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1
225	*Oxytricha granulifera quadricirrata*	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
226	*Oxytricha lanceolata*	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1
227	*Oxytricha longa*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
228	*Oxytricha longigranulosa*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
229	*Oxytricha opisthomuscorum*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
230	*Oxytricha siseris*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
231	*Parabryophrya etoschensis* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
232	*Paracineta lauterborni*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
233	*Paraenchelys brachyarmata* n. sp.	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
234	*Paraenchelys brachyoplites* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
235	*Paraenchelys pulchra* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
236	*Paraenchelys terricola*	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
237	*Paraenchelys wenzeli*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
238	*Parafurgasonia protectissima*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
239	*Parafurgasonia sorex*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
240	*Parafurgasonia terricola*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
241	*Paragastrostyla lanceolata*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
242	*Paragonostomum binucleatum* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
243	*Paragonostomum caudatum* n. sp.	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
244	*Paragonostomum multinucleatum* n. sp.	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
245	*Paragonostomum rarisetum* n. sp.	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
246	*Paraholosticha muscicola*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
247	*Parakahliella binucleata* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
248	*Parakahliella halophila* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–

Sp. No.	Sites / Samples 31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	%
186	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	1	–	–	–	–	1	–	–	–	6,8
187	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2,7
188	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
189	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	5,5
190	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1,4
191	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
192	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
193	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	5,5
194	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	1	1	–	–	1	–	–	1	1	–	–	–	–	–	–	1	1	1	–	–	1	1	–	–	1	27,4
195	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2,7
196	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2,7
197	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
198	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	6,8
199	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	4,1
200	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
201	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	1	–	–	–	–	9,6
202	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	1	1	1	–	1	–	–	–	1	–	–	–	–	1	–	–	–	–	11,0
203	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	4,1
204	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	1	–	–	–	–	–	–	–	–	1	–	1	1	–	–	–	–	8,2
205	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
206	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	2,7
207	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
208	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4,1
209	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1,4
210	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1,4
211	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
212	1	1	1	1	1	–	–	1	1	1	1	1	1	1	1	1	1	1	1	1	1	–	–	1	–	1	–	–	–	1	–	1	–	1	1	1	–	–	–	–	–	1	–	64,4
213	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
214	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
215	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
216	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
217	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
218	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4,1
219	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	2,7
220	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	2,7
221	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5,5
222	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4,1
223	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	8,2
224	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	8,2
225	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
226	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	1	–	–	1	1	–	–	–	–	1	–	–	–	–	15,1
227	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	1	1	–	–	6,8
228	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
229	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	4,1
230	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	4,1
231	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
232	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	5,5
233	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
234	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
235	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
236	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	1	–	1	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	12,3
237	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
238	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
239	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1,4
240	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
241	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
242	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5,5
243	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	1	–	–	–	–	11,0
244	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	5,5
245	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5,5
246	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
247	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	2,7
248	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	5,5

Sp. No.	Species	Sites / Samples 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
249	*Parakahliella namibicola* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–
250	*Pedohymena australiensis*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
251	*Periholosticha lanceolata*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
252	*Perisincirra longicirrata* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
253	*Perisincirra paucicirrata* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
254	*Phialina binucleata*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
255	*Phialina minima* n. comb.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
256	*Phialinides australis*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
257	*Plagiocampa bitricha*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
258	*Plagiocampa difficilis*	1	1	–	1	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
259	*Plagiocampa namibiensis* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
260	*Plagiocampa ovata*	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	1	–	–	–	1	–	–	–
261	*Plagiocampa pentadactyla* n. sp.	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
262	*Plagiocampa rouxi*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
263	*Plagiocampides halophilus* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
264	*Platyophrya binucleata*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
265	*Platyophrya macrostoma*	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–
266	*Platyophrya paoletti*	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
267	*Platyophrya spumacola hexasticha n+B33. ssp.*	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
268	*Platyophrya spumacola spumacola*	1	1	–	–	1	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	1	–	1	–	–	–
269	*Platyophrya vorax*	1	1	1	1	–	–	1	–	–	–	–	–	–	1	–	1	–	–	–	1	–	–	–	1	–	1	–	–	–	1
270	*Platyophryides latus*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
271	*Plesiocaryon elongatum* n. comb.	1	1	1	1	1	–	1	1	1	–	1	1	1	–	–	1	1	–	–	1	–	1	1	1	–	–	1	1	–	1
272	*Plesiocaryon terricola* n. sp.	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–
273	*Pleuroplites australis*	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
274	*Pleuroplitoides smithi*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
275	*Podophrya halophila*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
276	*Protocyclidium muscicola* n. comb.	1	–	–	1	–	–	–	1	1	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	1	–	1	1	1
277	*Protocyclidium terricola* n. comb.	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	1	–
278	*Protospathidium namibicola* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
279	*Protospathidium serpens*	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
280	*Pseudochilodonopsis mutabilis*	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
281	*Pseudocohnilembus binucleatus* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
282	*Pseudocohnilembus persalinus hexakineta* n. ssp.	–	–	–	–	–	–	–	1	–	1	1	1	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
283	*Pseudocohnilembus persalinus persalinus*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
284	*Pseudocyrtolophosis alpestris*	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1
285	*Pseudoholophrya minuta* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
286	*Pseudoholophrya terricola*	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	1	–	–	–	1
287	*Pseudokreyella australis*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
288	*Pseudokreyella etoschensis* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
289	*Pseudomicrothorax agilis*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
290	*Pseudomicrothorax dubius*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
291	*Pseudomonilicaryon angustistoma* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
292	*Pseudomonilicaryon massutii* n. comb.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
293	*Pseudoplatyophrya nana*	1	1	–	1	1	1	1	1	1	–	–	1	–	–	1	1	1	–	–	1	–	1	1	1	–	1	1	1	1	1
294	*Pseudoplatyophrya saltans*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	1
295	*Pseudouroleptus caudatus namibiensis* n. ssp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
296	*Pseudouroleptus procerus*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–
297	*Pseudourostyla franzi*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
298	*Pseudovorticella sphagni*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
299	*Reticulowoodruffia terricola*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
300	*Rostrophrya fenestrata* n. sp.	–	–	–	–	–	–	–	1	–	–	1	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
301	*Rostrophrya namibiensis maldivensis* n. sp. n. ssp.	–	–	–	–	–	–	–	1	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
302	*Rostrophrya namibiensis namibiensis* n. sp. n. ssp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
303	*Rostrophryides africana africana*	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
304	*Rostrophryides africana etoschensis* n. ssp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
305	*Sagittaria hyalina*	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
306	*Sathrophilus muscorum*	–	–	–	1	1	–	–	1	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	1	–	–	–	1
307	*Semiplatyophrya acrostoma* n. sp.	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
308	*Semiplatyophrya foissneri*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
309	*Semispathidium armatum* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
310	*Semispathidium enchelyodontides* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
311	*Sikorops minor* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Sp. No.	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	%
249	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5,5
250	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1,4
251	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	2,7
252	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1,4
253	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	2,7
254	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	2,7
255	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	5,5
256	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1,4
257	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1,4
258	-	-	-	1	-	-	-	-	-	1	1	-	-	1	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	17,8
259	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	4,1
260	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	17,8
261	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5,5
262	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	4,1
263	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	5,5
264	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1,4
265	-	-	1	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	12,3
266	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6,8
267	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5,5
268	-	-	1	-	-	-	-	-	-	-	1	1	-	-	1	-	-	1	1	-	1	1	-	1	-	1	-	-	-	1	-	1	1	-	-	-	-	-	-	-	-	-	-	27,4
269	1	1	1	1	-	-	-	-	-	1	1	1	-	-	-	1	-	1	-	-	1	-	-	-	-	-	1	-	-	1	-	1	1	1	1	-	-	-	1	-	-	-	1	39,7
270	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1,4
271	1	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-	-	-	-	-	1	-	1	1	1	-	-	-	-	-	-	-	-	1	65,8
272	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6,8
273	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	8,2
274	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1,4
275	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	2,7
276	-	1	1	-	-	-	-	-	-	-	1	-	1	1	1	-	-	1	1	1	1	-	1	1	-	1	1	-	-	1	-	-	1	-	1	1	-	-	-	1	-	-	-	39,7
277	-	-	1	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	1	1	1	-	-	1	-	-	-	-	-	-	-	-	1	1	-	1	-	-	-	-	-	-	1	21,9
278	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2,7
279	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	1	8,2
280	-	-	1	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	1	1	-	1	-	-	-	1	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	16,4
281	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1,4
282	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	1	-	-	-	-	-	1	1	1	-	-	-	-	19,2
283	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2,7
284	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	13,7
285	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1,4
286	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	1	1	1	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	17,8
287	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1,4
288	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1,4
289	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	4,1
290	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1,4
291	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1,4
292	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1,4
293	1	1	1	1	1	1	1	1	-	1	1	-	-	1	-	1	1	-	1	1	1	-	-	-	1	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	54,8
294	-	-	1	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	15,1
295	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1,4
296	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2,7
297	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	4,1
298	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	5,5
299	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2,7
300	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6,8
301	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	12,3
302	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	4,1
303	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2,7
304	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	2,7
305	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	1	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	11,0
306	1	-	1	-	-	-	-	-	-	1	1	-	1	-	-	-	-	1	1	1	-	1	1	-	-	1	-	-	-	1	-	-	1	1	-	-	-	-	-	-	-	1	-	31,5
307	-	-	-	-	-	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5,5
308	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1,4
309	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1,4
310	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1,4
311	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1,4

Sp. No.	Species	Sites / Samples 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
312	*Sikorops namibiensis* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
313	*Sorogena stoianovitchae*	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
314	*Spathidium aciculare* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
315	*Spathidium anguilla*	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
316	*Spathidium bavariense*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
317	*Spathidium claviforme*	1	–	–	–	1	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
318	*Spathidium contractile* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
319	*Spathidium etoschense* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
320	*Spathidium extensum*	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
321	*Spathidium lanceoplites* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
322	*Spathidium namibicola* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–
323	*Spathidium procerum*	–	–	–	–	–	–	–	1	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
324	*Spathidium rusticanum*	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
325	*Spathidium seppelti etoschense* n. ssp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
326	*Spathidium spathula*	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
327	*Spathidium turgitorum* n. sp.	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–
328	*Sphaerophrya terricola*	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
329	*Stammeridium kahli*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
330	*Sterkiella cavicola*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
331	*Sterkiella histriomuscorum*	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
332	*Supraspathidium armatum* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
333	*Supraspathidium etoschense* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
334	*Tachysoma granulifera*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
335	*Tachysoma humicola humicola*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
336	*Tectohymena terricola*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
337	*Terricirra livida*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
338	*Terricirra matsusakai*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
339	*Tetrahymena rostrata*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1
340	*Trachelophyllum africanum* n. sp.	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
341	*Trachelophyllum apiculatum*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
342	*Trihymena terricola*	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
343	*Uroleptus notabilis*	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	1	–
344	*Uroleptus paranotabilis* n. sp.	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
345	*Urosoma emarginata*	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
346	*Urosoma karinae*	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
347	*Urosomoida agiliformis*	1	–	1	1	–	–	–	–	–	–	1	–	1	–	1	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–
348	*Urosomoida agilis*	1	1	–	1	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
349	*Urosomoida antarctica*	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
350	*Urosomoida deserticola* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
351	*Urosomoida monostyla* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
352	*Urosomoida namibiensis* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
353	*Urosomoida reticulata* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
354	*Vermioxytricha arenicola* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–
355	*Vermioxytricha muelleri*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
356	*Vorticella astyliformis*	1	–	1	1	1	–	–	–	1	–	–	–	1	–	1	–	–	1	–	–	–	–	1	1	–	–	–	–	1	1
357	*Vorticella echini*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
358	*Vorticella infusionum*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
359	*Wallackia bujoreani*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
360	*Wallackia elegans* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
361	*Wolfkosia loeffleri* n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
362	*Woodruffia australis*	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
363	*Woodruffia rostrata*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
364	*Woodruffides metabolicus*	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
365	*Woodruffides terricola*	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
I	Number of taxa identified	39	24	24	80	43	10	8	35	36	1	17	18	16	5	21	30	17	12	2	15	2	7	26	21	2	31	24	23	41	65
II	Number of new species	2	1	1	11	11	0	1	4	1	1	4	3	1	1	0	3	2	2	0	1	0	0	5	4	1	3	1	2	5	7
III	Number of unidentified taxa [a]	3	0	0	10	3	1	0	2	0	0	2	0	0	0	0	0	2	0	0	0	0	0	1	0	0	3	0	0	2	3
IV	Number of unidentified, likely undescribed taxa [b]	3	0	0	6	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
V	Total number of taxa	42	24	24	90	46	11	8	37	36	1	19	18	16	5	21	30	19	12	2	15	2	7	27	21	2	34	24	23	43	68
VI	Site / sample number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30

[a] Most of these taxa (122 if simply added up) occurred at only one site, adding about 100 to the 365 identified species.
[b] Most of these species (58 if simply added up) occurred at only one site, adding about 50 to the 128 new taxa.

Sp. No.	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	%
312	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
313	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4,1
314	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
315	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	1	–	–	–	–	–	–	6,8
316	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
317	–	–	1	–	–	–	–	–	–	1	–	1	–	–	–	–	–	1	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	17,8
318	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
319	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
320	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
321	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
322	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
323	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	12,3
324	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	8,2
325	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	1	–	–	–	5,5
326	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
327	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9,6
328	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5,5
329	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
330	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
331	–	–	–	–	–	–	–	–	–	–	1	1	1	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	1	–	–	1	16,4
332	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	4,1
333	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	2,7
334	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1,4
335	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
336	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
337	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
338	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
339	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	9,6
340	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4,1
341	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
342	–	–	1	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8,2
343	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	12,3
344	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5,5
345	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	5,5
346	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4,1
347	1	1	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	1	1	1	–	1	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	1	26.0
348	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	9,6
349	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5,5
350	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
351	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
352	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
353	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
354	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4,1
355	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4,1
356	1	–	–	–	–	–	–	–	–	1	1	–	1	–	–	–	1	1	1	1	1	1	1	1	–	1	1	1	1	1	1	–	–	1	–	–	1	–	1	1	–	1	1	49,3
357	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	2,7
358	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,4
359	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	1	–	–	6,8
360	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
361	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1,4
362	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2,7
363	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	4,1
364	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	5,5
365	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	9,6
I	27	15	47	13	10	8	12	10	11	28	55	27	52	16	18	19	16	43	126	51	46	28	20	53	11	55	34	8	7	49	15	28	35	36	36	16	19	2	13	69	10	14	35	
II	5	1	7	0	0	2	2	0	2	1	6	1	9	0	1	0	1	4	34	3	4	5	6	16	1	10	11	2	4	9	8	1	0	2	7	1	8	1	3	17	2	0	6	
III	0	0	2	0	0	0	1	0	0	0	1	3	7	1	0	0	0	2	15	2	2	2	2	4	0	4	2	0	1	0	5	2	2	4	4	0	5	0	2	6	2	0	6	
IV	0	0	2	0	0	0	1	0	0	0	0	1	2	0	0	0	0	1	13	0	1	1	1	2	0	1	1	0	1	0	0	1	1	2	1	0	3	0	1	1	2	0	4	
V	27	15	49	13	10	8	13	10	11	28	56	30	59	17	18	19	16	45	141	53	48	30	22	57	11	59	36	8	8	49	20	30	37	40	40	16	24	2	15	75	12	14	41	
VI	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	

Sites / Samples (columns 31–73)

Table 5. Soil ciliates from the Etosha Pan region sensu stricto (sites 53, 54, 56, 57, 59, 60, 61, 65, 67, 69, 70, 71) and sensu lato (55, 62, 63, 64, 66). (n. sp.) = species discovered in this region and described in previous papers.

Species	Sites																		
	53	54	56	57	58	59	60	61	65	67	68	69	70	71	55	62	63	64	66
Acaryophrya collaris	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Afroamphisiella multinucleata n. sp.	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Amphisiella elegans n. sp.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amphisiella magnigranulosa	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-
Amphisiella namibiensis n. sp.	-	1	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-
Amphisiella terricola	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Apertospathula inermis n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Apobryophyllum etoschense (n. sp.)	-	-	-	1	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-
Apobryophyllum terricola	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Apocolpodidium etoschense n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Apourosomoida halophila n. sp.	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Arcuospathidium etoschense n. sp.	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-
Arcuospathidium multinucleatum	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-
Arcuospathidium vlassaki (n. sp.)	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Bakuella granulifera n. sp.	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Bilamellophrya etoschensis n. sp.	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-
Blepharisma hyalinum	-	1	1	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-
Bresslaua insidiatrix	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Bresslaua vorax	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bryometopus atypicus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Bryometopus pseudochilodon	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bryometopus triquetrus	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bryophyllum lingua multistriatum n. ssp.	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Bryophyllum loxophylliforme	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bryophyllum paucistriatum n. sp.	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bursaria truncatella	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Cinetochilum margaritaceum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Clavoplites edaphicus n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Colpoda aspera	-	-	1	-	-	-	-	-	-	-	-	-	1	1	-	-	1	-	-
Colpoda cavicola amicronucleata n. ssp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Colpoda cucullus	-	1	-	1	-	-	1	-	-	1	-	-	1	-	1	1	1	1	1
Colpoda ecaudata	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	1	-
Colpoda henneguyi	-	1	-	1	-	-	-	-	-	-	-	-	1	-	-	1	1	-	-
Colpoda inflata	-	1	1	1	-	-	1	-	-	-	-	-	1	-	1	1	-	1	-
Colpoda lucida	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Colpoda magna	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Colpoda maupasi	-	1	1	1	-	-	1	-	-	-	-	-	1	1	1	1	1	1	1
Colpoda minima	-	1	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-
Colpoda orientalis	-	-	1	1	-	-	-	-	1	-	-	-	1	-	-	-	1	1	-
Colpoda steinii	-	1	1	-	-	-	1	-	-	1	-	-	-	1	1	1	1	1	-
Colpoda variabilis	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Colpodidium caudatum	-	1	-	1	-	-	-	-	1	-	-	-	1	-	-	-	-	1	-
Colpodidium horribile n. sp.	1	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Condylostomides etoschensis n. sp.	-	-	-	-	-	-	1	-	1	-	-	-	1	-	-	-	-	-	-
Cyrtohymena citrina	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyrtohymena quadrinucleata	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-
Cyrtolophosis mucicola	1	-	-	-	-	-	1	-	1	-	-	-	1	-	-	-	-	-	-
Deviata bacilliformis	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-
Dileptus mucronatus	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dileptus terrenus	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Dioplitophrya otti n. sp.	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Drepanomonas pauciciliata	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Drepanomonas revoluta	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-

(continued)

Species	Sites																			
	53	54	56	57	58	59	60	61	65	67	68	69	70	71	55	62	63	64	66
Drepanomonas sphagni	1	-	1	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-
Enchelyodon nodosus	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Enchelyodon terrenus	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Enchelys longitricha n. sp.	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Enchelys multinucleata	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Epispathidium ascendens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Epispathidium polynucleatum n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Epistylis alpestris	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Etoschophrya oscillatoriophaga n. sp.	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Etoschothrix terricola n. sp.	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Euplotopsis incisa n. sp.	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-
Euplotopsis muscicola	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	1	-	1
Euplotopsis muscicola alatus	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Exocolpoda augustini	-	1	1	1	-	-	-	-	-	-	-	-	1	-	-	1	-	1	-
Frontonia angusta obovata n. ssp.	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Frontonia angusta solea	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Frontonia depressa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Frontonia terricola	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-
Furgasonia theresae	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Fuscheria nodosa	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-
Fuscheria terricola	1	1	1	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-
Gastrostyla steinii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Gonostomum affine	1	1	1	1	-	-	1	-	1	-	-	-	1	-	-	1	1	1	-
Gonostomum algicola	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-
Gonostomum namibiense n. sp.	1	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-
Grossglockneria acuta	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Grossglockneria hyalina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Halteria grandinella	1	-	-	1	-	-	1	-	1	1	-	-	1	-	-	-	1	-	-
Hausmanniella discoidea	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Hausmanniella patella	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-
Hemiamphisiella granulifera	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Hemiamphisiella terricola	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Hemisincirra gellerti verrucosa	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Hemisincirra inquieta	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	1
Hemiurosoma goertzi n. sp.	-	-	1	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-
Hemiurosoma terricola n. sp.	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holophrya salinarum n. sp.	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Holosticha australis	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Holosticha brachysticha n. sp.	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holosticha stueberi	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Holosticha tetracirrata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Holostichides terricola	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Homalogastra setosa	1	1	-	1	1	-	1	-	1	1	-	1	1	1	-	1	1	1	1
Idiocolpoda pelobia	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Ilsiella palustris	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kahlilembus attenuatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-
Keronopsis dieckmanni	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kuklikophrya ougandae	-	-	-	1	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-
Lamtostyla australis	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lamtostyla edaphoni	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Lamtostyla halophila n. sp.	-	-	-	-	-	-	-	-	-	-	1	1	-	1	-	-	-	-	-
Leptopharynx costatus	-	1	1	-	-	-	1	1	1	-	-	-	1	-	-	1	1	-	-
Litonotus muscorum	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Maryna antarctica	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Maryna minima	-	-	1	-	-	-	1	-	1	-	-	-	1	-	-	-	-	-	-
Maryna umbrellata	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
Meseres corlissi	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Metopus hasei	1	-	1	1	-	-	-	-	1	-	-	1	1	-	-	-	-	1	1

(continued)

Species	Sites																		
	53	54	56	57	58	59	60	61	65	67	68	69	70	71	55	62	63	64	66
Metopus palaeformis	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Metopus setosus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Mykophagophrys terricola	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	1	-	-
Nassula dragescoi n. sp.	-	1	1	1	1	-	1	-	1	-	-	-	1	-	-	-	-	-	-
Nassula etoschensis n. sp.	-	1	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-
Nassula granata n. sp.	1	1	-	1	-	-	-	-	-	1	-	1	1	-	-	-	-	-	-
Nassula longinassa	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nassula parva	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-
Nassulides labiatus	-	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nassulides pictus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Naxella lucida	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Naxella rosea	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nivaliella plana	-	1	1	-	-	-	1	-	1	-	-	-	-	-	-	1	-	1	1
Odontochlamys convexa	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Opercularia curvicaule	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Orthoamphisiella breviseries n. sp.	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-
Ottowphrya dragescoi	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oxytricha africana	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oxytricha elegans	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Oxytricha granulifera	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Oxytricha granulifera quadricirrata	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oxytricha lanceolata	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	1	1	-
Oxytricha longa	1	-	-	-	1	-	-	-	-	-	-	1	1	1	-	-	-	-	-
Oxytricha opisthomuscorum	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Oxytricha siseris	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-
Parabryophrya etoschensis n. sp.	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paracineta lauterborni	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Paraenchelys pulchra n. sp.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paraenchelys terricola	-	1	1	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-
Paraenchelys wenzeli	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Parafurgasonia sorex	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Paragonostomum binucleatum n. sp.	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paragonostomum caudatum n. sp.	-	-	-	-	-	-	1	-	1	-	-	-	1	-	-	-	-	-	-
Paragonostomum multinucleatum n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Parakahliella binucleata n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Parakahliella halophila n. sp.	-	1	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-
Periholosticha lanceolata	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Perisincirra paucicirrata n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-
Phialina binucleata	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Phialina minima	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-
Plagiocampa difficilis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Plagiocampa ovata	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Plagiocampa rouxi	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Plagiocampides halophilus n. sp.	-	-	-	1	1	-	-	1	-	-	-	1	-	-	-	-	-	-	-
Platyophrya paoletti	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Platyophrya spumacola hexasticha n. ssp.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Platyophrya spumacola spumacola	-	1	1	-	-	-	1	-	-	-	-	-	-	-	-	1	1	-	-
Platyophrya vorax	-	-	-	1	-	-	1	-	1	-	-	1	-	-	-	1	1	1	-
Platyophryides latus	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Plesiocaryon elongatum	1	1	-	-	-	-	1	-	-	-	-	-	-	-	-	1	1	1	-
Plesiocaryon terricola n. sp.	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pleuroplites australis	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-
Podophrya halophila	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Protocyclidium muscicola	1	1	1	1	-	-	1	-	1	-	-	-	1	-	-	-	1	-	1
Protocyclidium terricola	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1
Protospathidium serpens	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-
Pseudochilodonopsis mutabilis	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-
Pseudocohnilembus binucleatus n. sp.	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-

(continued)

Species	Sites																			
	53	54	56	57	58	59	60	61	65	67	68	69	70	71	55	62	63	64	66
Pseudocohnilembus persalinus hexakineta n. ssp.	-	1	-	1	-	-	-	1	-	1	1	1	-	-	-	-	-	-	-
Pseudocyrtolophosis alpestris	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-
Pseudoholophrya terricola	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Pseudokreyella etoschensis n. sp.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pseudomicrothorax agilis	-	-	1	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-
Pseudomicrothorax dubius	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Pseudomonilicaryon massutii	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Pseudoplatyophrya nana	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-
Pseudoplatyophrya saltans	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-
Pseudourostyla franzi	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-
Pseudovorticella sphagni	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-
Rostrophrya fenestrata n. sp.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rostrophrya namibiensis maldivensis n. ssp.	-	1	-	1	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-
Rostrophrya namibiensis namibiensis n. ssp.	1	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Rostrophryides africana etoschensis n. ssp.	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Sagittaria hyalina	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Sathrophilus muscorum	1	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	1	1	-
Sikorops minor n. sp.	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Spathidium anguilla	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	1	-
Spathidium claviforme	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Spathidium etoschense n. sp.	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Spathidium extensum	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Spathidium procerum	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Spathidium rusticanum	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Spathidium seppelti etoschense n. ssp.	-	1	-	-	-	1	1	-	-	-	-	-	1	-	-	-	-	-	-
Spathidium turgitorum n. sp.	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sterkiella cavicola	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Sterkiella histriomuscorum	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	1
Supraspathidium armatum n. sp.	-	1	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Supraspathidium etoschense n. sp.	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Tachysoma granulifera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Tectohymena terricola	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tetrahymena rostrata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
Uroleptus notabilis	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Uroleptus paranotabilis n. sp.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Urosoma emarginata	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Urosoma karinae	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Urosomoida agiliformis	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-
Urosomoida agilis	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Urosomoida monostyla n. sp.	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vorticella astyliformis	1	1	1	1	1	1	1	1	-	1	-	1	1	-	-	-	-	1	-
Vorticella echini	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-
Wallackia bujoreani	-	1	-	-	-	1	1	-	-	-	-	-	-	1	-	-	-	-	-
Wolfkosia loeffleri n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Woodruffia rostrata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Woodruffides metabolicus	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Woodruffides terricola	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Number of species: 216	20	53	55	34	8	7	49	15	36	19	2	13	69	10	11	28	35	36	16

Table 6. Soil ciliates from the central (Sossus Vlei; sites 19–27) and marginal (sites 9, 17, 28, 29, 30, 33) dunes of the Central Namib Desert (Fig. 2).

Species	Sites														
	19	20	21	22	23	24	25	26	27	9	17	28	29	30	33
Afrothrix multinucleata n. sp.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Amphisiella elegans n. sp.	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Amphisiella magnigranulosa	-	-	-	-	-	1	-	1	-	-	-	-	1	1	-
Amphisiella polycirrata	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Amphisiella procera n. sp.	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Amphisiella terricola	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-
Amphisiella vitiphila	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-
Apertospathula dioplites n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Apertospathula inermis n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Apocyclidium obliquum	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Apospathidium atypicum	-	-	-	-	-	-	-	-	1	1	1	-	-	-	-
Arcuospathidium cultriforme lionotiforme	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Arcuospathidium muscorum	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Balantidioides dragescoi	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Blepharisma hyalinum	-	-	-	-	-	-	-	-	-	1	-	-	-	1	1
Bryometopus pseudochilodon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Bryophyllum loxophylliforme	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Chilodonella uncinata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Cinetochilum margaritaceum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Circinella filiformis	-	-	-	-	1	-	-	1	-	1	-	-	-	-	1
Clavoplites edaphicus n. sp.	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Colpoda aspera	-	-	-	-	-	1	1	-	-	1	-	1	-	-	-
Colpoda cucullus	-	-	1	1	1	-	-	-	1	1	1	1	1	1	-
Colpoda ecaudata	-	1	-	-	-	-	-	1	-	-	-	-	-	-	1
Colpoda edaphoni	-	1	-	-	-	-	-	-	-	1	-	-	-	1	-
Colpoda elliotti	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-
Colpoda henneguyi	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Colpoda inflata	-	1	-	1	1	1	-	1	1	1	1	1	-	1	1
Colpoda lucida	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Colpoda maupasi	-	1	-	1	1	1	-	1	1	1	1	1	1	1	1
Colpoda steinii	1	1	1	1	1	1	-	1	1	-	1	1	1	1	1
Colpoda variabilis	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Colpodidium caudatum	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Cyrtohymena quadrinucleata	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-
Cyrtolophosis mucicola	-	-	-	-	1	-	-	1	-	-	1	-	1	1	-
Dileptus similis	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Dileptus terrenus	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-
Diplites arenicola n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Diplites telmatobius	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Drepanomonas pauciciliata	-	-	-	-	-	-	-	1	1	-	-	-	-	-	1
Drepanomonas revoluta	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-
Drepanomonas sphagni	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Enchelyodon longinucleatus	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-
Epispathidium ascendens	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-
Epitholiolus chilensis	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Erimophrya arenicola n. sp.	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-
Erimophrya glatzeli n. sp.	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Eschaneustyla terricola	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Euplotopsis muscicola	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-
Exocolpoda augustini	-	1	-	-	1	1	-	1	1	1	1	1	-	-	1
Frontonia terricola	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Fuscheria nodosa	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Fuscheria terricola	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-

(continued)

Species	Sites														
	19	20	21	22	23	24	25	26	27	9	17	28	29	30	33
Gonostomum affine	-	-	-	-	-	1	-	1	1	1	1	1	-	1	1
Gonostomum namibiense n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Grossglockneria acuta	-	1	-	-	1	-	-	-	-	-	-	1	1	-	1
Grossglockneria hyalina	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Halteria grandinella	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Hausmanniella discoidea	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-
Hausmanniella patella	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-
Hemiamphisiella granulifera	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Hemiamphisiella terricola	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-
Hemisincirra gellerti verrucosa	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-
Hemisincirra inquieta	-	-	-	-	1	-	-	-	1	-	-	1	-	-	1
Hemisincirra muelleri	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Hemisincirra namibiensis n. sp.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Hemiurosoma terricola n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Holostichides terricola	-	-	-	-	-	-	-	1	-	1	-	-	-	1	1
Homalogastra setosa	-	-	-	-	1	1	-	-	1	-	-	-	1	1	1
Lamtostyla australis	1	-	-	-	1	1	-	1	1	-	1	1	-	-	1
Lamtostyla islandica	-	-	-	1	-	1	-	-	-	1	-	1	-	-	-
Lamtostyla kirkeniensis	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Leptopharynx costatus	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1
Maryna atra	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Maryna minima	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Maryna namibiensis namibiensi n. ssp.	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Maryna ovata	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Metacineta namibiensis n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Metopus gibbus	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Metopus hasei	-	-	-	-	-	-	-	-	-	1	-	-	1	1	-
Metopus inversus	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Metopus palaeformis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Metopus setosus	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Nivaliella plana	-	1	-	-	1	1	-	1	1	1	1	1	1	1	1
Odontochlamys convexa	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Ottowphrya dragescoi	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Oxytricha elegans	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-
Oxytricha granulifera	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-
Oxytricha lanceolata	-	-	-	-	-	-	-	1	-	-	-	-	-	1	1
Oxytricha longigranulosa	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Paracineta lauterborni	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Paraenchelys terricola	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Paragastrostyla lanceolata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Paragonostomum binucleatum n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Paragonostomum caudatum n. sp.	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Paragonostomum rarisetum n. sp.	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1
Parakahliella namibicola n. sp.	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-
Pedohymena australis	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Phialinides australis	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Plagiocampa bitricha	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Plagiocampa difficilis	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Plagiocampa namibiensis n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-
Plagiocampa ovata	-	-	-	-	1	-	-	-	1	-	1	-	-	-	-
Platyophrya macrostoma	-	1	-	-	-	-	-	-	1	-	-	-	-	-	1
Platyophrya paoletti	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Platyophrya spumacola spumacola	-	-	-	-	-	-	-	1	-	-	-	1	-	-	1
Platyophrya vorax	-	1	-	-	-	1	-	1	-	-	-	-	-	1	1
Plesiocaryon elongatum	-	1	-	1	1	1	-	-	1	1	1	1	-	1	1
Plesiocaryon terricola n. sp.	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-

(continued)

Species	Sites														
	19	20	21	22	23	24	25	26	27	9	17	28	29	30	33
Pleuroplitoides smithi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Protocyclidium muscicola	-	-	-	-	1	-	-	1	-	1	-	1	1	1	1
Protocyclidium terricola	-	-	-	-	-	-	-	-	1	-	-	-	1	-	1
Protospathidium namibicola n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Protospathidium serpens	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Pseudochilodonopsis mutabilis	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
Pseudocyrtolophosis alpestris	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-
Pseudoholophrya terricola	-	-	-	-	1	-	-	1	-	1	-	-	-	1	-
Pseudoplatyophrya nana	-	1	-	1	1	1	-	1	1	1	1	1	1	1	1
Pseudoplatyophrya saltans	-	1	-	-	1	-	-	-	-	-	-	-	-	1	1
Pseudouroleptus caudatus namibiensis n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Pseudouroleptus procerus	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Pseudourostyla franzi	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Pseudovorticella sphagni	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Rostrophrya fenestrata n. sp.	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Rostrophrya namibiensis maldivensis n. ssp.	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Sagittaria hyalina	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Sathrophilus muscorum	-	-	-	-	-	1	-	1	-	1	-	-	-	1	1
Spathidium anguilla	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Spathidium claviforme	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
Spathidium lanceoplites n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Spathidium namibicola n. sp.	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-
Spathidium procerum	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
Spathidium rusticanum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Spathidium turgitorum n. sp.	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-
Sterkiella histriomuscorum	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Tectohymena terricola	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Tetrahymena rostrata	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-
Trachelophyllum africanum n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Trihymena terricola	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
Uroleptus notabilis	-	-	-	-	-	-	-	1	1	-	-	-	1	-	1
Uroleptus paranotabilis n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Urosomoida agiliformis	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-
Urosomoida agilis	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Urosomoida deserticola n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Vermioxytricha arenicola n. sp.	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Vorticella astyliformis	-	-	-	-	1	1	-	-	-	1	-	-	1	1	-
Vorticella infusionum	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Wallackia elegans n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Woodruffia rostrata	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Woodruffides metabolicus	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-
Number of species: 61	2	15	2	7	26	21	2	31	24	36	17	23	41	65	46

Similarity analysis was performed with the computer programs SPSS 10.0 for Windows, Freetree (http://www.natur.cuni.cz/~flegr/freetree.htm), and Treeview (http://taxonomy.zoology.gla.ac.uk/rod/treeview.html). Several similarity coefficients and cluster algorithms were tried, as suggested by BIRKS (1987). The most meaningful results were obtained with JACCARD's and DICE's similarity coefficients and the average-linkage and UPGMA cluster algorithms. "Meaningful" was tested by a priori grouping of the 73 sites into the following habitat types: Etosha Pan sensu stricto (Pan and Pan margin, usually highly saline; sites 53, 54, 56, 57, 59, 60, 61, 65, 67, 69, 70, 71); Etosha Pan sensu lato (Etosha Pan sensu stricto plus surroundings;

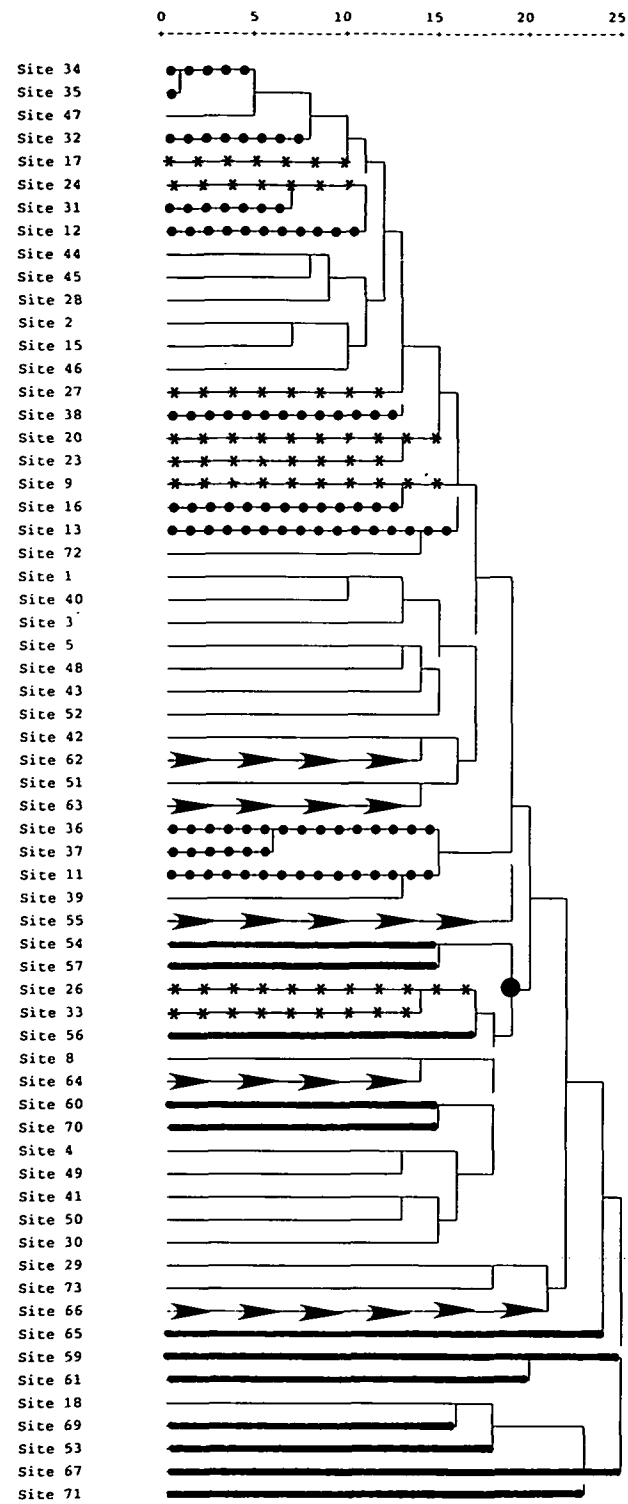

Fig. 5. Average-linkage similarity cluster of the sites investigated (except of special sites; see chapter 3.1.2) with JACCARD's coefficient. Thick lines: Etosha Pan sensu stricto; Arrowed lines: Etosha Pan sensu lato; Asterisk lines: Namib Desert sensu stricto; Dotted lines: Namib Desert sensu lato. Large dot marks subcluster containing most sites with high number of species.

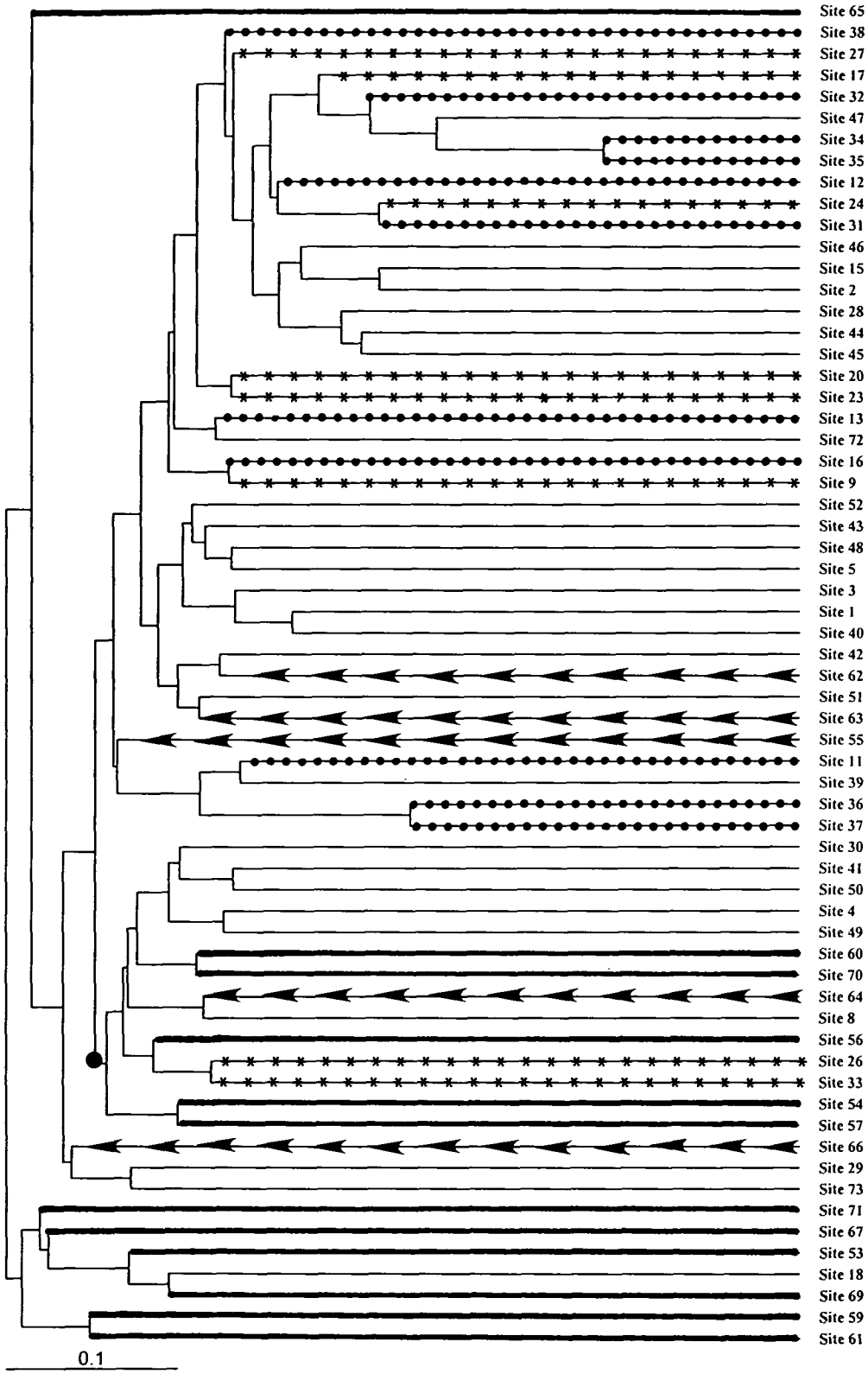

Fig. 6. UPGMA similarity cluster of the sites investigated (except of special sites; see chapter 3.1.2) with Dice's coefficient. Symbols as in cluster vis à vis.

sites 53, 54, 55, 56, 57, 59, 60, 61, 62, 63, 64, 65, 66, 67, 69, 70, 71); Namib Desert sensu stricto ("dune sea Namib"; sites 9, 17, 20, 23, 24, 26, 27, 33); Namib Desert sensu lato ("dune sea Namib" plus the about 100 km wide stripe along the Atlantic sea coast; sites 9, 11, 12, 13, 16, 17, 20, 23, 24, 26, 27, 31, 32, 33, 34, 35, 36, 37, 38); savannahs (sites 1, 2, 3, 5, 13, 15, 16, 17, 28, 33, 40, 43, 44, 45, 46, 47, 48, 50, 51, 52, 62, 64, 72, 73); riverine and lacustrine sites (4, 8, 18, 29, 30, 41, 42, 49, 66, 69, 73). Some special sites (6, 7, 10, 14, 19, 21, 22, 25, 58, 68) were excluded because they contained very few species (< 10), which would disturb calculation of both similarity coefficients and cluster algorithms.

Both coefficients and algorithms produce similar clusters, indicating stability of the results (Fig. 5, 6). However, habitat discrimination remains blurred, either due to poor habitat selectivity of ciliates or methodological shortcomings. Likely, the latter are the main problem because (i) the cultivation method used can stimulate only about one third of the ciliate species to reproduce to detectable numbers (chapter 3.1.1) and (ii) all sites with a high number of species (≥ 47; 4, 30, 33, 41, 49, 50, 54, 56, 60, 70) accumulate into a single sub-cluster (marked by a thick dot in Fig. 5, 6), irrespective the habitat type (riverine, savannah, and Pan sites). However, some patterns are recognizable and indicate habitat specificity of ciliates, as do literature data reviewed by FOISSNER (1987d).

(i) A fairly distinct separation of the Etosha and Namib sites is recognizable, the former are in the lower half of the clusters, the latter in the upper half. Site (18) matches the Pan sites because it is a highly saline habitat.

(ii) A large sub-cluster is formed by the sites from the Namib Desert and Namib Escarpment (sites 2, 12, 15, 17, 24, 27, 28, 31, 32, 34, 35, 38, 44, 45, 46, 47).

(iii) The savannah sites are nearer to the Namib Desert than to the Etosha sites.

(iv) Several micro-clusters contain, for instance, rock-pools (sites 29, 66, 73) riverine and puddle sites (4, 30, 41, 49, 50), and highly saline coastal sites (11, 36, 37, 39).

3.1.3 Species Numbers and Local Centres of Ciliate Diversity

3.1.3.1 Large scale comparison

With 365 taxa identified, that is more than half the known global soil ciliate diversity (FOISSNER 1998a), our investigation is by far the most comprehensive available worldwide. From Germany, for instance, only 270 soil ciliate species have been reported, in spite of the fairly detailed investigations by KAHL (1930–35) and WENZEL (1953), who described many new species from moss. Thus, one can speculate that Africa and/or Namibia is a soil ciliate biodiversity centre. There are indeed indications for this (FOISSNER 1997c), but undersampling is a more likely reason. As shown in chapter 3.1.7, further sampling would increase Namibian soil ciliate diversity to about 1000 species!

Ironically, the high number of species makes comparison with literature data difficult. It is, however, remarkable that similar species numbers have been reported from limnetic ecosystems, suggesting that both carry a similar number of species and the 2000 global soil ciliate diversity (FOISSNER 1997c) is an underestimate, as indicated also by other evidence (chapter 3.1.7). DRAGESCO & DRAGESCO-KERNÉIS (1986) report 267 species (30% undescribed) from tropical Africa (including some marine and soil species). FOISSNER (1980a) found

194 species (34% undescribed) in 77 small water bodies of the Austrian Central Alps. SCHMITZ (1986) identified 212 ciliate species in the Rhine, and FOISSNER (unpubl.) found nearly 400 species in the eutrophic Amper River near Munich. The last two studies report only few new species because the goal was water quality evaluation and little time remained to identify rare, possibly new species.

3.1.2.2 Local centres of ciliate biodiversity

Using total species number and the proportion of new species, at least four local ciliate diversity centres were discovered in the region investigated (Table 4). Generally, species number varies highly in the individual samples, viz. from 1 to 126 (141 if the unidentified taxa are added), which is not surprising considering the variety of biota, but the highest value (141) is unsurpassed by any other sample we ever studied. It even surpasses the numbers found in the "rich" floodplain soils of Austria, Costa Rica, Brazil, and Australia (Table 8), and it is also distinctly higher than the values reported from manipulated limnetic samples (ESTEBAN et al. 1993, 85 species; FINLAY et al. 1993, 65 species).

Fortunately, the most important local ciliate centres of diversity (Etosha region, Namib Desert) have already been protected by the Namibian government due to their uniqueness and richness of higher animals and plants (BARNARD 1998). Our data emphasize the need for protection because these areas now contain the loci classici of many new species. Unfortunately, the richest site (49) has been lost (see below).

- Etosha Pan region (general description, see chapter 2.1.1.2): 216 ciliate species, of which 61 were undescribed, occurred in the 19 samples from the Etosha Pan region (Table 5). This number is considerably higher than the 158 species identified at 17 sites in Austria (FOISSNER 1987d; Table 14, sites c–h) and the 139 taxa found in 21 Australian samples (BLATTERER & FOISSNER 1988). There is an obvious correlation between salinity and species number in the Namibian samples, viz., the total number of species decreases with increasing salinity (extremity), while the number of undescribed species increases with increasing salinity, likely because such habitats are poorly explored (Table 7). In fact, the high number of species in the Etosha Pan region is likely correlated with the steep vertical and horizontal salinity gradients, producing a sharp zonation of the vegetation (Fig. 3) and a great number of soil microhabitats.

Table 7. Etosha Pan transect. Total species number increases with decreasing salinity, while the number of undescribed species increases with increasing salinity.

Sites	Salinity (‰)	pH	Total species (identified and unidentified)	Total number of undescribed species
59	80	9.0	8	5
61	40	9.0	20	8
57	15	8.7	36	12
60	10	8.6	49	9
62	< 2	7.7	30	2
63	< 2	7.7	37	1

When dry, the upper 10 to 20 cm soil layer is like stone, hardly showing a distinct zonation, but in wet conditions it doubles the volume (Fig. 250, 251) and many, only partially decayed plant residues become visible. This mixture of soil and plant debris produces a nutrient-rich, spongious matrix containing countless microhabitats. Salinity within the microhabitats shows more or less distinct seasonal (floods) and daily changes because the strong insolation pulls up salt from the deeper to the upper zones (GANSSEN 1963, GANSSEN & MOLL 1961, HERDTFELDER 1984). The richness in microhabitats explains why there are so many species in the Pan region although most individual samples contain comparatively few species: each sample contains many, often undescribed species not found in other samples (Tables 4, 5).

• Namib Desert (general description, see chapter 2.1.1.3): The Namib has been arid for at least 55 million years and is fed with moisture by the coastal fogs and with nutrients by the savannahs at the east margin. This fortunate combination of geological stability, moisture, and nutrients produced a rich fauna and flora with many endemic species, now probably also some protists (BARNARD 1998, GRIFFIN 1998, SEELY 1988).

Likely, it is this special combination of features that causes the high ciliate diversity. About 60 species, of which 12 were undescribed, occurred in the nine samples from the "dune sea" of the Southern Namib Desert (mainly the Sossus Vlei, that is, the dead end of an ephemeral river). If we add the six samples from the marginal dunes, which are even more diverse, we arrive at 150 species, of which 32 were undescribed (Table 6). This is an impressive number when considering the 50 mm annual rainfall and 59 Antarctic samples which contained only 64 species (FOISSNER 1996a)! Indeed, ciliate diversity of the Namib approaches that of temperate regions from Austria and semi-arid soils from Australia (see above). Another impressive aspect is the high abundances that developed in the non-flooded Petri dish cultures only two to three days after rewetting, that is, before logarithmic growth of the organisms commenced. This shows that the dunes are full of resting cysts, and protists likely play an important, yet unrecognized role in dune life.

Similar to the Etosha Pan region, the new ciliate species of the Namib Desert have a very patchy distribution occurring in only one or two samples, even if sites are close together, for instance, *Erimophrya arenicola*, *E. glatzeli*, *Paragonostomum caudatum*, *Protospathidium namibicola*, and *Diplites arenicola*. Several of the 32 new species occur only in this area (Table 4), and those with a slender and/or small body, indicating adaptation to sand life, might even be endemic, for instance, *Protospathidium namibicola*, *Afrothrix multinucleata*, and *Hemisincirra namibiensis*.

• *Aloe dichotoma* (Quiver tree) forest and Bukaos River floodplain on the outskirts of Keetmanshoop: The two samples from these sites each contained 11 new species and several unidentified, likely also new species, indicating a further local ciliate diversity centre. With 90 species the sample from the Bukaos River floodplain has the second highest diversity in the whole collection (Table 4), showing that this habitat type is among the richest not only worldwide but also in Namibia (Table 8). In spite of this, floodplain soils have never been investigated systematically for ciliates. The data now available suggest that floodplain soils contain thousands of undescribed ciliate species (Table 8).

• Site (49), the Bambatsi Guest Farm: At this site, which is in the Mopane (*Colophospermum mopane*) savannah, we collected dark mud and surface soil from some road puddles on the farm. The sample was not only the richest of the whole collection, but also the richest we have ever investigated: 126 identified plus 15 unidentified species, of which at least 40 were

undescribed! In contrast, DINGFELDER (1962), who investigated nearly 800 samples from similar habitats in Germany, found only 132 species! Again, this is an indication that Namibia is a ciliate diversity centre. However, other samples from this region and similar habitats (sites 48, 50, 51, 52, 63) were not exceedingly rich, suggesting the following explanations: (i) road puddles belong to the mixed (limnetic/edaphic) biotope type which are often very rich; (ii) many species might have been introduced over the years by soil adhering to the car wheels of the guests.

Unfortunately, all puddles were filled with sand and gravel in year 2000 when the road was upgraded. As it was not tarred, there is hope that puddles will form again over the years!

Table 8. Diversity and structure of floodplain soil ciliate communities (from FOISSNER, unpubl.).

Floodplains	Total number of species	Freshwater species	New or supposedly new species
Danube River, Austria (2 samples from close sites)	86	28 (33%)	8 (10%)
Rio Corobici, Costa Rica (1 sample)	87	14 (16%)	5 (8%)
Amazon River, Brazil (2 samples from close sites)	112	27 (24%)	23 (21%)
Murray River, Australia (2 samples from close sites)	110	35 (32%)	25 (23%)
Bukaos River, Namibia (1 sample)	90	22 (24%)	17 (19%)

3.1.4 Functional Groups and C/P Quotient

Most main taxonomic formations of ciliates are functional groups in an ecological sense. In soil, their general significance was discussed by FOISSNER (1987d, 1998a). The Namibian soil ciliate community shows some remarkable differences to the world community (Table 9). Specifically, gymnostomatids and nassulids as well as the respective feeding groups are over-represented, while hypotrichs and peritrichs are under-represented (Table 9).

The nassulids obviously profit from the filamentous cyanobacteria, their preferred food, covering wide areas of the Etosha region and the crust soil in the more arid landscapes. Likewise, several cyanobacteria-feeding colpodids are unusually frequent, such as *Kuklikophrya ougandae* and *Rostrophrya* spp., and even a new genus, *Etoschophrya*, possibly developed in the Pan scooping off the rich cyanobacterial growth. The over-representation of the gymnostomes, most being rapacious carnivores, is difficult to understand, but shows that Namibian soils can sustain a rich predatory protist community. Possibly, the over-representation is partially related to the complex taxonomy of the group, that is, several of these often small and inconspicuous ciliates might previously have been lumped or not identified at all.

LÜFTENEGGER et al. (1985) and WODARZ et al. (1992) showed that the ratio of colpodean and polyhymenophoran (hypotrichs, oligotrichs, heterotrichs) ciliates, the so-called C/P quotient, is an excellent measure of habitat extremity: r-selected colpodids dominate (C/P quotient ≥ 1)

in unpredictable "extreme" habitats, while k-selected polyhymenophorans dominate (C/P quotient ≤ 1) in predictable, temperate habitats. This relationship is perfectly recognizable also in the arid and/or saline Namibian soils, where hypotrichs, oligotrichs, and heterotrichs are distinctly under-represented, when compared to the world soil ciliate community (Table 9). However, the overall C/P quotient is 0.6, showing that Namibian soils are not an extreme habitat for the ciliates living there, likely because they had sufficient time (at least 55 million years!) to evolve adapted populations and species (Table 9). In contrast, the C/P quotient is 1.3 in the young, postglacial European coastal dunes (VERHOEVEN 1999), where ciliates "adapted"

Table 9. Comparison of taxonomic and functional groups of the world (from FOISSNER 1998a) and the Namibian soil ciliate community.

Characteristics [a]	World community		Namibian community	
	number of species	%	number of species	%
Total number of species	643	100.0	365	100.0
Colpodids	129	21.8	78	21.3
Cyrtophorids	14	2.2	4	1.1
Gymnostomatids	105	17.8	101	27.6
Heterotrichs	24	4.1	14	3.8
Hymenostomes	23	4.0	15	4.1
Hypotrichs	214	36.0	105	28.7
Nassulids	26	4.4	29	7.9
Oligotrichs	1	0.1	2	0.5
Peritrichs	35	5.9	6	1.6
Prostomatids	10	1.7	8	2.2
Suctorians	12	2.0	4	1.1
C/P quotient [a)]	0.47	–	0.60	–
Omnivores [b)]	103	20.2	48	13.2
Mainly bacteriophagous	196	38.5	155	42.7
Mainly predaceous	172	34.1	136	37.5
Mainly (filamentous) cyanobacteria	18	3.6	17	4.7
Mainly mycophagous	8	1.6	7	1.9
Aerobics	582	98.3	357	97.8
Anaerobics	10	1.7	8	2.2
Recorded from 1 geographical region only [c]	265	44.5	100	27.4
Recorded from 2 geographical regions only [c]	95	16.0	77	21.1
Recorded from 3 geographical regions only [c]	64	10.8	52	14.2
Recorded from 4 geographical regions [c]	103	17.4	75	20.5
Recorded from all (5) geographical regions [c]	67	11.3	61	16.7
Occurring only in terrestrial habitats (***) [d]	133	22.5	120	32.9
Probably occurring only in terrestrial habitats (**) [d]	310	52.2	155	42.5
Occurring in soil and freshwater (*) [d]	151	25.3	90	24.6

[a] Colpodea/Polyhymenophora (heterotrichs, oligotrichs, hypotrichs) quotient: ≥ 1 in extreme habitats, ≤ 1 in ordinary habitats (see LÜFTENEGGER et al. 1985).

[b] Feeding on ≥ than three items.

[c] Only terrestrial records considered.

[d] See footnote (d) in table 3.

by selecting for common, euryoecious species. Nonetheless, the Namibian soils are basically extreme habitats, which becomes obvious when the C/P quotient is calculated not from the whole community but from the most frequent species: then, it amounts to 8.0, showing that most frequent species are r-selected colpodids, while the quotients are between 1.3 and 1.6 in the temperate central European area (Table 10).

Most peritrichs are sessile, filter-feeding ciliates and thus generally rare in the soil environment, where filter space is restricted by the small soil pores. In Namibia, peritrichs are especially rare because most soils are very sandy and thus lack stable pores. Nonetheless, one species, *Vorticella astyliformis*, is among the most frequent species in Namibia and worldwide (Table 10). As the name says, this species easily leaves the stalk when the environment becomes unfavourable and then behaves like a free-swimming filter feeder, that is, changes its functional group.

3.1.5 Frequencies and Characteristic Species Communities

200 of the 365 ciliate species identified occur at only one or two sites, showing (i) a very patchy distribution of most species and (ii) a high proportion of possibly rare species. No species occurred in all samples, and the euryoecious *Colpoda steinii* was most frequent, occurring in 77% of the samples (Table 4, Fig. 7). The contribution of methodological short

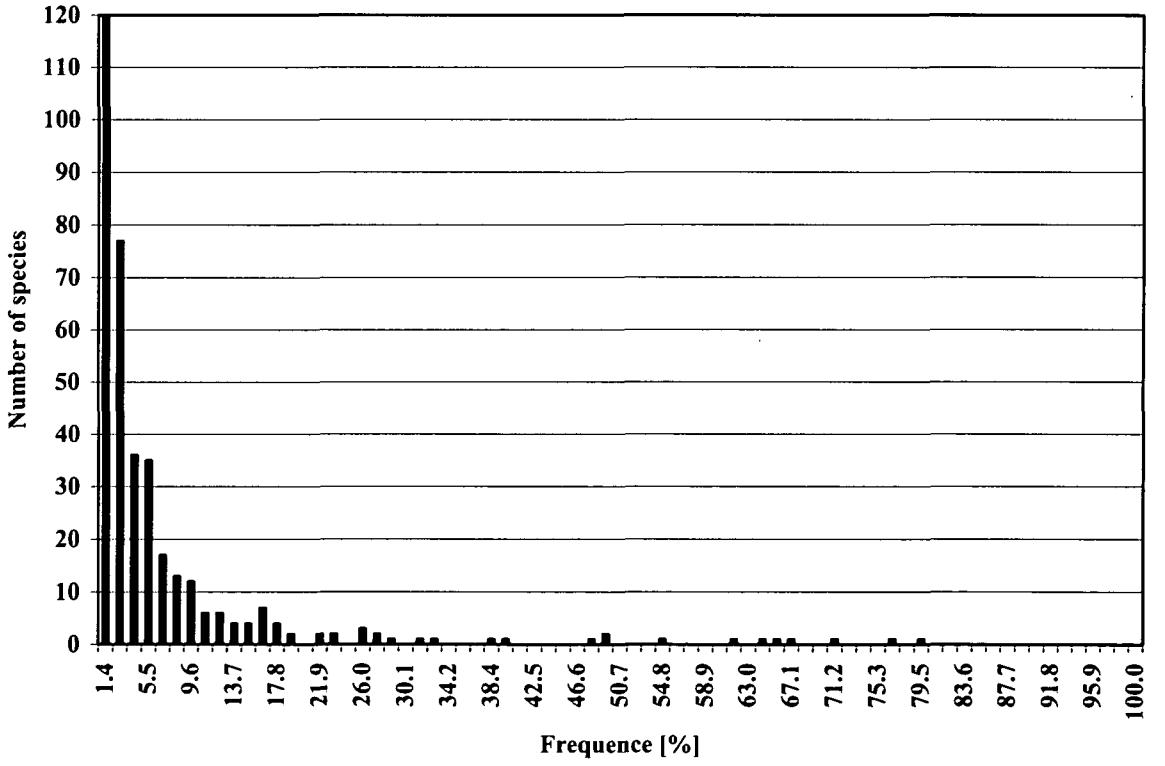

Fig. 7. Frequencies of 365 ciliate species in 73 samples from terrestrial biotopes of Namibia.

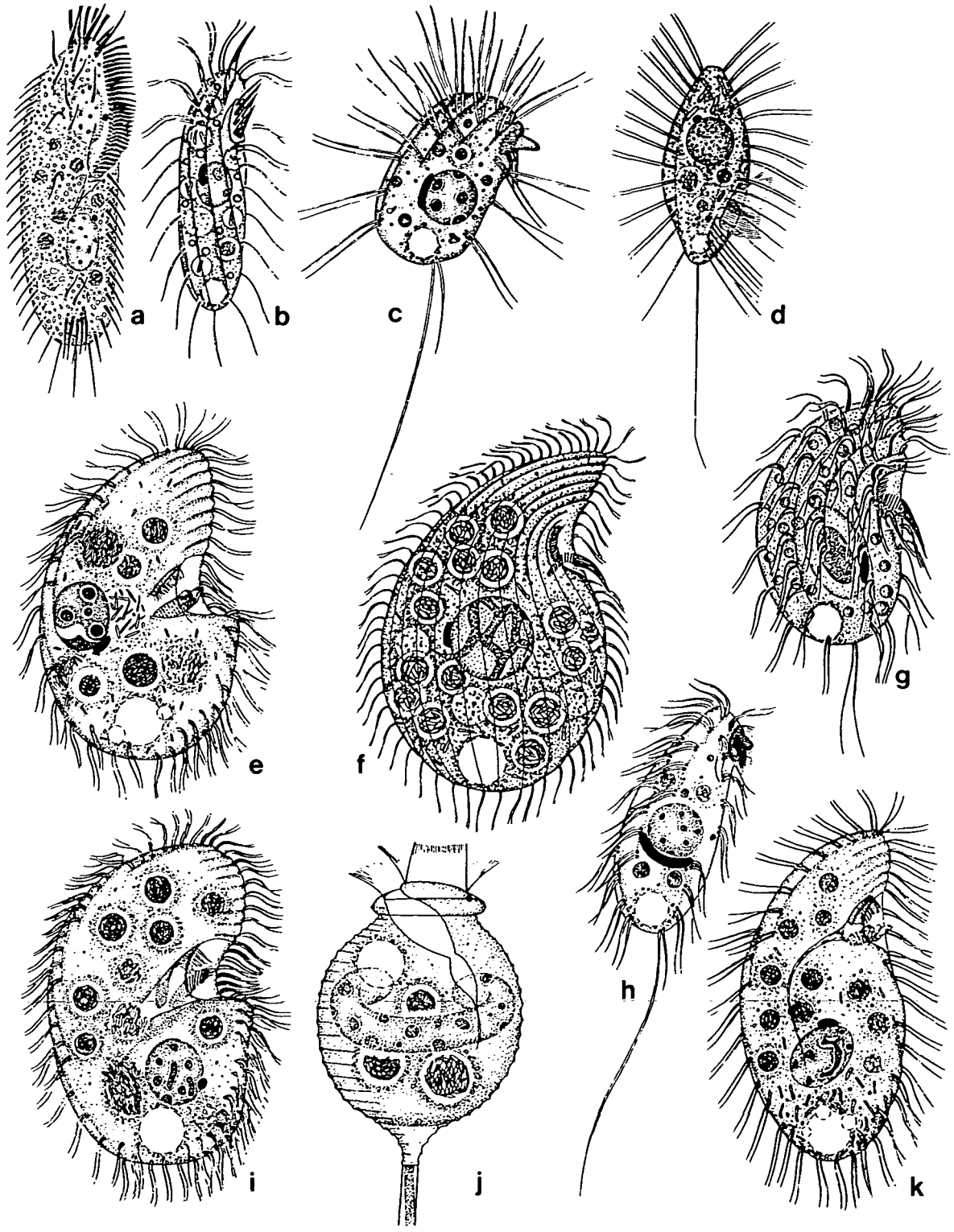

Fig. 8. The 11 most frequent ciliate species in Namibian soils: *Gonostomum affine* (a), *Plesiocaryon elongatum* (b), *Nivaliella plana* (c), *Homalogastra setosa* (d), *Colpoda inflata* (e), *Exocolpoda augustini* (f), *Colpoda steinii* (g), *Pseudoplatyophrya nana* (h), *Colpoda cucullus* (i), *Vorticella astyliformis* (j), and *Colpoda maupasi* (k).

comings to these results is unknown, but probably significant (chapter 3.1.1). On the other hand, this or similar patterns are common in all ordinary protist, plant and animal communities (FENCHEL 1987, SCHWERDTFEGER 1975).

Only 11 species have frequencies of ≥ 40%, viz., *Colpoda cucullus*, *C. inflata*, *C. maupasi*, *C. steinii*, *Exocolpoda augustini*, *Gonostomum affine*, *Homalogastra setosa*, *Nivaliella plana*, *Plesiocaryon elongatum*, *Pseudoplatyophrya nana*, and *Vorticella astyliformis* (Fig. 8, Table 10). Most of these species are frequent in soils globally and feed on bacteria, except for the obligate fungivorous *N. plana* and *P. nana*; further, most belong to the r-selected, fast-growing colpodids adapted to utilize the usually very short, wet periods in Namibia (chapter 3.1.4). *Pseudoplatyophrya nana*, a minute (25 µm) fungi and yeast feeder, is common in soils worldwide, while the high frequency of *N. plana* is unique to Namibia and indicates high abundances and wide distribution of certain fungi. However, this very minute (15 µm) ciliate is easily overlooked and thus likely more frequent than data indicate.

Table 10. Comparison of frequent (usually occurring in ≥ 40% of samples) soil ciliate species worldwide. + = present, – = absent.

Species [a]	Namibia[b]	Kenya[c]	Australia[d]	Antarctica[e]	Germany[f]	Austria[g] Tullnerfeld	Austria[h] alpine habitats	South America[i]
Blepharisma hyalinum	-	+	+	-	+	-	-	-
Bryometopus pseudochilodon	-	-	+	-	-	-	-	-
Colpoda aspera	-	-	-	-	-	+	+	-
Colpoda cucullus	+	+	+	-	+	+	-	+
Colpoda ecaudata	-	-	-	+	-	-	-	-
Colpoda henneguyi	-	+	+	-	-	-	-	-
Colpoda inflata	+	+	+	+	+	+	+	+
Colpoda lucida	-	-	+	-	-	-	-	+
Colpoda maupasi	+	+	+	-	+	+	-	+
Colpoda steinii	+	+	+	+	+	+	+	+
Cyclidium glaucoma	-	-	-	+	-	-	-	-
Cyclidium muscicola	-	+	+	+	+	-	+	+
Cyrtolophosis mucicola	-	+	+	+	+	-	-	+
Dileptus alpinus	-	-	+	-	-	-	-	-
Drepanomonas pauciciliata	-	+	+	-	-	-	-	+
Drepanomonas revoluta	-	+	-	-	+	-	-	-
Epispathidium terricola	-	+	+	+	+	+	+	+
Euplotopsis muscicola	-	-	-	-	+	-	-	-
Exocolpoda augustini	+	-	-	-	-	-	-	-
Gonostomum affine	+	-	+	-	+	+	-	-
Hemisincirra gellerti	-	-	-	-	-	+	-	-
Hemisincirra gracilis	-	-	-	-	-	+	-	-
Hemisincirra inquieta	-	-	-	-	+	-	-	-
Holosticha sigmoidea	-	-	-	+	-	-	-	-
Homalogaster setosa	+	-	+	-	+	-	-	-
Leptopharynx costatus	-	+	-	-	-	-	-	-
Microdiaphanosoma arcuatum	-	-	-	+	-	-	-	-
Mykophagophrys terricola	-	-	+	-	-	-	-	-

(continued)

Species [a]	Namibia[b]	Kenya[c]	Australia[d]	Antarctica[e]	Germany[f]	Austria[g] Tullnerfeld	Austria[h] alpine habitats	South America[i]
Nivaliella plana	+	-	-	-	-	-	-	-
Oxytricha opisthomuscorum	-	-	-	+	-	-	-	-
Oxytricha setigera	-	+	-	-	+	+	-	-
Paraenchelys terricola	-	+	-	-	-	-	-	-
Platyophrya macrostoma	-	-	-	-	-	+	+	-
Platyophrya vorax	-	-	+	+	+	-	+	+
Plesiocaryon elongatum	+	-	-	-	-	+	-	-
Pleuroplitoides smithi	-	-	-	+	-	-	-	-
Pseudochilodonopsis mutabilis	-	-	-	-	-	+	-	-
Pseudocyrtolophosis alpestris	-	+	+	+	+	-	+	+
Pseudoholophrya terricola	-	+	-	-	-	-	-	-
Pseudoplatyophrya nana	+	-	+	+	+	+	-	+
Sathrophilus muscorum	-	+	+	-	+	+	-	-
Sterkiella histriomuscorum	-	-	+	-	+	-	-	-
Tetrahymena rostrata	-	-	+	-	+	-	-	-
Urosomoida agiliformis	-	+	-	-	-	-	-	-
Urosomoida agilis	-	-	-	-	-	+	-	-
Vorticella astyliformis	+	+	+	+	-	+	-	-
C/P quotient[j]	8.0	2.3	4.0	4.0	1.3	1.6	6.0	9.0

[a] Nomenclature adapted to FOISSNER (1998a), who also provides authorship and date for species. All data based on non-flooded Petri dish cultures.

[b] From table 4. Species with ≥ 48% frequency are included.

[c] From FOISSNER (1999b). Nine samples containing 125 taxa from the Shimba Hills near Mombasa. Species with ≥ 55% frequency are included.

[d] From BLATTERER & FOISSNER (1988). Twenty-one samples containing 139 taxa were investigated. Species with ≥ 50% frequency are included.

[e] From FOISSNER (1996a). Fifty-nine samples containing 64 taxa were investigated. Many samples contained no or few species causing very low frequency values. Thus, species with a frequency of ≥ 5.1% are included.

[f] From FOISSNER (2000a). Twenty samples and sample groups containing 270 species were investigated. Species with ≥ 50% frequency are included.

[g] From FOISSNER et al. (1985). Seven sites, each investigated ten times during a period of 27 months, containing 132 taxa. Species with a frequency of ≥ 50% are included.

[h] From FOISSNER (1981c). Fifteen sites, some investigated several times, containing 81 taxa. Species with ≥ 50% frequency are included.

[i] From FOISSNER (1997d). Seventeen samples from rain forests in Amazonia and Costa Rica. Species with ≥ 50% frequency are included.

[j] Quotient of Colpodea and Polyhymenophora (heterotrichs, oligotrichs, hypotrichs), as described by LÜFTENEGGER et al. (1985). The higher the value, the extremer the habitat. The high value from South America is a methodological artifact (FOISSNER 1997d).

Thus, there remains a single, outstanding species, viz., *Exocolpoda augustini*, whose morphology and life cycle are described in detail in the systematic section. *Exocolpoda augustini* feeds on bacteria and looks like an ordinary *Colpoda*, but has two special features:

(i) it divides in freely motile condition, while all other colpodids s. str. generate a division cyst; and (ii) the resting (dormant) cyst has an extraordinarily thick wall. Both specializations enable this species to survive in adverse, very short-lived habitats, such as dune seas of the

Namib Desert and the gravel plains along the Atlantic sea coast and in the Central Namib Desert. Indeed, *E. augustini* is much more common in arid than temperate environments, and is thus very rare in central Europe (FOISSNER 2000a). Interestingly, it is absent from the Antarctic (FOISSNER 1998a), emphasizing that it is a thermophilic species.

Division in cysts is considered as an r-selected life strategy because it usually generates four offspring and can occur under already suboptimal conditions (FOISSNER 1987d, 1993c). The data from *E. augustini* cast doubts on this interpretation, although the advantage of the freely motile division remains obscure; possibly it proceeds faster than cystic division, which would be a great advantage in arid environments, where the wet periods are often very short-lived.

Interestingly, almost the same ciliate species are most frequent in soils globally, indicating global distribution of many euryoecious species (Table 10). On the other hand, differences exist, with *Exocolpoda augustini* being the most remarkable example, showing that even frequent species are **not** globally ubiquitous, as suggested by FINLAY and FENCHEL. Further, only few of the most frequent soil ciliate species commonly occur in limnetic habitats, mainly *Cyclidium glaucoma*, *Sterkiella histriomuscorum*, and *Cyrtolophosis mucicola*. Thus, both biotopes have highly distinct ciliate communities, as already shown by FOISSNER (1987d).

3.1.6 Not Everything is Everywhere – Evidences from Literature and Namibian Soil Ciliates

3.1.6.1 Literature

There is no direct way to prove endemism in microscopic organisms. Only careful analysis of a great number of habitats with a variety of methods will provide sufficient pros and cons over time. However, the trachelophyllids with their specific cortical scales would be an ideal group for a closer examination of free-living ciliate endemism, just as FINLAY & CLARKE (1999) did with the scale-bearing chrysomonad genus *Paraphysomonas*. They found 78% of the described species in Priest Pot, a small pond in England. This is an impressive result, and thus it is difficult to understand why FINLAY & CLARKE (1998) provided scale micrographs from only 5 out of the 32 species found. In contrast, 22 of the 59 northern temperate *Mallomonas* species, a genus closely related to *Paraphysomonas*, are endemic; and 18 taxa are restricted to the tropics (KRISTIANSEN 2001). As concerns the trachelophyllids mentioned above, the main problem is that their rarity makes global studies difficult. The present monograph is, indeed, the first in-deep investigation of trachelophyllid diversity, but data are still too meagre for any firm conclusion, even if the four unpublished species found recently are included.

Evidence is accumulating, mainly from refined molecular methods, that both, free-living bacteria (CHO 2000) and protists (FOISSNER 1999d, FOISSNER et al. 2001, HOLZMANN et al. 2001, KRISTIANSEN 2001, LA TERZA et al. 2001, NANNEY et al. 1998) have more or less distinct biogeographies, contradicting the views of FENCHEL (1993) and FINLAY et al. (1996) that, in micro-organisms, "everything is everywhere". Indeed, FINLAY & ESTEBAN (1998) state: **"As protozoan species are probably globally ubiquitous, there is every reason to believe that all species of freshwater protozoa could eventually be discovered in one**

small pond". In our opinion and to our best literature knowledge, there is no pond in the world with the capacity to carry all protozoan species, and only 256 ciliate taxa have been reported from Priest Pot, FINLAY's well-studied model pond (FINLAY & MABERLY 2000). The limited carrying capacity of single biotopes is a well known ecological principle, and thus FINLAY will never find all free-living ciliates in his pond, even not his 3000 species.

While FOISSNER (1999d) provides convincing examples for a restricted geographic distribution of several protozoan species and suggests that many more can be discovered in more detailed investigations, ESTEBAN et al. (2001) state: **"We remain unconvinced that there exists a single example of a ciliate species whose distribution is restricted by geographical barriers"**. We shall show in chapter 3.1.6.3 that this conclusion is based on very selective literature citation and unusual taxonomic practices. The rather lengthy discussion of this issue is necessary to save our former (FOISSNER 1998a) and the present data from incomplete and/or incorrect citation by FINLAY's group.

3.1.6.2 Namibian evidence

As explained above, "evidence" in the strict sense of the word cannot be obtained from our data, but some "indications" making endemism and/or restricted geographic distribution of at least some species likely. To clarify our view once more: **We believe that most, but not all, protists are morphological cosmopolitans.** This is substantiated by the most frequent species, which are almost the same in a wide variety of habitats and geographic regions (Table 10).

(a) Most of the 143 new taxa were found only in Namibia or tropical Africa, although we analyzed about 1000 soil and moss samples from all main biogeographic regions (FOISSNER 1998a). Certain genera or genus groups possibly occur only in Africa or Gondwanaland. The most impressive example is a group of slender hypotrichs with a bipartited adoral zone of membranelles: *Erniella* (saline coastal soil of the Cape Verde Islands), → *Etoschothrix* (highly saline soil from the Etosha Pan), and → *Afrothrix* (sand dune in the Namib escarpment and, another species, in an ordinary grassland soil of Kenya).

(b) Many of the new species were found only at type location, even if several samples were taken from, admittedly different, habitats nearby. Thus, either the distribution is very patchy, suggesting high habitat-specificity, or the investigation method very incomplete. Likely, the latter is a main drawback, as explained in chapter 3.1.1, but habitat specificity is also involved because similar sites group to more or less distinct clusters (Fig. 5, 6) and, for instance, many species from saline soils do not occur in ordinary soils.

(c) Populations from different biogeographic regions tend to be more different from each other than those from the same area, for instance, → *Maryna namibiensis namibiensis* and → *Maryna namibiensis costaricensis*. Similar examples are → *Rostrophryides africana africana* and → *R. africana etoschensis*, as well as *Bryophyllum lingua lingua* and → *B. lingua multistriatum*. Sequence data are still rare and conflicting, but if both sequences and morphological traits are combined some biogeographic pattern becomes recognizable (FOISSNER et al. 2001).

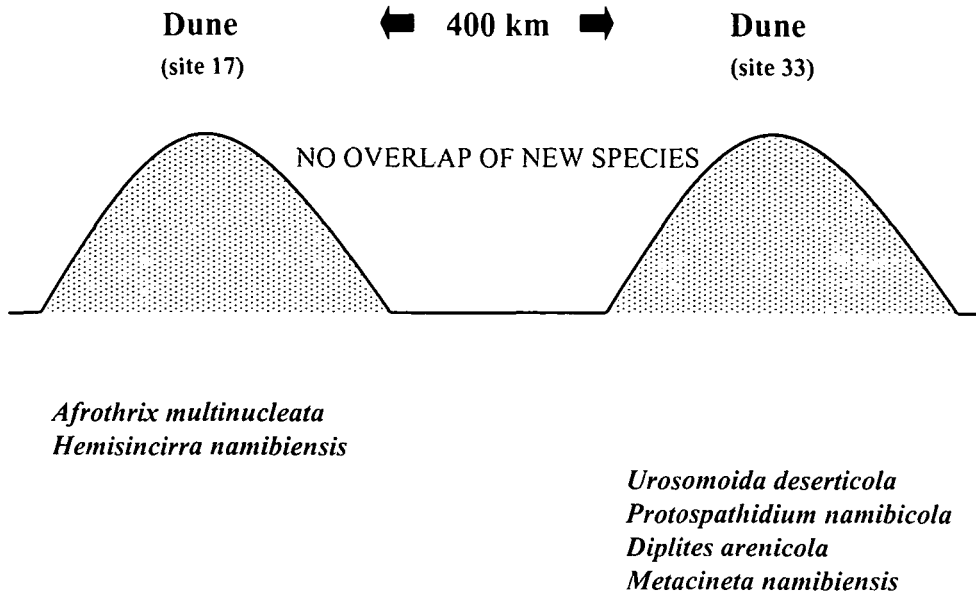

Fig. 9. Patchy distribution of new ciliate species in dunes of the Namib Desert.

Table 11. New species overlap (underlined) in sand dune ciliates of deserts in Namibia, Australia, USA, and Tunisia (from FOISSNER, unpubl.).

Namib Desert (n = 12)	Australia (n = 6)	USA (n = 4)	Tunisia (n = 1)
Hemisincirra namibiensis			
Afrothrix multinucleata			
Parakahliella namibicola			
Urosomoida deserticola			
Erimophrya arenicola			
Erimophrya glatzeli			
Spathidium namibicola			
Protospathidium namibicola			
Diplites arenicola			
Metacineta namibiensis			
Lamtostyla decorata	*Lamtostyla decorata*		
	Coriplites australis		
	Oxytricha granulifera quadricirrata		
	Rostrophryides australis		
	Kuehneltiella terricola		
	Bilamellophrya australiensis		
	Enchelydium n. sp.		
	Australocirrus n. sp.		
Paragonostomum multinucleatum		*Paragonostomum multinucleatum*	
		Circinella arenicola	
		Urosoma n. sp.	
		Tectohymena terricola	
		Rostrophrya terricola	
		Reticulowoodruffia terricola	
		Dexiotricha sp.	
Vermioxytricha arenicola			*Vermioxytricha arenicola*
			Pseudocyrtolophosis terricola

(d) A different species each of → *Kuehneltiella* occurs in Europe (moss), Australia (semi-desert), and Namibia (bark). A similar kind of vicariance is shown by species of the genera → *Bilamellophrya* and → *Parakahliella*.

(e) Several new species and new genera were discovered in the dunes of the Namib desert. Most of them show a very patchy distribution in the Namib dunes (Fig. 9) and do not occur in dunes of deserts of the USA and Australia, where many other new species were discovered (Table 11). The same is true for most new species from the coastal Namib and the Etosha Pan.

There are, however, also contrasting examples, most notably → *Kuklikophrya ougandae* and → *Reticulowoodruffia terricola*, two euryhaline, possibly rare species. The first occurs also in saline soils of Austria, and the second was discovered in highly saline sand from the Death Valley, USA. Further, *Idiocolpoda pelobia*, a minute and possibly rare species discovered by FOISSNER (1993b) in dry mud of a stream in Hawaii, was found in Namibia and, most recently, also in leaf litter in the surroundings of Salzburg, Austria.

As concerns the trachelophyllids mentioned above, morphologically indistinguishable populations of the "Eurasian" → *Trachelophyllum apiculatum* were found in Venezuela, and the "South American" *Trachelophyllum chilense* (now → *Epitholiolus chilensis*) occurred in the Namib Desert. However, identity of the Chilean and Namibian *T. chilense* still has to be proved by scanning electron microscopy of the epicortical scales.

3.1.6.3 Critique of a recent paper on ciliate endemism by ESTEBAN, FINLAY, CHARUBHUN & CHARUBHUN (2001)

a) The paper mainly deals with *Loxodes rex*, an almost 1 mm long and thus very conspicuous anaerobic ciliate recorded as yet only from tropical Africa. ESTEBAN et al. (2001) claim to have found this ciliate in Thailand.

Loxodes species are distinguished by the following main features (DRAGESCO & DRAGESCO-KERNÉIS 1986, FOISSNER 1996d, KAHL 1931): body size, body shape, number of macronuclei, number of micronuclei, arrangement of macronuclei, macro-micronucleus pattern, arrangement of Müller vesicles, number of Müller vesicles, arrangement of cortical granules, colour of cortical granules, number of somatic ciliary rows, various morphometrics of the oral apparatus, and details of the infraciliature (known of only few species, but likely important; FOISSNER 1996d). Of these features, all necessary for a reliable identification and, especially, biogeographic comparison of populations, ESTEBAN et al. (2001) investigated only body size, body shape (without indication of variability), and the number of Müller vesicles. Accordingly, this study is insufficient for any firm conclusion and simply shows that there is a *Loxodes* in Thailand similar to the African *L. rex* in body size and shape, and the number of Müller vesicles. However, such similarities are quite common in congeners and even among different genera, and thus tell us nothing about the species' identity (FOISSNER 1993c). The same applies to another Gondwanan species, *Neobursaridium gigas*, which ESTEBAN et al. (2001) claim to have found in Thailand.

Further, ESTEBAN et al. (2001) found their *Loxodes* in an artificial, 20 years old pond at the Burapa University Campus, about 80 km east of Bangkok. Thus, it seems possibly that, if it is *L. rex* at all, it was introduced by guest students or scientists, just like some North American rotifers (SEGERS 2001), having a similar size to *L. rex*. This possibility must be taken into

account in modern times and, especially, regarding anaerobic organisms needing no oxygen during transport.

Whatever might be true, it remains a fact that records of *L. rex* are lacking from the much better investigated Central European waters, especially from Priest Pot, where, according to FINLAY & ESTEBAN (1998), all species of freshwater protozoa can be found (full citation, see chapter 3.1.6.1).

b) Part of the cosmopolitan distribution of FINLAY's Protozoa is caused by superficially discussed and premature synonymies. Several examples will be shown in the following paragraphs because this is an important issue influencing both distribution and number of species recognized.

ESTEBAN & OLMO (1997) synonymize *Paurotricha cyclidiformis* DRAGESCO & DRAGESCO-KERNÉIS (1991) from Lake Tanganyika with the holarctic *Cristigera pleuronemoides*. However, the African species has two caudal cilia, while *C. pleuronemoides* has only one, a significant difference not discussed by ESTEBAN & OLMO (1997), but widely used as a species character by many ciliatologists. Further, *Paurotricha* lacks the two equatorial ciliary girdles present in *Cristigera*, another significant difference also recognized by ESTEBAN & OLMO (1997), but considered as unimportant. Certainly, one cannot exclude that DRAGESCO's description contains heavy mistakes, viz., his species is *C. pleuronemoides*. However, this is unlikely because DRAGESCO discussed relationships with *Cristigera* and another similar genus, *Paracyclidium*, also lacking equatorial cilia. Accordingly, there is no objective reason to synonymize *Paurotricha cyclidiformis* with *Cristigera pleuronemoides*. Even if these differences are considered as unimportant at species level, the fact remains that the populations differ in at least two conspicuous features and are thus not identical in a biogeographic context.

Next, ESTEBAN et al. (2001) discuss two studies on Lake Baikal ciliates, used by FOISSNER (1999d) as examples for endemic species. While it is true that several Lake Baikal ciliates described by GAJEWSKAJA (1933) were later found in other lakes, there is still a considerable number of species which were not (yet?) found elsewhere and thus might be endemics. A representative example is *Liliimorpha viridis*, which ESTEBAN et al. (2001) synonymize with *Stockesia vernalis*: "However, GAJEWSKAJA (1933) may have been unaware of some earlier literature. Her drawing of a living *Liliimorpha viridis* closely resembles the *Stockesia vernalis* WENRICH, 1929. More recently, OBOLKINA (1995a) described the infraciliature of *L. viridis*; however, the infraciliature shown in OBOLKINA (1995a) actually correspond to the well-known ciliate *Askenasia*". See FOISSNER et al. (1999) for a detailed review of all species mentioned.

Obviously, ESTEBAN et al. (2001) found only one reason for the synonymy suggested, viz., the overall shape similarity; meagre indeed! They do not, for instance, discuss the conspicuous, membranellar structures surrounding the distal margin of *Liliimorpha*, possibly because they are absent in *Stockesia*. It is true that *Liliimorpha* resembles an *Askenasia*, but not any described species, and there is no reason why *Liliimorpha* should not be related to this genus. Regardless of the taxonomic classification, the species shown by OBOLKINA (1995a) is either *L. viridis* or another, as yet undescribed, probably endemic ciliate of Lake Baikal.

ESTEBAN et al. (2001) also suggest synonymy of *Coleps grandis* VACELET, 1961 and *Baikalocoleps quadratus* OBOLKINA, 1995b, another supposed endemic of Lake Baikal. This

synonymy is also highly questionable because *C. grandis* is a marine species, is twice the size of *B. quadratus* (180 × 80 µm vs. 86 × 55 µm), and has more ciliary rows (about 28 vs. 21). However, the main issue is that ESTEBAN et al. (2001) make no mention of six other endemic Colepidae described by OBOLKINA (1995b) in the same paper; obviously, they did not find related species in the literature, suggesting that these species might indeed be endemic to Lake Baikal.

In other cases, the synonymies suggested by FINLAY's group are even more worse, for instance, they declare *Holophrya seyrli* FOISSNER, 1997b as a junior synonym of *Holophrya discolor* without providing any reason (ESTEBAN et al. 2000). Both differ in a prominent feature, viz., the presence vs. absence of 10 µm long toxicysts documented by micrographs. Such taxonomy not only unduely discredits other, more careful observers but also disrespects basic taxonomic practices. Likewise, ESTEBAN et al. (2000) disrespect nomenclature, that is, do not recognize fixed type species (of a genus), as is obvious from their use of the wrong genus name (*Prorodon*) for their *Holophrya* (for details, see FOISSNER et al. 1994).

c) ESTEBAN et al. (2000, 2001) state that they "found no endemic free-living ciliate species in the sediment of a volcanic crater-lake with brackish water in Australia. All 85 species recorded had previously been found in Northern Europe". However, four taxa were not identified to species level and several others are so poorly known and/or difficult to identify that we took an interest in the voucher preparations, especially *Perisincirra kahli*, → *Protospathidium bonneti*, *Holosticha grisea*, *Microdiaphanosoma terricola*, *Rhagadostoma completum*, *Trachelocerca fusca*, and *Tracheloraphis caudata*. On request, we obtained the following information: "Our policy here is that we do not keep either permanent preparations or samples". This is indeed a strange policy, far removed from good taxonomic practice, especially when just these species are used to disprove the existence of autochthonous soil ciliates (p. 186)! Thus, the identifications of ESTEBAN et al. (2000) cannot be falsified and the study cannot support the statement cited above. Further, in the same paper the authors describe a new species, *Lembadion curvatum*, which is very conspicuous and thus a good candidate for an Australian endemic.

d) In their passion to disprove a restricted geographic distribution and/or endemism of free-living ciliates, ESTEBAN et al. (2001) fail to mention that hundreds of well-defined soil ciliate species have been recorded from only one or two biogeographical regions (for a review, see FOISSNER 1998a). Certainly, we cannot exclude that some, or even many, will be found at other sites in more detailed investigations. For the present, however, it is a fact that they were absent in nearly 1000 samples from all main biogeographic regions.

e) FOISSNER (1999d) showed, and the above examples emphasize, that FINLAY's group often refers to literature data in an incomplete and/or inaccurate way. This is also the case in ESTEBAN et al. (2001), where they state: "*Bryometopus hawaiiensis* FOISSNER, 1994, **described as "endemic" to Hawaii** (FOISSNER, 1994c), then was found in a freshwater stream in Spain (OLMO & TÉLLEZ, 1996)". We agree that the Hawaiian and Spanish populations belong to the same morphospecies, but emphasize that FOISSNER (1994c) did not "describe" it as an endemic but supposed that it could be endemic: "*Bryometopus hawaiiensis* must be a rare species since I have not found it in about 1000 other soil and moss samples collected worldwide; it is **probably** endemic to the Hawaiian Archipelago". FOISSNER's paper is written in English, and thus there is no excuse for changing "probably" to "described". The

same kind of misquotation applies in the case of *Holostichides terricola* FOISSNER, 1988a, which has been recorded from all main biogeographic regions (FOISSNER 1998a).

3.1.7 How Many Soil Ciliate Species in Namibia and Globally?

We identified 365 species and subspecies, of which 128 (34%) were undescribed, in the 73 samples from Namibia. Thus, each sample contained an average of 26.5 species, of which 1.75 were undescribed. About 100 rare species, half likely undescribed, were not identified (Table 4). Adding these numbers to the identified species, we arrive at 465, respectively, 178 (40%) taxa. Considering the methodological problems discussed in chapter 3.1.1, we must at least double these figures, that is, can expect about 650 described and 350 undescribed soil ciliate species in Namibia. Thus, our monograph contains only one third of the species actually living in terrestrial habitats of Namibia. This is substantiated by the following observation: We investigated five samples from the year 2001 collection, all from habitats and/or regions not sampled in 1994 (eutrophic soil from margin of water-holes in the Etosha National Park, soils from coastal floodplain of the Uniab River). They contained 10 new species, that is, an average of 2 new species per sample, which is even more than the 1.75 species calculated from the 1994 collection. Further, few of the diverse riverine, lacustrine, palustrine, and estuarine wetland soils were collected in year 1994. Certainly, they contain a significant number of undescribed species.

The total number of ciliates reliably reported from terrestrial habitats globally presently stands at 643 species (FOISSNER 1998a). With the new and several redescribed species contained in the present monograph, we arrive at 800 species, that is, half the number (1330–2000 species) suggested by probability statistics (FOISSNER 1997c). Further, FOISSNER still has 400 undescribed species in his notes from soil ciliates globally. Accordingly, 2000 global soil ciliate species can be reached, provided sufficient man-power. Considering the 143 new taxa described in the present monograph, it is even likely that there are many more than 2000 species.

As concerns global diversity of free-living ciliates, the reader is referred to FOISSNER (1999d) and the "Introduction" to the present monograph, which summarize the present state of knowledge. However, we would like to reinforce that global diversity of free-living ciliates must be much higher than the 3060 species proposed by FINLAY (2001). This is not only indicated by the many new taxa found in Namibian and floodplain soils (Table 8), but also by some other observations:

a) FOISSNER (in preparation) discovered three new ciliate genera and species in the tanks of three Brazilian *Bromelia* species. Considering that the group contains about 3000 species, we can expect that their detailed investigation will considerably increase free-living ciliate diversity.

b) Habitat specificity of free-living ciliates has probably been greatly underestimated due to superficial sampling and, especially, misidentification of species (FOISSNER 1987d). We shall demonstrate this with a few examples, suggesting a further significant increase in species number when well-trained specialists investigate properly defined habitats: (i) A different species each of *Diplites* lives in the Namib Desert (→ *D. namibicola*) and Namibian riverine habitats (→ *D. telmatobius*); (ii) *Parakahliella* species not only show habitat but likely also some biogeographic specificity: → *P. binucleata* occurs in alluvial Namibian soils; → *P.*

halophila occurs in aperiodically flooded, highly saline soils (sites 18, 54, 59, 61) and shows some geographic specializations; → *P. namibicola* has been found only in the Namib Desert and Namib Escarpment; *P. macrostoma* occurs in alluvial, agricultural soil and alpine grassland in Austria; and *P. haideri* was discovered in Austria in a bundle of straw used for mushroom cultivation; (iv) Habitat specificity occurs also in larger systematic groups, for instance the Colpodea (FOISSNER 1993c): The mycophagous grossglockneriids (*Pseudoplatyophrya*, *Grossglockneria*, *Mykophagophrys*, etc.) are strictly terricolous; most *Colpoda* species prefer terrestrial habitats; most *Maryna* species live in semiterrestrial habitats, such as road puddles and bark; and *Bursaridium* is euplanktonic; (v) Frequently, the "extreme" members of a group have specific life strategies and/or food requirements: → *Exocolpoda augustini*, which prefers hot and dry habitats, lacks division cysts and is strictly bacteriophagous; *Sorogena stoianovitchae*, a phyllocolous colpodid, produces aerial sorocarps and feeds on small *Colpoda* species (for a review, see FOISSNER 1993c); and a still unnamed, bacteriophagous *Colpoda* from Australian and Brazilian floodplains has a cover of fine clay particles, probably protecting it from predation.

3.2 Description of Insufficiently Known and New Species

3.2.1 Summary of New Taxa Described in this Book and of Nomenclatural Acts

New order: Colpodidiida (p. 464).

New suborder: Trachelophyllina (p. 142).

New families: Enchelyodontidae (p. 121), Exocolpodidae (p. 921), Fuscheriidae (p. 189).

New genera: *Afroamphisiella* (p. 698), *Anatoliocirrus* (p. 615), *Apertospathula* (p. 318), *Apocolpodidium* (p. 492), *Apocyclidium* (p. 518), *Apoenchelys* (p. 112), *Apospathidium* (p. 334), *Apourosomoida* (p. 759), *Bilamellophrya* (p. 170), *Clavoplites* (p. 212), *Dioplitophrya* (p. 199), *Dragescozoon* (p. 912), *Enchelaria* (p. 220), *Epitholiolus* (p. 164), *Erimophrya* (p. 791), *Etoschophrya* (p. 986), *Etoschothrix* (p. 593), *Exocolpoda* (p. 921), *Hemiurosoma* (p. 834), *Nassulides* (p. 413), *Nudiamphisiella* (p. 693), *Obliquostoma* (p. 115), *Ottowphrya* (p. 967), *Paragonostomum* (p. 819), *Plagiocampides* (p. 547), *Plesiocaryon* (p. 962), *Semispathidium* (p. 327), *Vermioxytricha* (p. 749), *Wolfkosia* (p. 458).

New subgenera: *Echinovorticella* (p. 553), *Kleinstyla* (p. 723), *Phagoon* (p. 497), *Pseudocolpodidium* (p. 488), *Spetastyla* (p. 723).

New species: *Actinobolina multinucleata* (p. 383), *Afroamphisiella multinucleata* (p. 699), *Afrothrix multinucleata* (p. 588), *Amphisiella elegans* (p. 674), *Amphisiella longiseries* (p. 680), *Amphisiella multinucleata* (p. 685), *Amphisiella namibiensis* (p. 656), *Amphisiella procera* (p. 670), *Anatoliocirrus capari* (p. 617), *Apertospathula armata* (p. 322), *Apertospathula dioplites* (p. 322), *Apertospathula inermis* (p. 318), *Apobryophyllum vermiforme* (p. 357), *Apocolpodidium etoschense* (p. 493), *Apocolpodidium macrostoma* (p. 498), *Apoenchelys bamforthi* (p. 112), *Apospathidium terricola* (p. 334), *Apourosomoida halophila* (p. 761), *Arcuospathidium etoschense* (p. 292), *Arcuospathidium lorjeae* (p. 295), *Arcuospathidium novaki* (p. 303), *Bakuella granulifera* (p. 561), *Bilamellophrya australiensis* (p. 170), *Bilamellophrya etoschensis* (p. 177), *Bilamellophrya hawaiiensis* (p. 183), *Bryophyllum paucistriatum* (p. 340), *Clavoplites australiensis* (p. 217), *Clavoplites edaphicus* (p. 213), *Colpoda formisanoi* (p. 905), *Colpodidium bradburyarum* (p. 489), *Colpodidium horribile* (p. 474), *Colpodidium microstoma* (p. 485), *Colpodidium trichocystiferum* (p. 480), *Condylostomides etoschensis* (p. 893), *Condylostomides trinucleatus* (p. 899), *Dioplitophrya otti* (p. 199), *Diplites arenicola* (p. 193), *Dragescozoon terricola* (p. 912), *Enchelaria multinucleata* (p. 221), *Enchelydium blattereri* (p. 121), *Enchelyodon armatides* (p. 130), *Enchelyodon kenyaensis* (p. 128), *Enchelyodon megastoma* (p. 139), *Enchelyodon minutus* (p. 136), *Enchelyotricha jesnerae* (p. 186), *Enchelys longitricha* (p. 101), *Epispathidium polynucleatum* (p. 312), *Erimophrya arenicola* (p. 796), *Erimophrya glatzeli* (p. 791), *Eschaneustyla lugeri* (p. 572), *Etoschophrya oscillatoriophaga* (p. 987), *Etoschothrix terricola* (p. 594), *Euplotopsis incisa* (p. 868), *Gastrostyla bavariensis* (p. 743), *Gonostomum namibiense* (p. 810), *Hemisincirra namibiensis* (p. 857), *Hemisincirra rariseta* (p. 865), *Hemiurosoma goertzi* (p. 843), *Hemiurosoma terricola* (p. 835), *Holophrya salinarum* (p. 537), *Holosticha brachysticha* (p. 579), *Ilsiella elegans* (p. 950), *Kuehneltiella namibiensis* (p. 916), *Lamtostyla decorata* (p. 712), *Lamtostyla halophila* (p. 706), *Metacineta namibiensis* (p. 404), *Nassula dragescoi* (p. 424), *Nassula etoschensis* (p. 438), *Nassula granata* (p. 427), *Nassula*

tuberculata (p. 433), *Nudiamphisiella interrupta* (p. 694), *Obliquostoma enchelyodontides* (p. 116), *Obliquostoma namibiense* (p. 119), *Orthoamphisiella breviseries* (p. 703), *Parabryophrya etoschensis* (p. 957), *Paraenchelys brachyarmata* (p. 106), *Paraenchelys brachyoplites* (p. 109), *Paraenchelys pulchra* (p. 104), *Paragonostomum binucleatum* (p. 826), *Paragonostomum caudatum* (p. 820), *Paragonostomum multinucleatum* (p. 828), *Paragonostomum rarisetum* (p. 831), *Parakahliella binucleata* (p. 607), *Parakahliella halophila* (p. 598), *Parakahliella namibicola* (p. 611), *Perisincirra longicirrata* (p. 632), *Perisincirra paucicirrata* (p. 628), *Phialinides armatus* (p. 224), *Plagiocampa namibiensis* (p. 542), *Plagiocampa pentadactyla* (p. 539), *Plagiocampides halophilus* (p. 548), *Plesiocaryon terricola* (p. 963), *Podophrya tristriata* (p. 396), *Protospathidium namibicola* (p. 305), *Protospathidium vermiforme* (p. 310), *Pseudocohnilembus binucleatus* (p. 530), *Pseudoholophrya minuta* (p. 99), *Pseudokreyella etoschensis* (p. 1023), *Pseudomonilicaryon angustistoma* (p. 381), *Pseudomonilicaryon japonicum* (p. 378), *Rostrophrya fenestrata* (p. 997), *Semiplatyophrya acrostoma* (p. 1019), *Semispathidium armatum* (p. 331), *Semispathidium enchelyodontides* (p. 327), *Sikorops minor* (p. 209), *Sikorops namibiensis* (p. 203), *Spathidium aciculare* (p. 258), *Spathidium contractile* (p. 263), *Spathidium etoschense* (p. 255), *Spathidium lanceoplites* (p. 267), *Spathidium namibicola* (p. 246), *Spathidium turgitorum* (p. 234), *Supraspathidium armatum* (p. 280), *Supraspathidium etoschense* (p. 274), *Trachelophyllum africanum* (p. 151), *Trachelophyllum costaricanum* (p. 160), *Trachelophyllum pannonicum* (p. 155), *Uroleptus paranotabilis* (p. 566), *Urosomoida deserticola* (p. 787), *Urosomoida monostyla* (p. 784), *Urosomoida namibiensis* (p. 780), *Urosomoida reticulata* (p. 771), *Vermioxytricha arenicola* (p. 751), *Wallackia elegans* (p. 643), *Wolfkosia loeffleri* (p. 459).

New subspecies: *Amphisiella binucleata multicirrata* (p. 663), *Arcuospathidium cultriforme megastoma* (p. 300), *Arcuospathidium namibiense namibiense* (p. 285), *Arcuospathidium namibiense tristicha* (p. 288), *Bryophyllum lingua multistriatum* (p. 345), *Colpoda cavicola amicronucleata* (p. 910), *Frontonia angusta obovata* (p. 511), *Maryna namibiensis costaricensis* (p. 942), *Maryna namibiensis namibiensis* (p. 935), *Odontochlamys alpestris biciliata* (p. 390), *Platyophrya spumacola hexasticha* (p. 960), *Pseudocohnilembus persalinus hexakineta* (p. 533), *Pseudouroleptus caudatus namibiensis* (p. 652), *Rostrophrya namibiensis maldivensis* (p. 994), *Rostrophrya namibiensis namibiensis* (p. 992), *Rostrophryides africana etoschensis* (p. 1000), *Spathidium seppelti etoschense* (p. 229).

New combinations

Balantiophorus elongatus SCHEWIAKOFF transferred to genus *Plesiocaryon*, p. 963.
Colpoda augustini FOISSNER transferred to genus *Exocolpoda*, p. 922.
Condylostoma luteum KAHL transferred to genus *Condylostomides*, p. 899.
Condylostoma tardum PENARD transferred to genus *Condylostomides*, p. 899.
Condylostoma terricola FOISSNER transferred to genus *Condylostomides*, p. 899.
Cyclidium citrullus COHN transferred to genus *Protocyclidium*, p. 524.
Cyclidium muscicola KAHL transferred to genus *Protocyclidium*, p. 524.
Cyclidium obliquum KAHL transferred to genus *Apocyclidium*, p. 520.
Cyclidium sphagnetorum ŠRÁMEK-HUŠEK transferred to genus *Protocyclidium*, p. 524.
Cyclidium terricola KAHL transferred to genus *Protocyclidium*, p. 524, 525.
Dileptus massutii KAHL transferred to genus *Pseudomonilicaryon*, p. 373.
Enchelydium polynucleatum FOISSNER transferred to genus *Enchelys*, p. 127.
Enchelydium terrenum FOISSNER transferred to genus *Clavoplites*, p. 213.
Euplotes labiatus RUINEN transferred to genus *Euplotopsis*, p. 868.

Hemisincirra muelleri FOISSNER transferred to genus *Vermioxytricha*, p. 750.
Hemisincirra polynucleata FOISSNER transferred to genus *Hemiurosoma*, p. 835.
Lacrimaria chilensis BÜRGER transferred to genus *Epitholiolus*, p. 165.
Lacrymaria minima KAHL transferred to genus *Phialina*, p. 227.
Lamtostyla abdita FOISSNER transferred to genus *Afroamphisiella*, p. 698.
Nassula labiata KAHL transferred to genus *Nassulides*, p. 448.
Nassula lucida REUTER transferred to genus *Naxella*, p. 445.
Nassula picta KAHL transferred to genus *Nassulides*, p. 413.
Nassula pratensis CZAPIK & JORDAN transferred to *Nassulides*, p. 413.
Nassula rosea TUCOLESCO transferred to genus *Naxella*, p. 441.
Nassula theresae FABRE-DOMERGUE transferred to genus *Furgasonia*, p. 457.
Nassula vernalis GELEI & SZABADOS transferred to *Nassulides*, p. 413.
Perisincirra similis FOISSNER transferred to genus *Hemiurosoma*, p. 835.
Platyophryides dragescoi FOISSNER transferred to genus *Ottowphrya*, p. 969.
Platyophryides magnus FOISSNER transferred to *Ottowphrya*, p. 975.
Prorodon spirogyrophagus LEIPE transferred to *Holophrya*, p. 538.
Spathidium atypicum BUITKAMP & WILBERT transferred to genus *Apospathidium*, p. 338.
Spathidium lagyniforme KAHL transferred to genus *Semispathidium*, p. 327.
Trachelophyllum attenuatum FOISSNER transferred to genus *Epitholiolus*, p. 164.

Nomina correcta

Colpodidium viride pro *C. viridis* (MIRABDULLAYEV, 1986) JANKOWSKI, 1992, p. 467.
Euplotopsis apsheronica pro *E. apsheronicus* (AGAMALIEV, 1966) BORROR & HILL, 1995, p. 868.
Euplotopsis bisulcata pro *E. bisulcatus* (KAHL, 1932) BORROR & HILL, 1995, p. 868.
Euplotopsis encystica pro *E. encysticus* (YONEZAWA, 1985) BORROR & HILL, 1995, p. 868.
Euplotopsis tegulata pro *E. tegulatus* (TUFFRAU, 1960) BORROR & HILL, 1995, p. 868.
Frontonia roqueae pro *F. roquei* DRAGESCO, 1970, p. 504.
Pedohymena australiensis pro *P. australiense* FOISSNER, 1995, p. 466.
Supraspathidium multistriatum pro *S. multistriata* FOISSNER & DIDIER, 1981, p. 278.

3.2.2 Descriptions

GYMNOSTOMATEA

The Gymnostomatea were founded by BÜTSCHLI (1889) for a group of ciliates with simple (gymnostomous) oral ciliature. Later, many other names were suggested, such as Litostomatea, Haptorida, Filicorticata, and Homotricha, for basically the same ciliates. Thus, and for reasons of stability (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE 1999), we prefer BÜTSCHLI's time-honoured name Gymnostomata.

Gymnostome ciliates are very frequent in soils globally and, for obscure reasons, especially in Namibia (chapter 3.1.4). Many are inconspicuous and look alike at first glance. More detailed analysis, however, reveals quite a lot of organization types, especially of the circumoral ciliature and extrusomes, which are highly evolved in this basically rapacious group of ciliates. This is emphasized by the present study, which discovered 10 new gymnostomatous genera and 57 new species.

Workers not familiar with the group tend to underrate the differences. ESTEBAN et al. (2000), for instance, state: "Living cells of *Pleuroplites australis* are indistinguishable from ciliates of the following genera: *Coriplites*, *Enchelys*, *Enchelyodon*, *Foissnerides*, *Fuscheria*, *Pleuroplitoides*, from some of KAHL's *Spathidium* species, and from *Placus ovum* (KAHL, 1926)". This is nonsense; just the reverse is the case, especially with *Placus ovum*, which has a unique, spiral kinety course and cortex structure (for a review, see FOISSNER et al. 1994). But also the other genera and species are easily distinguished by quite a lot of features, such as the location (uniquely postcytostomal in *Pleuroplites* and *Pleuroplitoides*) and shape (uniquely nail-like in *Fuscheria*) of the extrusomes, the presence/absence (uniquely lacking in *Enchelys*) of a circumoral kinety and extrusomes (uniquely lacking in *Coriplites*), and the fine structure of the dorsal brush (uniquely multi-rowed and with ordinary cilia interspersed in *Pleuroplites* and *Foissnerides*). All these and other features can be recognized in vivo and/or good protargol preparations. It is only the selective use of a single silver stain and insufficient live observation which make these well-defined genera so similar to ESTEBAN et al. (2000). Clearly, they have to improve their methodological diversity, otherwise they will be also unhappy with most of the new genera described in this book.

Family Pseudoholophryidae BERGER, FOISSNER & ADAM, 1984

Improved diagnosis: Haptorid gymnostomes with spiral ciliary rows. Dorsal brush in anterior half of few to many kineties, composed of numerous minute kinetofragments with shortened bristles interspersed between ordinary cilia. Silverline system narrowly meshed.

Type genus (by original designation): *Pseudoholophrya* BERGER, FOISSNER & ADAM, 1984.

Remarks: The original diagnosis of the family ("dorsal brush lacking") has to be improved because the reinvestigation of many *Pseudoholophrya terricola* populations showed that *Pseudoholophrya* has a similar brush as → *Paraenchelys*. The diagnosis of the genus *Pseudoholophrya* is still valid as given by BERGER, FOISSNER & ADAM (1984): "Pseudoholophryidae with rod-shaped extrusomes occupying the minute oral opening". Possibly, it should be supplemented by "rod-shaped to indistinctly acicular extrusomes" or, more simply, "basically rod-shaped extrusomes".

The brush pattern of *Pseudoholophrya* is very constant and more or less distinctly different from that of other gymnostomes. It resembles those of → *Paraenchelys* (FOISSNER 1984), *Ovalorhabdos* (FOISSNER 1984, FOISSNER & GSCHWIND 1998), as well as *Prorodon armatides*, as described by FOISSNER (1997b), and *Prorodon emmae*, as redescribed by SONG & WILBERT (1989). In *P. armatides*, which has, like *Ovalorhabdos sapropelicus*, an oblong oral opening, the brush consists of two ordinary dikinetidal kineties plus several rows in which dikinetids and monokinetids irregularly alternate. This pattern is distinctly different from those of *Ovalorhabdos*, → *Paraenchelys*, → *Pseudoholophrya*, and *Prorodon emmae*, which lack conventional brush dikinetids. These genera (and *Prorodon emmae*, which is likely distinct at genus level) form a natural assemblage, which can be united in the family Pseudoholophryidae BERGER, FOISSNER & ADAM, 1984. They differ from each other mainly by the shape of the oral opening (circular and minute, except for *Ovalorhabdos*, in which it is oblong and large) and the arrangement (in oral bulge, except for *P. emmae* which also has distinct lateral bundles) and shape of the extrusomes (rod-shaped to acicular in *Pseudoholophrya*, *Ovalorhabdos* and *P. emmae* vs. drumstick-shaped in *Paraenchelys*).

Pseudoholophrya terricola BERGER, FOISSNER & ADAM, 1984 (Fig. 10a–l, 11a–z; 301a–v; Table 12)

Description of a Maldivean population: Because the original description of *P. terricola* is in German and Maldivean-like populations occur in Namibia, we redescribe this "difficult" species in detail. The sample was collected by Dr. Wolfgang PETZ at the North-Male Atoll near the village of Himmafuchi. The highly saline and alkaline (pH 8.6) material was taken about 2 m inshore and consisted mainly of shrub litter mixed with some sand.

Size 50–80 × 20–40 µm in vivo, distinctly shrunken in protargol preparations (50 × 20 µm; Table 12). Slightly asymmetrical and flattened up to 2:1, broad-side view ellipsoidal to somewhat dumb-bell-shaped, narrow-side view ovate and often slightly curved (Fig. 10a, e, h, i; 301g, m); very flexible but acontractile. Nuclear apparatus usually in middle body third. Macronucleus mostly reniform, rarely ellipsoidal or semicircular, or in two nodules connected by a broad bridge; nucleoli globular, small, numerous. Usually two micronuclei attached to macronucleus at various positions; individual micronuclei discoidal and surrounded by a distinct membrane (Fig. 10a, e, h, i; 301a, f). Contractile vacuole in posterior body end, several excretory pores in pole area. Oral bulge extrusomes form conspicuous bundle in anterior pole centre, slightly acicular and about 5 µm long; cytoplasmic extrusomes scattered and shaped like oral ones or, occasionally, fusiform; exploded toxicysts drumstick-shaped, hyaline, about 13 µm long (Fig. 10a–d). Cortex very flexible, contains innumerable granules,

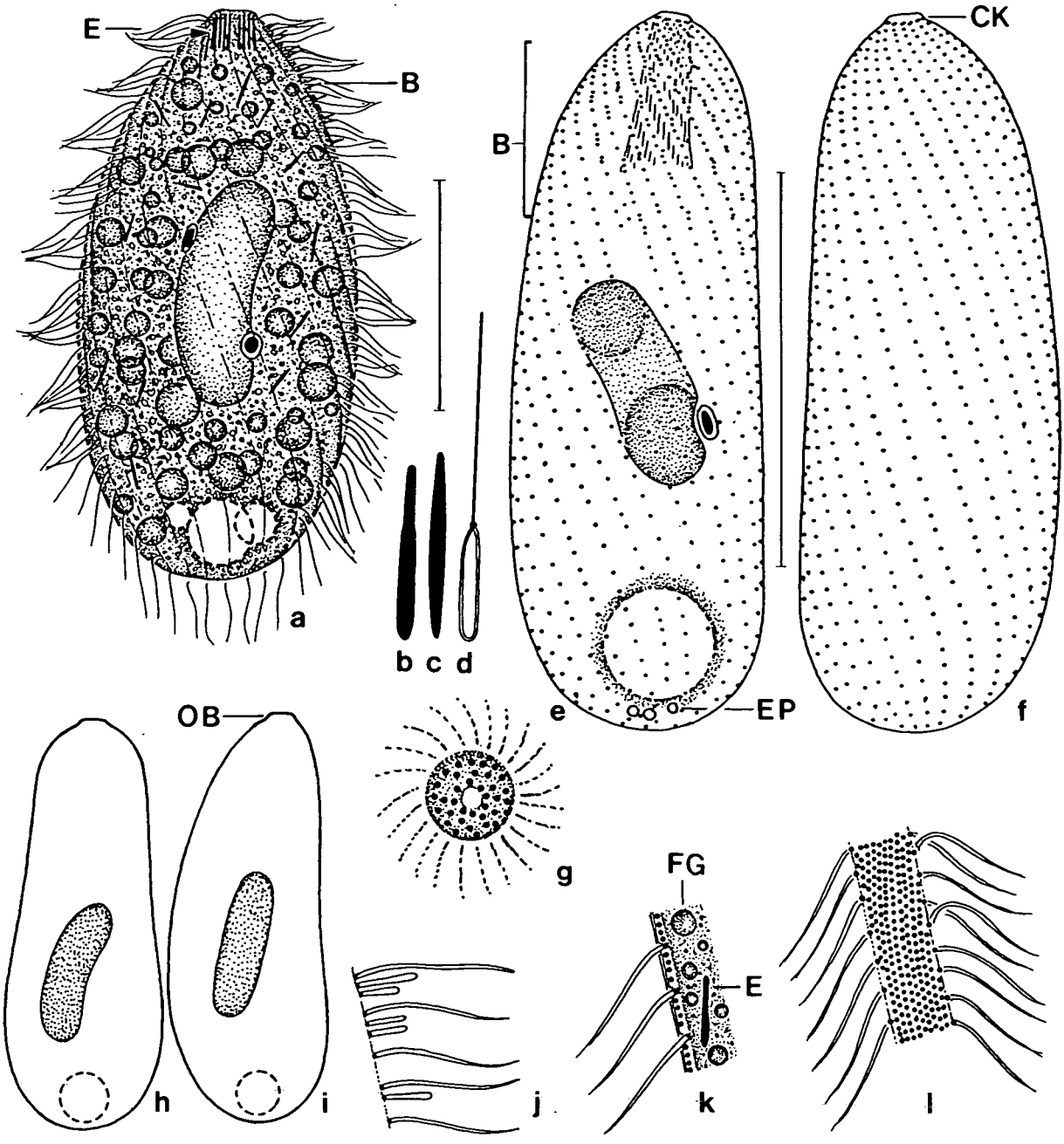

Fig. 10a–l. *Pseudoholophrya terricola*, Maldivean specimens from life (a–d, g–l) and after protargol impregnation (e, f). **a, j:** Broad-side view of a representative specimen with reniform macronucleus having two flattened micronuclei attached. Note the extrusome bundle in the inconspicuous oral bulge. The dorsal brush, difficult to recognize in live specimens, consists of 2–4 μm long bristles interspersed between ordinary cilia (j). **b:** Resting extrusome attached to the oral bulge, length 5 μm. **c:** Cytoplasmic extrusome, length 5 μm. **d:** Exploded toxicysts, length 13 μm. **e, f:** Ciliary pattern of dorsal and ventral side. The dorsal brush is difficult to recognize and consists of a field of kinetids slightly more closely and irregularly spaced than the ordinary cilia. **g:** Frontal view of oral bulge packed with extrusomes. **h, i:** Same specimen in broad and narrow-side view showing that *P. terricola* is slightly asymmetrical. Note the very flat, almost invisible oral bulge. **k, l:** Optical section and surface view showing the small (~ 0.3 μm) but rather strongly refractive cortical granules, likely mucocysts, which are a fairly typical feature of *P. terricola* (cp. figure 301 l, v). B – dorsal brush, CK – circumoral kinety, E – extrusomes, EP – excretory pores, FG – fat globule, OB – oral bulge. Scale bars 30 μm.

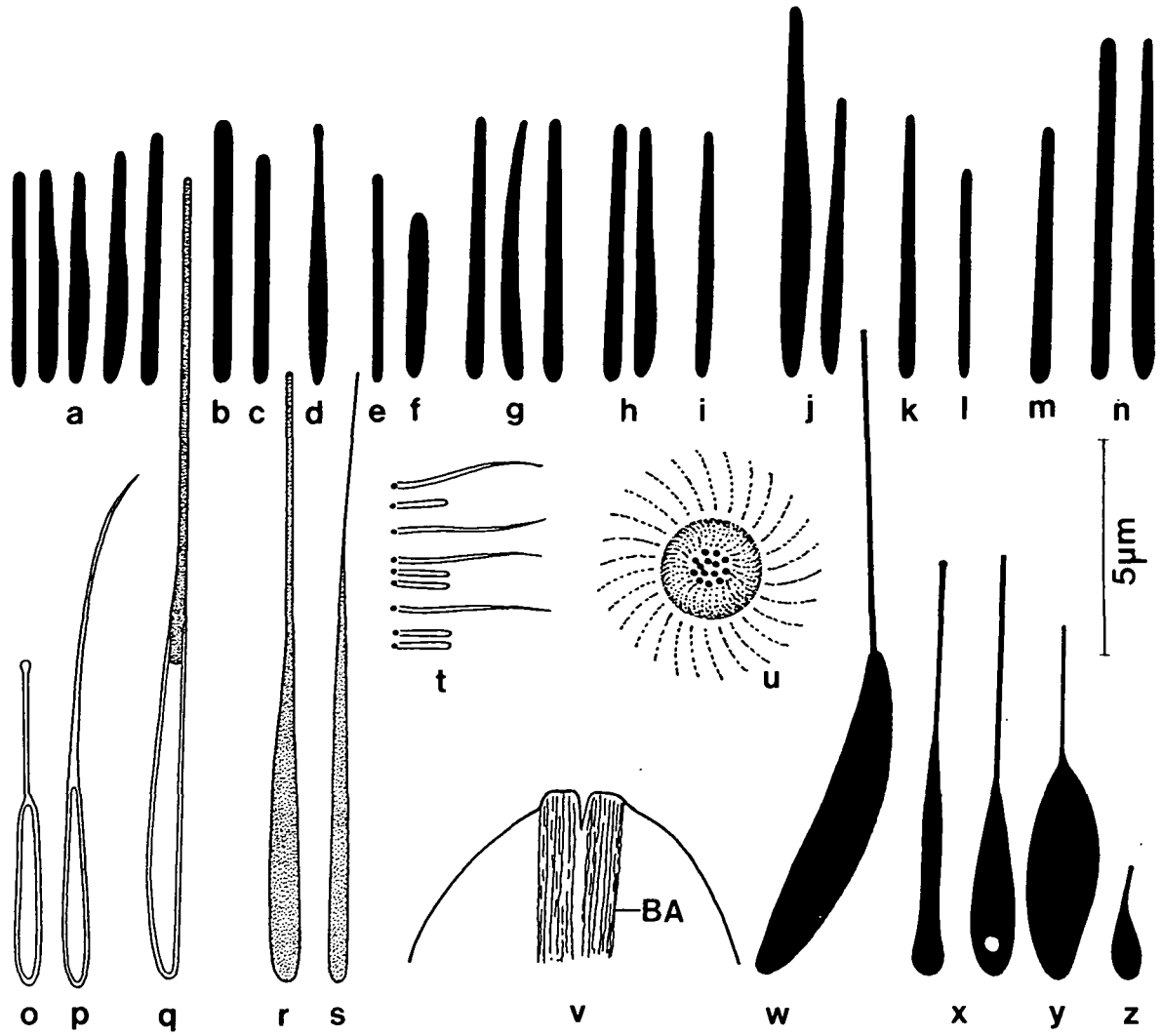

Fig. 11a–v. *Pseudoholophrya terricola* from life. All extrusomes (a–s) drawn to scale (5 µm) to show variability in length and width. The extrusomes of *P. terricola* are toxicysts and rather small (about 6 x 0.6 µm); thus, they are difficult to observe and measure. Accordingly, some subjectivity is unavoidable. Basically, the extrusomes of *P. terricola* are rod-shaped, the variability becomes recognizable only on careful observation. Part of the variability is possibly caused by a slight asymmetry of the toxicysts and by some differences between oral and (developing?) cytoplasmic organelles; furthermore, they become more distinctly acicular shortly before exploding. Thus, the variability shown is likely an over-estimation. However, all these details are difficult to recognize and quantify. The figures are free-hand sketches "polished" by the measurements. **a–n:** Extrusomes of populations from Greece (a; ~ 5–6 x 0.4 µm), Tunisian site 1 (b; length ~ 6 µm), Tunisian site 2 (c; 5–6 x 0.4 µm), Benin (d; ~ 6 x 0.4 µm), Namibian site 23 (e; length ~ 5 µm), Namibian site 30 (f; ~ 4 x 0.4 µm), South African site 35 (g; 5–6 x 0.5 µm), South African site 37 (h; length 5–7 µm), South African site 27 (i; ~ 5–6 x 0.3 µm), Venezuelan site 25 (j; 7–9 × 0.5–0.7 µm), Venezuelan site 60 (k; ~ 6–9 x 0.5 µm), Venezuelan site 15 (l; length 4–5 µm), St. Vincent Island (m; length ~ 6 µm), and Thailand (n; ~ 8–9 x 0.5 µm). **o–s:** Exploded toxicysts from specimens of Namibian site 30 (o; length 8 µm), Greece (p; length 12–15 µm), South Africa (q; ~ 20 x 1 µm), South Africa (r; length 15 µm), and Benin (s; length 15 µm). **t:** Brush portion from a Venezuelan site (60) specimen, bristles about 3 µm long. **u:** Frontal view of oral bulge of specimens from Venezuelan sites (25) and (60). Note that extrusomes are clustered in bulge centre. **v:** After the extrusomes are released, the oral basket (BA) becomes more distinct.

Fig. 11w–z. Extrusomes of *Paraenchelys wenzeli* (w; length ~ 15 µm), → *P. pulchra* and *P. terricola* (x; length ~ 10 µm each), *P. spiralis* (y; length ~ 8 µm), and → *P. brachyarmata* (z; length 2–3 µm). Drawn to scale, also with respect to the extrusomes of *Pseudoholophrya terricola* shown above. Clearly, all extrusomes of *Pseudoholophrya* are basically rod-shaped, while those of *Paraenchelys* are drumstick-shaped.

likely mucocysts, forming a conspicuous sheet; individual granules rather compact and about 0.3 µm across, conspicuous under interference contrast illumination and in the scanning electron microscope (Fig. 10k, l; 301e, h, l, u, v). Cytoplasm colourless, contains many fat globules 1–5 µm across. Likely feeds on ciliates. Swims rapidly by rotation about main body axis, showing conspicuous metachronal ciliary waves (Fig. 10a; 301g). Divides in freely-motile (non-encysted) condition.

Cilia about 11 µm long in vivo and rather closely spaced, form spiral rows; frequently, some rows shortened anteriorly and/or posteriorly, especially in brush area. Dorsal brush inconspicuous, although extending across anterior third of five to eight kineties, because composed of single and paired, only 2–4 µm long bristles interspersed among ordinary cilia (Fig. 10a, e, f, j; 301h, l–p, r–u).

Oral apparatus in anterior pole area, conspicuous due to the pharyngeal extrusome bundle contained; oral bulge, however, only 1–2 µm high and thus hardly recognizable in vivo and protargol preparations. Circumoral kinety at base of oral bulge, likely composed of dikinetids that are difficult to recognize. Oral basket hardly recognizable in vivo unless extrusomes have been released (Fig. 10a, e–i, 11u, v; 301a, e, r).

Observations on other populations: *Pseudoholophrya terricola* has few distinct features and is thus a "difficult" species. The supposed lack of a dorsal brush (BERGER et al. 1984) and the variability of the extrusomes motivated us to study many populations from soils world-wide. This showed: (i) Body shape and size are rather variable and indistinguishable from those of *Paraenchelys* spp., emphasizing the importance of extrusome shape (Fig. 11a–n, w–z); (ii) Although basically rod-shaped, the extrusomes show a variety of shapes (rod-shaped to acicular) and sizes (4–9 × 0.3–0.8 µm) on detailed investigation (Fig. 11a–s; 301a–e, i–k, q, t), but are never drumstick-shaped as in *Paraenchelys* (Fig. 11w–z); (iii) Invariably, the extrusomes form a conspicuous bundle attached to the inconspicuous oral bulge, occupying either the centre or the periphery (Fig. 10a, g, 11u; 301a, d–f, n, t); (iv) The composition and thus distinctiveness of the dorsal brush are highly variable because the number of brush rows varies from about three to eight, and few to many bristles are recognizable under interference contrast illumination in vivo, in good silver preparations, and the scanning electron microscope (Fig. 10a, e, j; 301h, l, n, r, s–u); (v) The nuclear pattern and the dense cortical granulation are very stable (Fig. 10a, e, k, l; 301a, f, u, v).

Occurrence and ecology: *Pseudoholophrya terricola* is a common ciliate in ordinary and saline soils globally (FOISSNER 1998a). However, we cannot exclude that it is a complex of morphospecies/subspecies, as discussed in the following section. Usually, *P. terricola* appears one to two weeks after rewetting a sample, indicating that it is more k- than r-selected.

Comparison with original description and of populations: The identification is very likely correct because all main features match, except for the dorsal brush which is lacking, according to BERGER et al. (1984). However, the brush is extremely difficult to recognize without interference contrast optics and silver carbonate impregnation, two methods not used by BERGER et al. (1984). Thus, it is reasonable to assume that they simply overlooked the dorsal brush. This is substantiated by a reinvestigation of specimens from near the type location. They have the same dorsal brush as the Maldivean specimens.

Table 12. Morphometric data on *Pseudoholophrya terricola* (PTA, PTF, PTM) and *Pseudoholophrya minuta* (PM).

Characteristics [a]	Pop [b]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	PTA	41.2	42.0	7.1	1.7	17.2	30.0	53.0	18
	PTF	53.2	53.0	4.9	1.6	9.2	44.0	61.0	9
	PTM	50.4	50.0	7.0	1.5	13.8	40.0	68.0	21
	PM	28.3	28.0	2.9	0.8	10.2	25.0	34.0	13
Body, width	PTA	24.4	24.5	4.2	1.0	17.2	15.0	31.0	18
	PTF	36.1	36.0	5.7	1.9	15.7	27.0	43.0	9
	PTM	20.8	20.0	4.3	0.9	20.9	16.0	33.0	21
	PM	16.9	17.0	2.1	0.6	12.2	14.0	21.0	13
Anterior body end to macronucleus, distance	PTM	17.2	17.0	3.6	0.8	20.7	11.0	22.0	21
	PM	11.7	11.5	4.1	1.3	34.7	6.0	18.0	10
Macronucleus, length	PTA	15.9	15.0	3.6	1.0	22.6	12.0	25.0	13
	PTF	22.1	23.0	3.7	1.2	16.7	17.0	27.0	9
	PTM	18.5	18.0	2.7	0.6	14.6	15.0	25.0	21
	PM	9.6	10.0	1.4	0.4	14.1	8.0	13.0	11
Macronucleus, width	PTA	12.3	12.0	4.2	1.2	34.3	7.0	20.0	13
	PTF	12.5	13.0	2.5	0.8	20.0	10.0	17.0	9
	PTM	8.1	8.0	1.3	0.3	16.0	7.0	12.0	21
	PM	7.3	7.0	1.0	0.3	13.9	6.0	9.0	11
Micronuclei, length	PTM	2.2	2.0	–	–	–	1.5	2.5	21
	PM	1.6	1.5	–	–	–	1.2	2.0	8
Micronuclei, width	PTM	2.2	2.0	–	–	–	1.5	2.5	21
	PM	1.2	1.0	–	–	–	1.0	1.5	8
Micronuclei, number	PTM	1.9	2.0	0.7	0.2	39.2	1.0	4.0	21
	PM	3.6	3.0	1.8	0.7	51.3	2.0	6.0	8
Oral bulge, diameter	PTF	3.7	3.5	–	–	–	3.0	4.0	9
	PTM	2.9	3.0	0.4	0.1	13.3	2.5	4.0	21
	PM	2.3	2.5	0.4	0.1	18.8	1.5	3.0	13
Somatic kineties, number	PTA [c]	36.9	38.0	4.1	1.1	11.1	30.0	44.0	14
	PTF [c]	33.8	32.0	4.8	1.6	14.2	28.0	45.0	9
	PTM	21.0	20.0	–	–	–	15.0	30.0	21
	PM	14.5	14.0	–	–	–	14.0	16.0	13
Kinetids in mid-body, number in 10 µm	PTM	7.0	7.0	0.9	0.2	12.4	5.0	8.0	21
	PM	7.7	8.0	1.2	1.2	15.4	6.0	10.0	13

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Populations: PM – *Pseudoholophrya minuta* from Namibia, PTA – *Pseudoholophrya terricola* from Austrian Central Alps (from BERGER et al. 1984), PTF – *P. terricola* from a mixed forest in lower Austria (from BERGER et al. 1984), PTM – *P. terricola* from the Maldives, as described in the present monograph.

[c] Values too high, as indicated by the figures. More likely numbers are between 25 and 30. Kinety number is difficult to count due to their spiral course and because they often impregnate poorly, that is, are partially hidden by the cortical granules.

It is much more difficult to answer the question as to whether all populations studied belong to the same species. The differences in the number of ciliary rows (on average 32 and 38 in two populations studied by BERGER et al., only 21 in the Maldivean specimens; likely, BERGER et al. overestimated the number, as indicated by the figures) and brush kineties (2–3 to about 8), as well as in extrusome length (4–9 µm) and shape (rod-shaped to rather distinctly acicular) indicate at least several distinct races. However, all these features are difficult to recognize and quantify, and thus we prefer to put all populations into a single morphotype: *Pseudoholophrya terricola*.

Pseudoholophrya minuta **nov. spec.** (Fig. 12a–f; Table 12)

Diagnosis: Size about 35 × 18 µm in vivo; ellipsoidal. Macronucleus ellipsoidal. Oral extrusomes rod-shaped, fine, about 7 µm long. On average 15 ciliary rows, about half of them differentiated to dorsal brush in anterior two thirds, that is, contain scattered dikinetids with minute bristles.

Type location: Mud from granitic rock-pools in a stream of the Daan Viljoen Game Park near Windhoek, Namibia, 22°35'S 17°05'E (site 73 in figure 2 and chapter 2.1.2).

Etymology: The Latin adjective *minuta* (small) refers to the minuteness of the organism.

Description: Size 30–40 × 15–20 µm in vivo, usually near 35 × 18 µm; length:width ratio 1.3–2.1:1, on average 1.7:1 in protargol preparations. Shape simple, that is, broadly to ordinarily ellipsoidal; unflattened, flexible but acontractile (Fig. 12a, e; Table 12). Macronucleus in or near mid-body, broadly ellipsoidal, dissociated into two to four globules in about half of 30 specimens observed. Micronuclei broadly ellipsoidal, usually near or attached to macronucleus at variable positions. Contractile vacuole in posterior body end, at least one excretory pore in pole centre. Oral bulge extrusomes form conspicuous bundle in anterior pole centre, rod-shaped and very fine, that is, 7–8 × ≤ 0.5 µm. Cortex flexible, hardly furrowed by ciliary rows, contains innumerable granules in indistinct rows, likely mucocysts, forming a conspicuous sheet; individual granules rather refractive and thus distinct (Fig. 12b). Cytoplasm colourless, contains many fat globules up to 5 µm across, indicating a predatory mode of life. Swims rapidly in wide spirals.

Cilia about 10 µm long in vivo and rather closely spaced in anterior body half, arranged in distinctly spiral rows; some rows shortened anteriorly and/or posteriorly. Dorsal brush inconspicuous, although occupying almost half of the body surface, because composed of few dikinetids with about 1 µm long bristles interspersed among ordinary cilia in anterior two thirds of six to eight kineties (Fig. 12a, c, e, f; Table 12).

Oral apparatus in anterior pole area, conspicuous due to the pharyngeal extrusome bundle contained, oral bulge, however, only 1 µm high and thus hardly recognizable in vivo or protargol preparations, like the circumoral kinety and the oral basket (Fig. 12a, e).

Occurrence and ecology: To date found only at type location, where it was rare but present for three weeks in the non-flooded Petri dish culture.

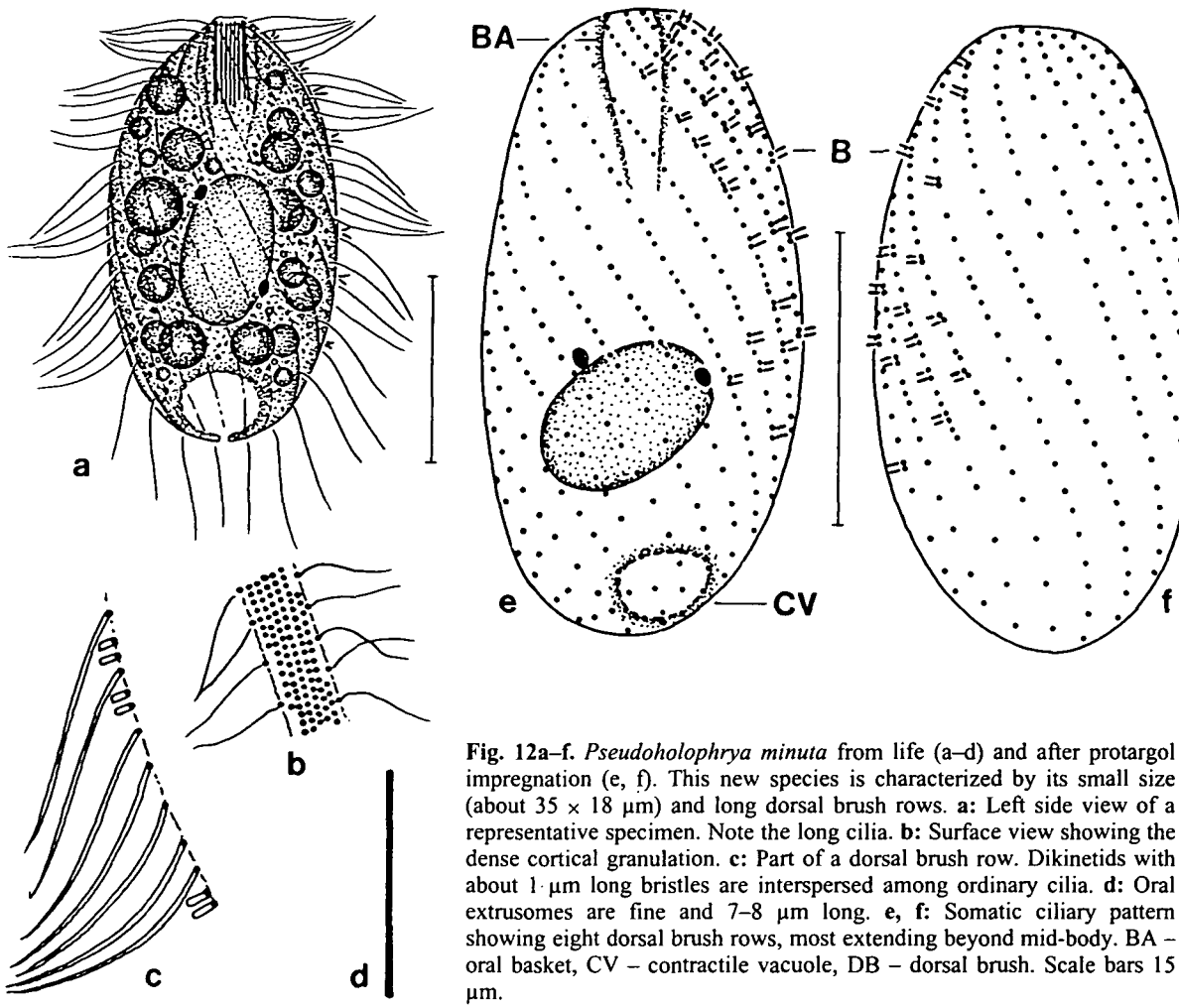

Fig. 12a–f. *Pseudoholophrya minuta* from life (a–d) and after protargol impregnation (e, f). This new species is characterized by its small size (about 35 × 18 µm) and long dorsal brush rows. **a:** Left side view of a representative specimen. Note the long cilia. **b:** Surface view showing the dense cortical granulation. **c:** Part of a dorsal brush row. Dikinetids with about 1 µm long bristles are interspersed among ordinary cilia. **d:** Oral extrusomes are fine and 7–8 µm long. **e, f:** Somatic ciliary pattern showing eight dorsal brush rows, most extending beyond mid-body. BA – oral basket, CV – contractile vacuole, DB – dorsal brush. Scale bars 15 µm.

Comparison with related species: We do not include this population in → *Pseudoholophrya terricola*, although we attribute to this species a profuse variability, because it is distinctly smaller (Table 12) and the dorsal brush rows extend almost to rear body end (Fig. 12f), while they terminate above mid-body in *P. terricola* (Fig. 10e). The cilia, the brush rows, and the extrusomes of *P. minuta* are disproportionally long, that is, about as long as in the larger → *P. terricola*, indicating that all differences are caused by body diminution. Likely, the small size is stable because we observed such specimens for three weeks in the culture and could not find a single large (*P. terricola*-like) individual in vivo or the protargol slides.

Pseudoholophrya spp. are easily confused with *Paraenchelys* spp. (extrusomes drumstick-shaped), *Enchelys* spp. (dorsal brush three-rowed and of ordinary fine structure), *Enchelyodon* spp. (dorsal brush three-rowed and of ordinary fine structure, oral bulge usually distinct), and several other small gymnostomatids. Thus, identification must be based on the unique structure of the dorsal brush.

Enchelys longitricha nov. spec. (Fig. 13a–i; 302a–g; Table 13)

Diagnosis: Size about 150 × 30 µm in vivo; cylindroidal. Macronucleus a long, tortuous strand; on average 9 micronuclei. Extrusomes in a row each between somatic kineties, rod-shaped with narrowed ends, about 6 µm long. On average 18 ciliary rows, 3 differentiated anteriorly to dorsal brush having conspicuous, up to 15 µm long bristles.

Type location: Moderately saline and alkaline (pH 8.1), dark-red sand mixed with some halophyte litter from the surroundings of the village of El Haouaria, about 100 m inshore of Cape Bon, Tunisia, 37°N 13°E.

Etymology: Composite of the Latin adjective *longus* (long) and the Greek adjective *tricho* (hairy), referring to the extraordinarily long brush bristles.

Description: This species is difficult to impregnate, that is, the cortical granules impregnate so intensely that the ciliary pattern is hidden. Thus, we cannot provide full morphometrics and description of the infraciliature. Anyway, the main feature of the species, the long dorsal bristles, must be determined from life.

Size 100–200 × 20–35 µm in vivo, usually near 150 × 30 µm, length:width ratio highly variable, viz., 3.2–9.6:1, on average 5.1:1 in protargol preparations (Table 13). Basically cylindroidal, respectively, very elongate ovoidal with anterior region distinctly narrowed and slightly convex in dorsal brush area (Fig. 13a, b); sometimes slightly curved and/or flattened, acontractile; prepared specimens usually rather distinctly shrunken in anterior and posterior third making cells more or less distinctly fusiform (Fig. 13i). Macronucleus usually in posterior two thirds of cell, highly tortuous and frequently rather distinctly nodular; contains many small, globular nucleoli. Micronuclei globular to ellipsoidal, most rather distant from macronucleus (Fig. 13a, i). Contractile vacuole in posterior end, on average four excretory pores in pole area. Extrusomes in oral bulge and perpendicularly attached to pellicle, forming a meridional row each between two somatic kineties; extrusome rows difficult to recognize in vivo and protargol preparations, but intensely impregnated by silver carbonate (Fig. 13a, d, g; 302a–c). Individual extrusomes 5–7 µm long, rod-shaped with more or less distinctly narrowed ends, stronger curved in population II than I, do not or only faintly impregnate with protargol, except for certain rather intensely impregnated developmental stages in the cytoplasm; released extrusomes acicular and up to 20 µm long (Fig. 13e, f; 302c, g). Cortex very flexible, about 0.8 µm thick, bright, indistinctly furrowed by ciliary rows, contains countless minute (0.2–0.4 µm) granules in closely spaced rows and extrusomes as described above; granules impregnate heavily with protargol, hiding the ciliary pattern (Fig. 13g; 302e–g). Cytoplasm colourless and usually rather opaque due to many fat globules up to 3 µm across. Food not observed and not recognizable in protargol-impregnated specimens, indicating that prey dissolves rapidly. Movement without peculiarities.

Ciliary pattern hidden by the strongly impregnated cortical granules, data thus incomplete (Fig. 13h, i; Table 13). Cilia about 8 µm long in vivo, closely spaced, especially in oral region, arranged in equidistant, longitudinal to slightly spiral rows, three of which anteriorly differentiated to dorsal brush composed of closely spaced, up to 15 µm long bristles forming conspicuous tuft in mid-brush area. Individual brush rows separated by two distinct ridges appearing like an oral slit at a magnification of ×100 (Fig. 13b); rows 1 and 3 shorter than

row 2, row 3, however, extends to mid-body with a monokinetidal tail composed of 1.5 µm long bristles; longest bristles 15 × 1 µm in size, that is, distinctly longer and slightly thicker than the ordinary somatic cilia, occasionally slightly inflated and/or with a thread-like projection distally; do not beat wave-like, but simply back and forth (Fig. 13a, c, h; 302d).

Oral bulge inconspicuous, about 6 µm across and 3 µm high in vivo, centre slightly concave. Details of infraciliature only partially recognizable in the protargol preparations, especially the fine nematodesmata originating from oralized somatic monokinetids in the anterior region of the ciliary rows (Fig. 13h, i; 302a–c). Thus, the oral apparatus is obviously similar to that of *E. geleii*, as redescribed by FOISSNER (2000a).

Occurrence and ecology: To date found at moderately saline (~10‰) Tunisian type location[1], at a site very near to type location[1] (slightly saline, brownish sand mixed with litter from *Erica multiflora* and *Andromeda* sp. about 200 m inshore Cape Bon, pH 7.7), and at Namibian site (53), which is also saline, indicating that *E. longitricha* prefers saline soils.

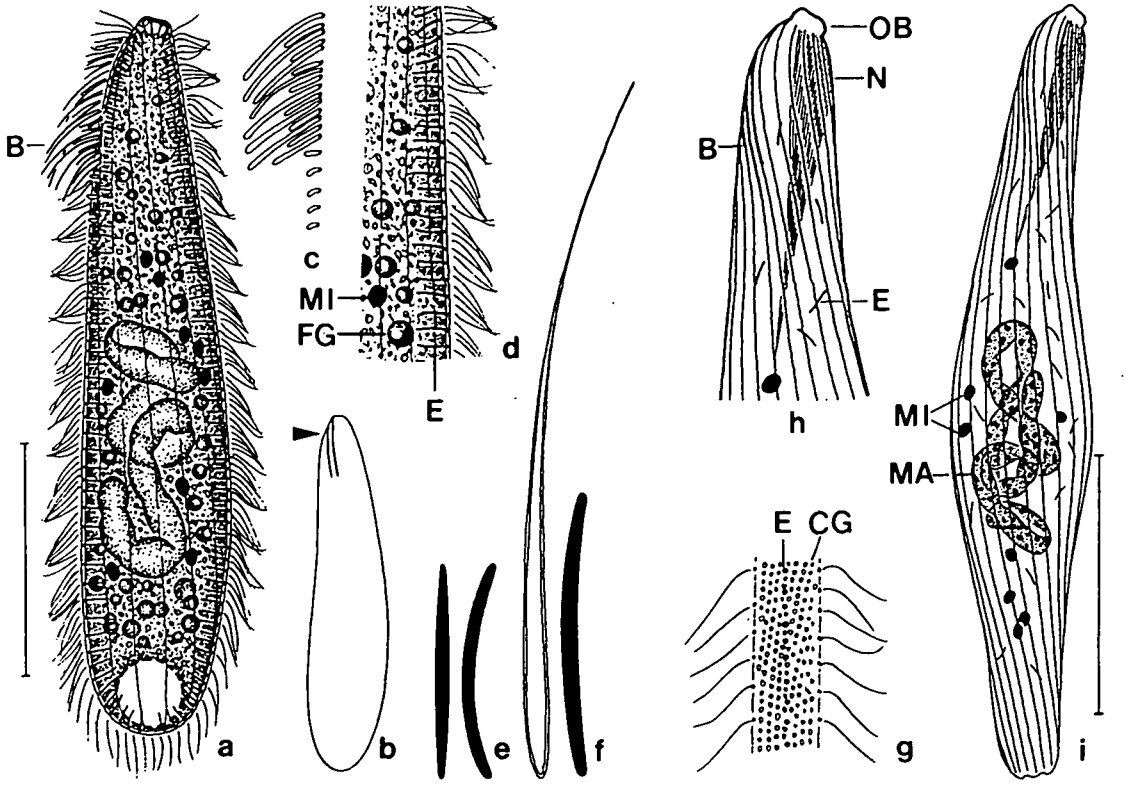

Fig. 13a–i. *Enchelys longitricha* from life (a–g) and after protargol impregnation (h, i). **a, c, d, g:** Right side view of a representative specimen (a) and details showing mid-region of dorsal brush row 3 (c) and the cortex (d, g), which contains a row of extrusomes (E) and several rows of granules (CG) between each two kineties. The dorsal brush bristles (B), which are up to twice as long as the ordinary somatic cilia and thus form a conspicuous tuft, are the main feature of the species. The fine cortical extrusomes (E) are easily overlooked! **b:** Shape variant. The arrowhead denotes the two ridges separating brush rows 2 and 3; at low magnification, the ridges might be misinterpreted as an oral cleft! **e:** Extrusome from Tunisian population II, length 6 µm. **f:** Exploded (15–20 µm) and resting (5–6 µm) extrusomes from Tunisian population I (type). **h, i:** Dorsolateral view of holotype specimen, which shows a distinct nematodesmal bundle produced by fibres originating from the basal bodies of the anterior region of the ciliary rows. B – dorsal brush, CG – cortical granules, E – extrusomes, FG – fat globules, MA – macronucleus, MI – micronucleus, N – nematodesmata, OB – oral bulge. Scale bars 50 µm.

[1] Sample collected by Mag. Aline BERTHOLD.

Comparison with related species: *Enchelys longitricha* is unique by the long cilia of the dorsal brush, a conspicuous feature easy to recognize in vivo. Otherwise, it is highly similar to *E. vermiformis* FOISSNER, 1987b and *E. geleii*, as redescribed by FOISSNER (2000a). As the long dorsal bristles are hardly recognizable in the protargol preparations, live observation is indispensable for identification. In vivo, *E. longitricha* may be confused with → *Enchelyodon* spp. and *Apoenchelys* spp., which, however, lack body extrusomes and long dorsal brush bristles.

Table 13. Comparison of morphometric data on *Enchelys longitricha* (upper line) and *E. geleii* (lower line; from FOISSNER 2000a).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	134.5	132.0	25.4	5.6	18.9	93.0	197.0	21
	133.4	136.0	27.8	7.2	20.8	91.0	185.0	15
Body, width	27.0	27.0	3.6	0.8	13.4	18.0	32.0	21
	29.9	28.0	5.4	1.4	17.9	21.0	43.0	15
Body length:width, ratio	5.1	5.1	1.3	0.3	25.3	3.2	8.6	21
	4.6	5.4	1.4	0.4	29.5	2.3	5.6	15
Oral bulge, width	5.1	5.0	0.7	0.2	13.3	4.0	6.0	21
	5.4	5.0	1.1	0.3	19.6	4.0	8.0	15
Oral bulge, height	2.5	2.5	–	–	–	2.0	3.0	21
	1.8	2.0	–	–	–	1.0	2.0	15
Macronuclear figure, length	43.1	43.0	7.3	1.6	16.9	27.0	60.0	21
	46.3	43.0	12.0	3.1	25.8	32.0	66.0	15
Macronucleus, length (spread) [b]	99.3	100.0	–	–	–	70.0	130.0	21
			not calculated					
Macronucleus, width	5.0	5.0	0.8	0.2	15.5	4.0	7.0	21
	4.6	5.0	0.7	0.2	16.0	3.0	6.0	15
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Micronuclei, length	3.5	3.5	–	–	–	3.0	4.0	21
	2.8	3.0	–	–	–	2.0	3.0	15
Micronuclei, width	2.8	3.0	–	–	–	2.0	3.7	21
	2.4	3.0	–	–	–	2.0	3.0	15
Micronuclei, number	8.6	9.0	2.0	0.4	23.1	6.0	15.0	21
	15.9	16.0	2.8	0.7	17.5	10.0	20.0	15
Somatic ciliary rows, number [b]	18.4	18.0	–	–	–	16.0	20.0	21
	23.5	23.0	1.1	0.3	4.5	22.0	25.0	15
Excretory pores, number [b]	4.3	4.0	–	–	–	3.0	6.0	16
			not investigated					

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Approximations in *E. longitricha*.

Paraenchelys pulchra nov. spec. (Fig. 14a–f; 303a–m; Table 14)

Diagnosis: Size about 90 × 50 µm in vivo; ovate with a length:width ratio near 1.8:1. Extrusomes amphoriform, about 10 µm long. About 60 ciliary rows.

Type location: Highly saline soil from margin of Etosha Pan, Namibia, 19°S 15°50'E (site 54 in figures 2, 3 and chapter 2.1.2).

Etymology: The Latin adjective *pulchra* (beautiful) refers to the pretty shape of the extrusomes.

Description: This species was rare and did not impregnate well with protargol, except for the extrusomes, the main diagnostic feature. Thus, morphometry is incomplete and the description based mainly on live observation and cells impregnated with silver carbonate.

Size 70–110 × 45–55 µm in vivo, usually about 90 × 50 µm; unflattened and acontractile. Ovoidal with narrowly rounded anterior end; occasionally an indistinct shoulder pre-equatorially (Fig. 14a, b). Macronucleus in or near cell centre without any preferred orientation, elongate ellipsoidal to reniform; nucleoli minute. Micronucleus not found. Contractile vacuole in posterior body end. Extrusomes (toxicysts) attached to oral bulge and scattered in cytoplasm, impregnate with protargol and silver carbonate, except for the filiform anterior half, which stains only faintly or not at all; thus extrusomes look different in vivo and silver preparations, although the basic shape is still recognizable in prepared cells (compare Fig. 303i with Fig. 303c, d, f, h, k–m). Fully developed extrusomes found mainly in oral region, 10–12 µm long and basically elongate clavate or amphoriform (Fig. 14d; 303i): globular posterior end about 1 µm across, gradually narrows and then widens to a fusiform mid-portion, which transits into the filiform anterior half with a minute granule at top. Developmental stages in cytoplasm lanceolate or simple club-shaped, similar to ripe extrusomes of *P. terricola* FOISSNER, 1984 (Fig. 14e; 303c, d, f, h, k–m). Cortex very flexible and rather thick because containing closely spaced rows of compact, ellipsoidal granules with a size of about 0.8 × 0.4 µm. Cytoplasm without conspicuous inclusions, usually packed with fat globules up to 10 µm across, indicating a predatory mode of life. Swims rapidly rotating about main body axis.

Somatic ciliary pattern as in congeners (FOISSNER 1984), as evident from silver carbonate-impregnated specimens. About 50–70 rather distinctly spiral ciliary rows and thus very densely ciliated (Fig. 14a; 303a, b, d, e). Dorsal brush in large subapical area, inconspicuous because consisting of minute, scattered kinetofragments, each composed of three to six closely spaced basal bodies bearing 2.5 µm long bristles (Fig. 303d).

Oral area slightly set off from body proper and very small compared to size of cell, that is, only 3–4 µm across; oral opening minute and surrounded by a smooth area. No circumoral kinety recognizable, but likely present, because the 3–4 µm wide pharyngeal basket is rather conspicuous and extends to mid-body (Fig. 14a–c; 303e, g, j).

Occurrence and ecology: To date found at type location and in a soil sample from the margin of a small lake (Sirkelsvlei) near Cape Town, Republic of South Africa. Thus, it is possibly restricted to Africa or Gondwana.

Table 14. Morphometric data on *Paraenchelys pulchra*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	79.8	81.0	9.9	2.6	12.5	60.0	100.0	15
Body, width	45.1	45.0	3.7	1.0	8.2	39.0	52.0	15
Anterior body end to macronucleus, distance	25.7	25.0	5.3	1.4	20.8	14.0	37.0	15
Macronucleus, length	30.5	30.0	3.0	0.8	9.8	26.0	37.0	15
Macronucleus, width	12.2	12.0	1.1	0.3	8.9	10.0	15.0	15

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

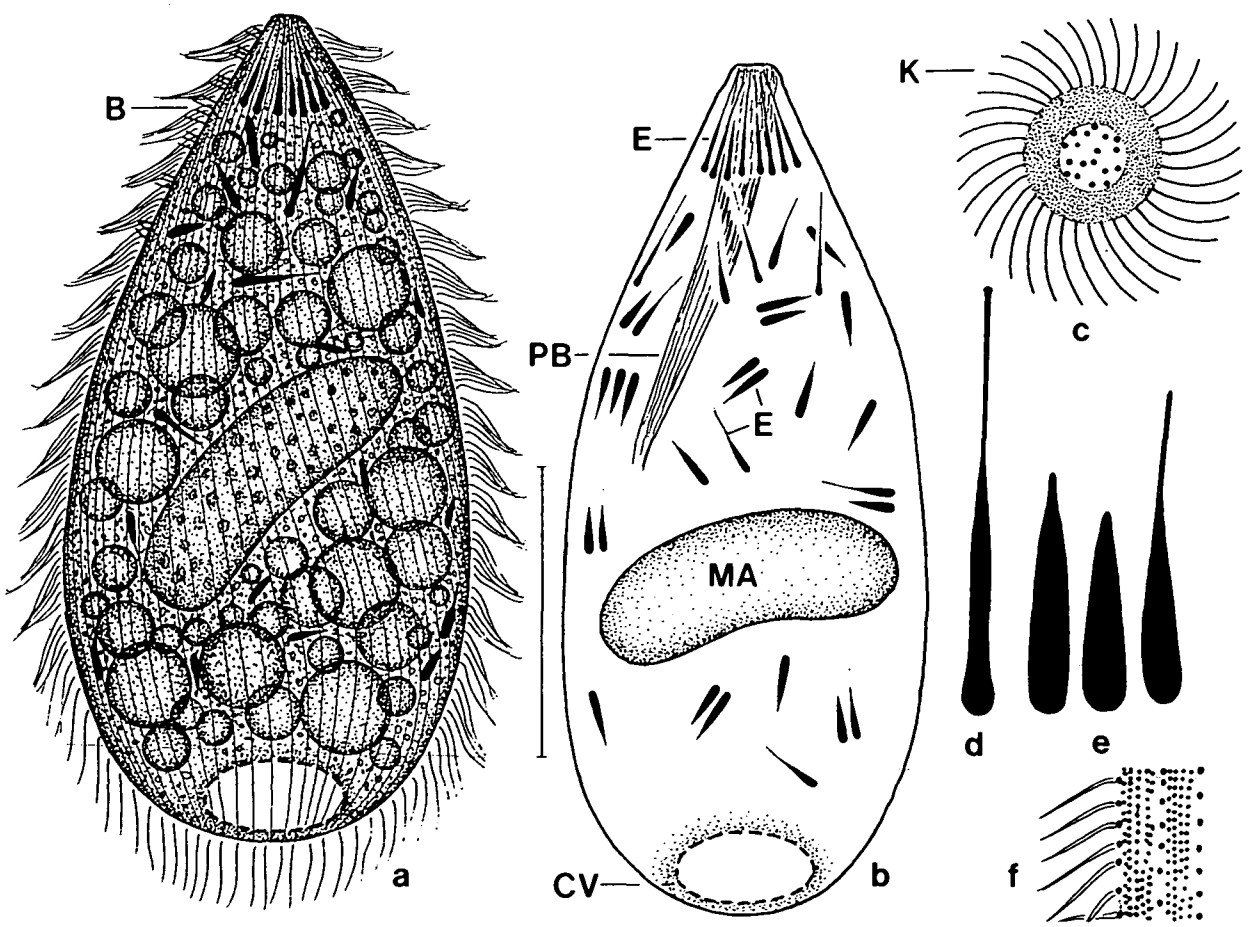

Fig. 14a–f. *Paraenchelys pulchra* from life. **a:** A representative specimen packed with up to 10 µm-sized fat globules. Note the minute and sparse brush cilia in left anterior region. **b:** Shape variant showing main cell organelles. Note that the extrusomes attached to the oral bulge are different in shape and size to those scattered in the cytoplasm. **c:** Anterior polar view. The oral bulge centre contains the extrusome tips and is surrounded by a smooth, unciliated area; both bulge centre and smooth area have a diameter of only about 4 µm. **d:** Fully developed extrusome attached to oral bulge, length 12 µm. **e:** Extrusome developmental stages found in cytoplasm. **f:** Surface view showing dense cortical granulation. B – dorsal brush, CV – contractile vacuole, E – extrusomes, K – ciliary rows, MA – macronucleus, PB – pharyngeal basket. Scale bar 30 µm.

Comparison with related species: *Paraenchelys pulchra* is well-defined by the neatly-shaped extrusomes (simply drumstick-shaped in congeners) and the high number of ciliary rows (50–70 vs. < 40). Body shape and size are similar to those of congeners and → *Pseudoholophrya terricola*. Thus, specimens must be checked for the extrusomes using high magnification.

Paraenchelys brachyarmata **nov. spec.** (Fig. 15a–o; Table 15)

Diagnosis: Size about 80 × 20 µm in vivo; slenderly ovate, that is, length:width ratio about 4:1. Extrusomes numerous and obclavate with short, rod-shaped anterior process, about 2.5 µm long. On average 20 ciliary rows, about 10 anteriorly differentiated to dorsal brush.

Type location: Savannah soil near the village of El Sapo, about 50 km north of Puerto Ayacucho, Venezuela, 07°N 67°W.

Etymology: Composite of the Latin adjectives *brachy* (short) and *armatus* (armed), referring to the minuteness of the extrusomes.

Description: Size 60–100 × 15–30 µm in vivo, usually near 80 × 20 µm; slightly flattened, acontractile. Elongate ovate, that is, length:width ratio about 4:1 in vivo, even more variable and slender in protargol preparations, viz., 2.7–6:1, on average 5:1; often slightly curved and, in protargol preparations, somewhat fusiform (Fig. 15a, j, m; Table 15). Macronucleus in or near centre of cell, elongate ellipsoidal (3:1) to semicircular (4–5:1), ends usually slightly inflated; contains many minute (≤ 2 µm) nucleoli; dissociated into four globules in one out of 60 specimens. Usually one discoidal micronucleus in indentation near or slightly above centre of macronucleus; possibly lacking in some specimens (Fig. 15a, j, o). Contractile vacuole in posterior body end, some excretory pores in pole area. Two to eight extrusomes, likely toxicysts, attached to oral bulge and up to 70 scattered in cytoplasm, except for posterior quarter. Individual extrusomes drop-shaped to claviform with filiform process occupying about half of extrusome length; minute, that is, about 2.5–3 × 0.8 µm in vivo, but strongly refractive and thus rather easy to recognize; look similar in vivo and protargol preparations, where they impregnate intensely, especially the posterior half (Fig. 15a–f, o). Cortex flexible, contains innumerable, colourless, minute (≤ 0.2 µm) granules in distinct rows; covered by bacterial rods in most Venezuelan specimens (Fig. 15g, h). Cytoplasm colourless, contains some fat globules 1–2 µm across and many about 5 µm-sized food vacuoles with spongy, indeterminable content; prey obviously quickly digested because not identifiable in the 60 protargol-impregnated specimens investigated. Swims rather rapidly by rotation about main body axis.

Cilia about 7 µm long in vivo, rather closely spaced in oral and brush area, form bipolar, distinctly spiralling rows slightly more closely spaced in brush region. Seven to twelve rows modified to indistinct dorsal brush anteriorly; brush as in congeners, that is, composed of many minute, slightly scattered kinetofragments, likely bearing minute bristles interspersed among ordinary cilia, as described in → *Pseudoholophrya terricola*. Kinetids associated with a fibre extending posteriorly at right side of kineties (Fig. 15a, j, k, m, n; Table 15).

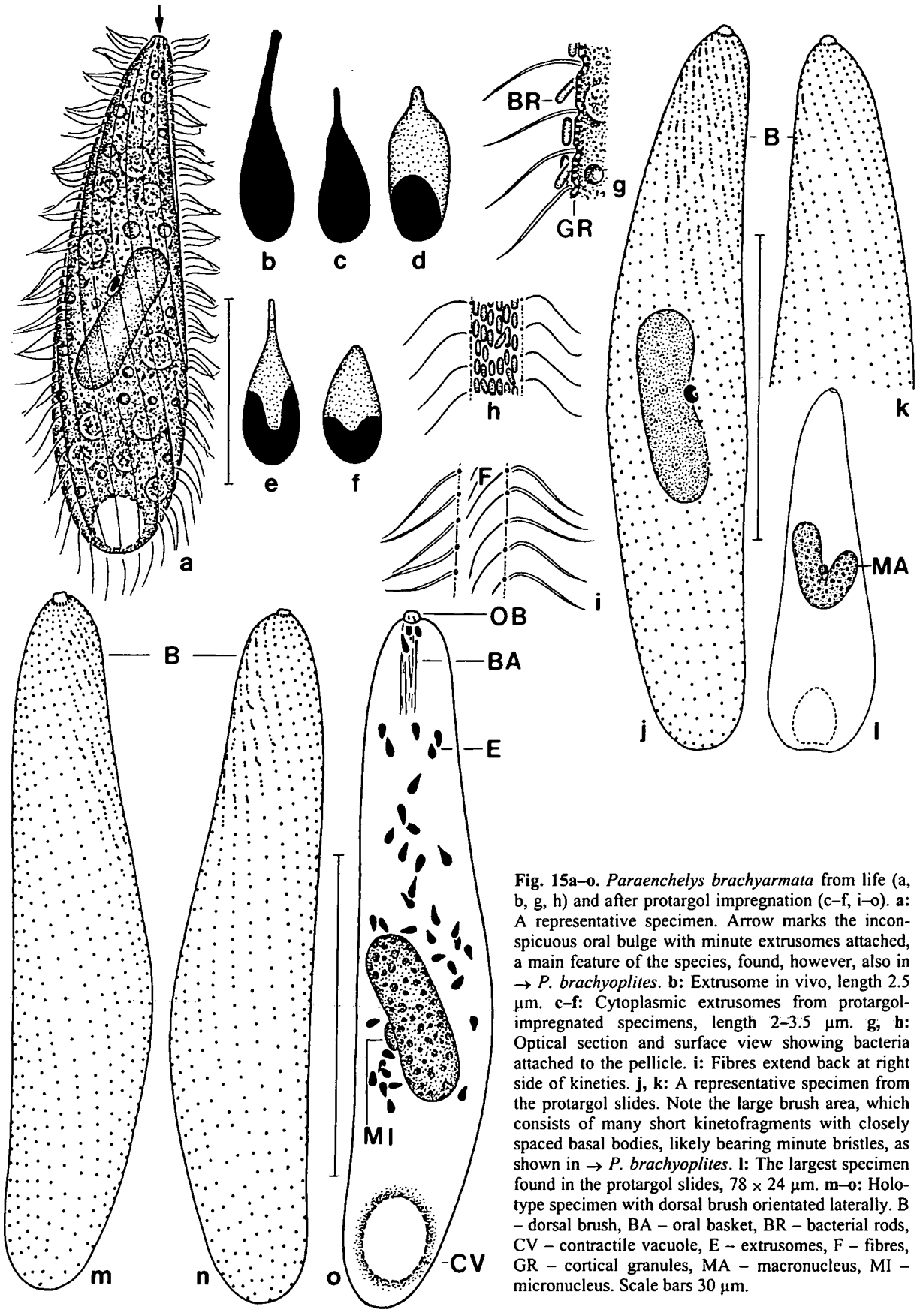

Fig. 15a–o. *Paraenchelys brachyarmata* from life (a, b, g, h) and after protargol impregnation (c–f, i–o). **a:** A representative specimen. Arrow marks the inconspicuous oral bulge with minute extrusomes attached, a main feature of the species, found, however, also in → *P. brachyoplites*. **b:** Extrusome in vivo, length 2.5 µm. **c–f:** Cytoplasmic extrusomes from protargol-impregnated specimens, length 2–3.5 µm. **g, h:** Optical section and surface view showing bacteria attached to the pellicle. **i:** Fibres extend back at right side of kineties. **j, k:** A representative specimen from the protargol slides. Note the large brush area, which consists of many short kinetofragments with closely spaced basal bodies, likely bearing minute bristles, as shown in → *P. brachyoplites*. **l:** The largest specimen found in the protargol slides, 78 × 24 µm. **m–o:** Holotype specimen with dorsal brush orientated laterally. B – dorsal brush, BA – oral basket, BR – bacterial rods, CV – contractile vacuole, E – extrusomes, F – fibres, GR – cortical granules, MA – macronucleus, MI – micronucleus. Scale bars 30 µm.

Oral area occupying anterior body end, minute, likely surrounded by a dikinetidal circumoral kinety associated with long, fine nematodesmata forming inconspicuous oral basket hardly recognizable in live specimens. Oral bulge extremely minute, that is, about 3 µm across and 1–1.5 µm high, has attached a bundle of extrusomes diverging posteriorly (Fig. 15a, j, k, m–o).

Occurrence and ecology: To date found at type location and Namibian site (4), that is, the floodplain of a river. The type location is in the floodplain of the Orinoco. Thus, *P. brachyarmata* is probably not a strictly edaphic species. Very recently, we found this species in a forest soil of Austria, showing our ignorance of even the European soil ciliate biota. Thus, *P. brachyarmata* is likely a cosmopolitan.

Comparison with related species: *Paraenchelys brachyarmata* differs from the congeners by the slender shape (4:1 vs. 1.6–2.3:1) and the low number of ciliary rows (about 20 vs. 30–70). Further, the extrusomes are distinctly smaller than in the other species (2–3 µm vs. 8–15 µm), except for → *P. brachyoplites*. See FOISSNER (1983b, 1984), SONG & WILBERT (1989), and the present book for description of other species. Take care not to confuse it with slender specimens of → *Pseudoholophrya*, which have rod-shaped extrusomes.

Table 15. Morphometric data on *Paraenchelys brachyarmata*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	71.1	72.0	6.2	1.4	8.7	58.0	78.0	21
Body, width	15.9	15.0	3.8	0.8	23.6	11.0	24.0	21
Body length:width, ratio	4.7	5.0	1.0	0.2	20.5	2.7	6.0	21
Oral basket (bulge), diameter at distal end	2.3	2.0	–	–	–	2.0	3.0	21
Anterior body end to macronucleus, distance	28.3	28.0	6.4	1.4	22.5	10.0	36.0	21
Macronucleus, length (spread) [b]	21.2	20.0	4.4	1.0	20.6	17.0	36.0	21
Macronucleus, width	6.2	6.0	0.5	0.1	8.6	5.0	7.0	21
Micronucleus, maximum size	2.6	3.0	–	–	–	2.0	3.0	19
Extrusomes, total length	2.5	3.0	–	–	–	2.0	3.5	21
Extrusomes, maximum width	1.0	1.0	–	–	–	0.8	1.2	21
Macronuclei, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Micronuclei, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	17
Extrusomes, number	50.6	50.0	11.6	2.5	23.0	30.0	70.0	21
Ciliary rows, number [c]	20.7	20.0	–	–	–	12.0	26.0	21
Kinetids in a ventral kinety, number	56.2	56.0	8.9	1.9	15.8	40.0	70.0	21

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] If curved, it was extended artificially; values thus approximations.

[c] Approximations because difficult to count due to the spiral course.

Paraenchelys brachyoplites nov. spec. (Fig. 16a–m; Table 16)

Diagnosis: Size about 90 × 40 µm in vivo; ovate with a length:width ratio near 2.3:1. Macronucleus almost globular. Extrusomes obclavate, 2–3 × 0.7–1 µm. On average 26 ciliary rows, about 8 anteriorly differentiated to a dorsal brush.

Type location: Soil from the surroundings of the Ameib Guest Farm, Namib Escarpment, Namibia, 21°50'S 15°35'E (site 43 in figure 2 and chapter 2.1.2).

Etymology: Composite apposition of the Latin adjective *brachy* (short) and the Greek noun *hoplites* (soldier ~ extrusome), referring to the minuteness of the extrusomes.

Description: Size 60–110 × 25–60 µm in vivo, usually near 90 × 40 µm; up to 2:1 flattened, acontractile. Ovate to obclavate and occasionally rather distinctly curved in narrow-side view, body length:width ratio highly variable, that is, 1.5:1 – 3.5:1, on average near 2.3:1 both in vivo and protargol preparations (Fig. 16a–e; Table 16). Macronucleus usually near or in body centre, globular to ellipsoidal (2:1), on average 17 × 13 µm in protargol preparations, fragmented into four globular nodules in one specimen; nucleoli pale in vivo, globular to lobate after protargol impregnation. A single micronucleus seen in a middle divider, does not impregnate with the protargol method used in morphostatic specimens. Contractile vacuole in posterior body end. Extrusomes attached to oral bulge and scattered in cytoplasm, obclavate without filiform process, only 2–3 × 0.7–1 µm in size but compact and thus fairly distinct in vivo; do not impregnate with the protargol method used; extruded toxicysts very transparent, with 2–3 µm long, filiform process (Fig. 16j–m). Cortex very flexible, contains innumerable, colourless, minute (≤ 0.3 µm) granules forming conspicuous, closely spaced rows. Cytoplasm colourless, packed with fat globules 1–3 µm across and 5–7 µm-sized food vacuoles containing bacterial remnants. Glides and swims rather rapidly by rotation about main body axis.

Cilia about 9 µm long in vivo, closely spaced, especially in oral and brush area, form bipolar, distinctly spiralling rows slightly more closely spaced in brush region; some kineties slightly shortened anteriorly and/or posteriorly. About eight rows modified to indistinct dorsal brush anteriorly; brush as in congeners and → *Pseudoholophrya terricola*, that is, composed of many minute, slightly scattered kinetofragments bearing 1–5 µm long bristles interspersed among ordinary cilia (Fig. 16a, f–h; Table 16).

Oral area occupying anterior body end, minute, likely surrounded by a dikinetidal circumoral kinety associated with long, fine nematodesmata forming inconspicuous oral basket hardly recognizable in live specimens. Oral bulge extremely minute, that is, about 3 µm across and 1 µm high, has a bundle of posteriorly slightly diverging extrusomes attached (Fig. 16a, f, g; Table 16).

Occurrence and ecology: To date found in the sandy soil of the type location; in South Africa (sandy forest soil in the Hluhluwe Game Reserve, picnic site near crocodile pool; Fig. 16e); and in a sandy, slightly saline soil (pH 7.7) near the village of Nyalam Togmy, Tibet, 5120 m above sea-level in the cushion plant zone (sample kindly collected by Dr. Norbert WINDING, Salzburg). Possibly, *P. brachyoplites* prefers sandy soils.

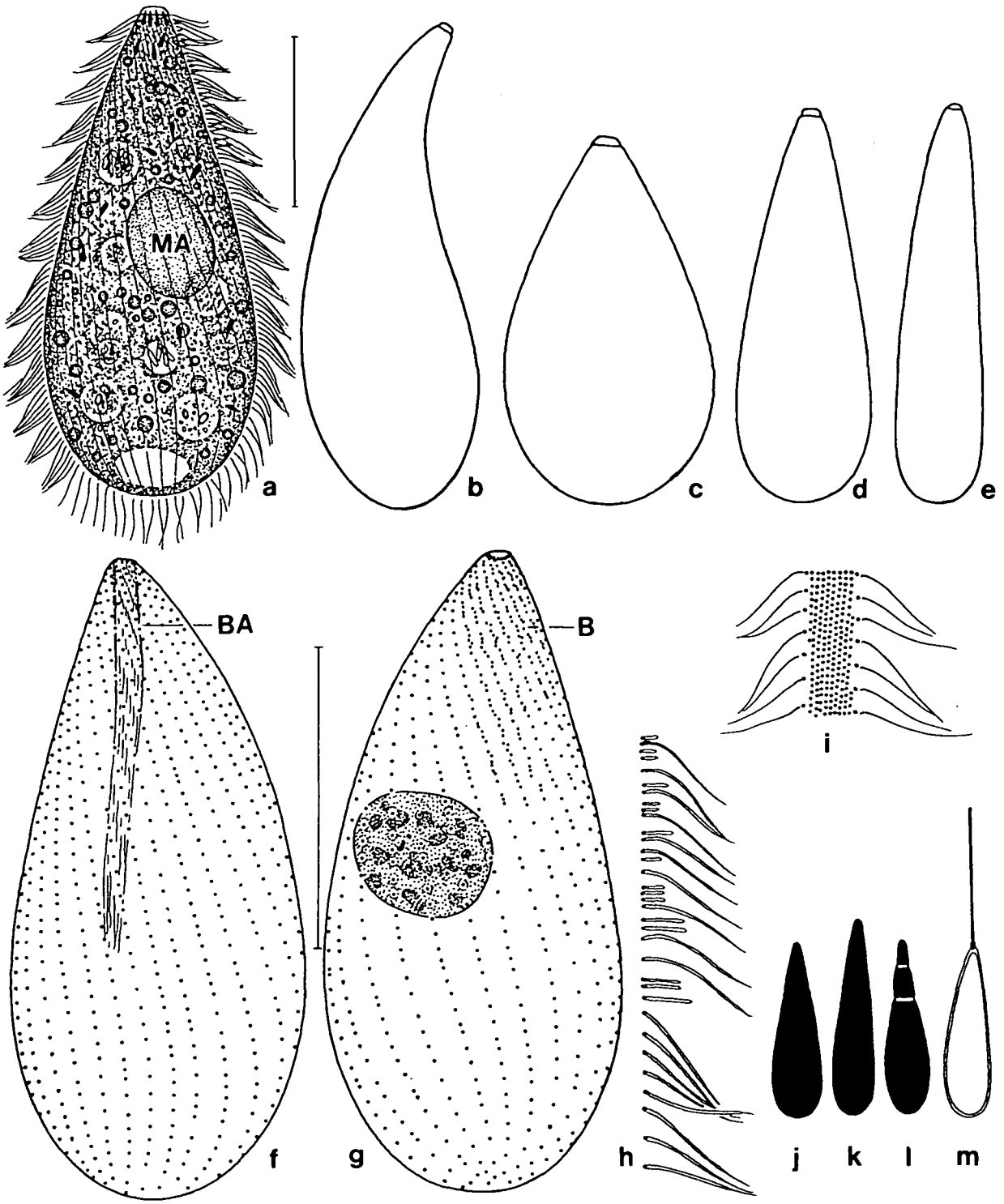

Fig. 16a–m. *Paraenchelys brachyoplites* from life (a–e, h–m) and after protargol impregnation (f, g). **a, b:** Broad and narrow-side view of a representative, slightly flattened specimen. **c, d:** Extreme shape variants. **e:** A very slender South African specimen. **f–h:** Ciliary pattern and nuclear apparatus of holotype specimen. The dorsal brush (B) consists of about eight rows of closely spaced, slightly irregularly arranged kinetids, many of which have shortened cilia (h). **i:** Surface view showing dense cortical granulation. **j, k:** Oral extrusomes, length 2.5–3 μm. **l:** An extrusome with two minute constrictions. **m:** Exploded extrusome, length about 5 μm. B – dorsal brush, BA – oral basket, MA – macronucleus. Scale bars 30 μm.

Table 16. Morphometric data on *Paraenchelys brachyoplites* (upper line) and *Paraenchelys terricola* (lower line) from Namibian site (43).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	79.3	80.0	9.4	2.4	11.9	57.0	95.0	16
	78.7	81.0	12.5	3.0	15.9	55.0	95.0	17
Body, width	37.6	36.0	9.5	2.4	25.3	25.0	58.0	16
	29.1	29.0	5.2	1.3	17.8	19.0	39.0	17
Body length:width, ratio	2.3	2.1	0.5	0.1	23.8	1.5	3.5	16
	2.8	2.9	0.7	0.2	23.4	1.4	3.8	17
Oral basket (bulge), diameter at distal end	3.1	3.0	–	–	–	2.5	4.0	16
	2.5	2.0	–	–	–	2.0	4.0	15
Anterior body end to macronucleus, distance	30.9	31.5	7.6	1.9	24.6	14.0	43.0	16
	24.3	23.0	8.1	2.0	33.5	10.0	40.0	17
Macronuclear figure, length	17.7	17.0	3.4	0.8	19.1	14.0	27.0	17
	27.0	27.0	5.9	1.4	21.8	15.0	35.0	17
Macronucleus, length (spread) [b]	17.7	17.0	3.4	0.8	19.1	14.0	27.0	17
	29.2	27.0	–	–	–	15.0	35.0	17
Macronucleus, width	12.7	13.0	2.2	0.5	17.2	9.0	17.0	17
	8.1	8.0	1.1	0.3	13.7	6.0	10.0	17
Macronucleus spread length:width, ratio	1.4	1.4	0.3	0.1	23.0	1.0	2.1	17
	3.6	3.9	0.9	0.2	23.9	1.9	5.0	17
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	17
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	17
Ciliary rows, number [c]	25.7	26.0	–	–	–	23.0	29.0	15
	23.9	23.0	–	–	–	20.0	28.0	7
Brush rows, number [c]	8.3	8.0	–	–	–	7.0	10.0	12
	12.4	12.0	–	–	–	10.0	15.0	8
Kinetids in a ventral kinety, number	80.0	77.5	19.3	6.1	24.1	60.0	120.0	10
	47.0	40.0	12.1	5.4	25.6	35.0	60.0	5

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Rough estimation.

[c] Approximations because difficult to count due to the spiral course.

Generic classification and comparison with related species: *Paraenchelys* has been diagnosed as having drumstick-shaped extrusomes, while those of *P. brachyoplites* are obclavate, that is, lack a filiform process. This could be considered as sufficient to separate this species at genus level because extrusome shape is an important feature. However, the extrusomes of *P. brachyoplites* are obviously the end of an evolutionary line ranging from *P. wenzeli*, which has large (15 µm) extrusomes with a conspicuous process, over → *P. brachyarmata*, where the extrusomes are as small as in *P. brachyoplites*, but still have a minute process.

Paraenchelys brachyoplites is likely most closely related to → *P. brachyarmata*, differing mainly in the shape of the body (broadly vs. slenderly ovate), the extrusomes (without vs. with filiform process), and the macronucleus (broadly vs. elongate ellipsoidal). Admittedly, these differences are not very conspicuous, but the best we have in this feature-poor group of ciliates.

Paraenchelys terricola FOISSNER, 1984 occurs in the same sample, differing from *P. brachyoplites* by the oblong macronucleus (29 × 8 µm; Table 16) and the protargol-affine, cytoplasmic extrusomes, which show a variety of shapes and sizes (3–9 µm), indicating that they are developmental stages. In vivo, the oral extrusomes are as described by FOISSNER (1984), that is, drumstick-shaped, 8–10 µm long, and contain a minute granule posteriorly.

Apoenchelys nov. gen.

Diagnosis: Enchelyidae with meridional ciliary rows more or less distinctly curved anteriorly; 2 rows differentiated to dorsal brush. Oral bulge cylindroidal, opens centrally. Nematodesmal bundles originate from ciliated oralized somatic monokinetids in anterior region of ciliary rows.

Type species: *Apoenchelys bamforthi* nov. spec.

Etymology: Composite of the Greek prefix *apo* (derived from) and the Greek generic name *Enchelys* (eel, referring to the oblong body), referring to the presumed nearest relative. Feminine gender.

Comparison with related genera: The oral basket of *A. bamforthi* consists of nematodesmata originating from the monokinetids in the anterior region of the somatic kineties, while oral dikinetids contribute to the basket of the → Fuscheriidae and → Acropisthiidae. Thus, *Apoenchelys* belongs to the family Enchelyidae EHRENBERG, as defined by FOISSNER (1984), specifically, it is related to *Enchelys*, differing mainly by the number of dorsal brush rows, viz., two vs. three. Admittedly, this is a rather inconspicuous generic feature which, however, likely represents a distinct evolutionary branch because the fairly large size of *A. bamforthi* excludes simple spatial constraints. The five *Enchelys* species investigated in detail so far not only have three dorsal brush rows but also rod-shaped extrusomes (FOISSNER 1984, 1987b, BERGER et al. 1984), while those of *A. bamforthi* are acicular, a difference probably also of generic significance.

Apoenchelys bamforthi nov. spec. (Fig. 17a–i; Table 17)

Diagnosis: Size 145 × 30 µm in vivo; obclavate. 2 globular, almost abutting macronuclear nodules with 1 micronucleus in between. Extrusomes acicular, about 5 µm long. On average 14 ciliary rows and 17 dikinetids each in dorsal brush rows 1 and 2.

Type location: Mud and soil from granitic rock-pools of the Spitzkoppe, an inselberg in the Namib Escarpment, Namibia, 21°45'S 15°8'E (site 41 in figure 2 and chapter 2.1.2).

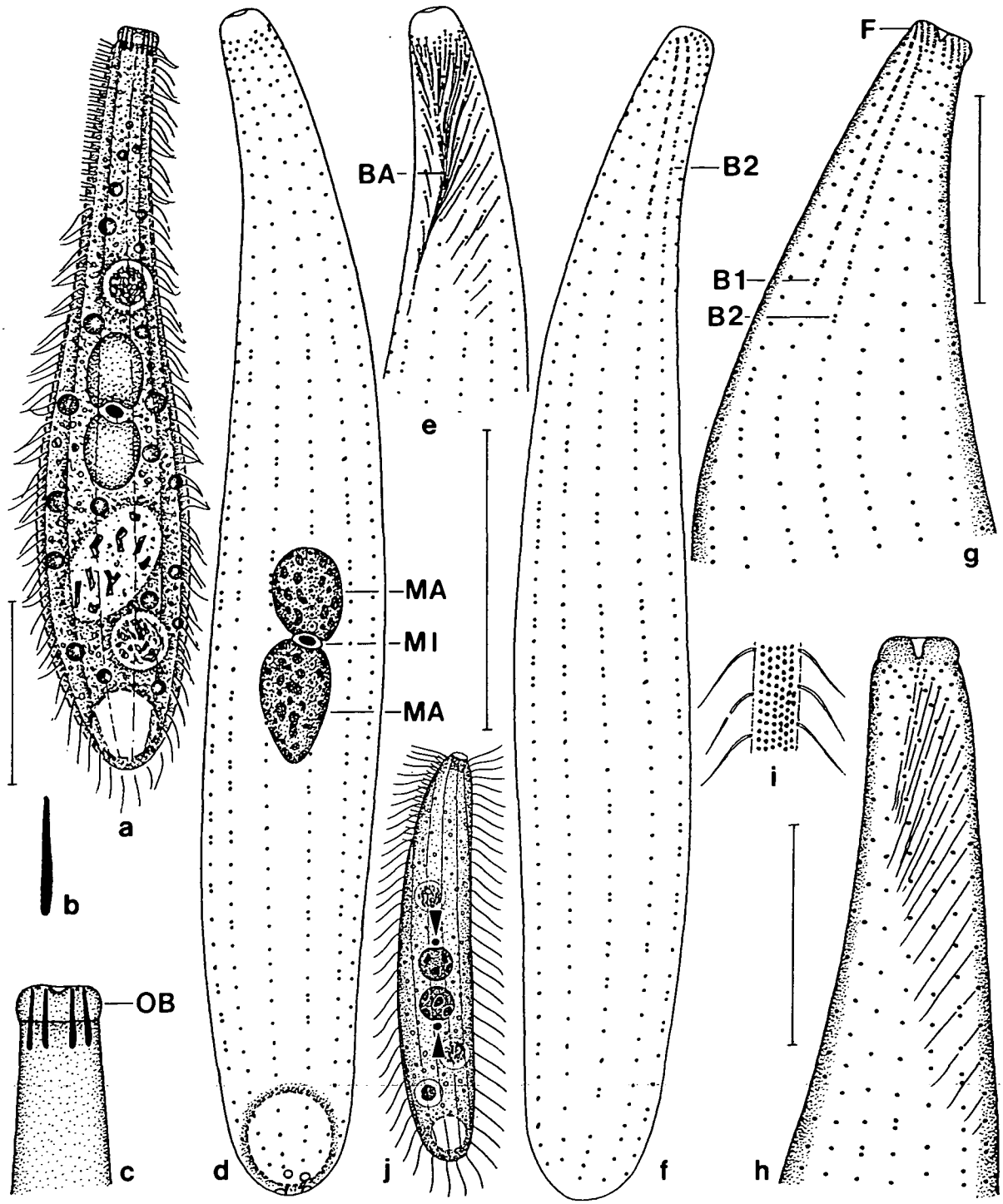

Fig. 17a–i. *Apoenchelys bamforthi* from life (a–c, i) and after protargol impregnation (d–h). **a:** Right side view of a representative specimen with a large vacuole containing crystalline remnants from a hypotrichous ciliate. **b, c:** Extrusomes are attached to the oral bulge and about 5 µm long. **d–f:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. **g, h:** Dorsal and lateral view of other specimens. *Apoenchelys* is characterized by having two dorsal brush rows and lacking oral dikinetids. Oral basket rods originate from the monokinetids of the anterior region of the ciliary rows (h, shown for one kinety). **i:** Surface view showing cortical granulation. BA – oral basket, B1, 2 – dorsal brush rows, F – bulge fibres, MA – macronuclear nodules, OB – oral bulge. Scale bars 35 µm (a, d–f) and 20 µm (g, h).

Fig. 17j. *Enchelys binucleata* FOISSNER, 1983b from life, length 70 µm. Arrowheads mark the opposed micronuclei.

Dedication: This new species is named in honour of Prof. Dr. Stuart S. S. BAMFORTH, Tulane University, USA, who dedicated a lifetime's research to soil protozoa.

Description: Size 100–200 x 20–40 µm in vivo, usually about 145 x 30 µm, length:width ratio also highly variable, viz., 3.4–6.7:1, on average near 5:1 in vivo and protargol preparations. More or less pronounced obclavate with anterior end distinctly narrower than widest subequatorial body portion; unflattened and acontractile. Nuclear apparatus near or in mid-body, conspicuous because composed of two almost abutting, globular to broadly ellipsoidal macronuclear nodules and an ellipsoidal micronucleus in between; nucleoli scattered, numerous, globular (Fig. 17a, d; Table 17). Contractile vacuole in posterior body end, several excretory pores in posterior pole area. Extrusomes attached to oral bulge, acicular, about 5 µm long, difficult to recognize because rather transparent; do not impregnate with the protargol method used (Fig. 17a–c). Cortex flexible, contains closely spaced rows of colourless granules about 1 µm across. Cytoplasm colourless, contains some fat globules up to 5 µm across and small and large food vacuoles with remnants of naked amoebae and ciliates. Swims rather rapidly by rotation about main body axis.

Table 17. Morphometric data on *Apoenchelys bamforthi*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	130.8	130.0	25.5	7.7	19.5	93.0	185.0	11
Body, width	27.7	29.0	6.6	2.0	23.9	17.0	36.0	11
Body length:width, ratio	4.9	5.0	1.2	0.4	23.7	3.4	6.7	11
Oral bulge, width	6.5	7.0	0.9	0.3	14.5	5.0	8.0	11
Oral bulge, height	2.5	2.0	–	–	–	2.0	3.0	11
Anterior body end to end of brush row 1, distance	32.4	31.0	4.7	1.4	14.6	24.0	39.0	11
Anterior body end to end of brush row 2, distance	32.0	31.5	6.1	1.9	19.5	23.0	40.0	11
Anterior body end to macronuclear figure, distance	63.1	60.0	16.5	5.0	26.2	41.0	95.0	11
Nuclear figure, length	25.5	26.0	5.2	1.6	20.6	17.0	32.0	11
Anterior macronuclear nodule, length	12.6	14.0	2.8	0.9	22.5	8.0	17.0	11
Anterior macronuclear nodule, width	9.7	10.0	1.6	0.5	16.6	7.0	12.0	11
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
Micronucleus, length	2.1	2.1	–	–	–	1.8	2.5	6
Micronucleus, width	1.4	1.4	–	–	–	1.0	2.0	6
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10
Somatic kineties, number	13.6	14.0	1.8	0.5	12.9	11.0	16.0	11
Ciliated kinetids in a ventral kinety, number	53.6	58.0	14.5	4.4	27.1	27.0	73.0	11
Dikinetids in brush row 1, number	16.5	17.0	3.5	1.1	21.3	9.0	21.0	11
Dikinetids in brush row 2, number	16.7	17.0	4.2	1.3	25.4	10.0	23.0	11
Dorsal brush rows, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

On average 14 bipolar, equidistant ciliary rows slightly curved anteriorly (Fig. 17d–h; Table 17); two rows anteriorly differentiated to dorsal brush, both of about same length and composed of an average of 17 comparatively widely spaced dikinetids. Bristles not studied in detail.

Oral bulge occupies anterior body end, cylindroidal and about 8 µm wide in vivo, indistinctly set off from body proper but fairly conspicuous because about 3 µm high and distinctly depressed in centre; contains fibres originating from the anterior basal body of the ciliary rows, as, for instance, in → *Sikorops*. No circumoral kinety. Oral basket weir-like, made by fine, moderately long nematodesmata originating from 10–15 monokinetids in anterior region of each somatic and brush row.

Occurrence and ecology: To date found at type location, a semiterrestrial habitat, and in a forest soil from the east slope of Mt. Kenya near the town of Nanyuki. *Apoenchelys bamforthi* was very rare in both samples (one specimen per slide).

Comparison with related species: There is only one species with a similar nuclear configuration, viz., *Enchelys binucleata* FOISSNER, 1983b, a limnetic, up to 75 µm long species with a micronucleus each attached to the abutting macronuclear nodules (Fig. 17j). No similar species occur in related genera. However, there are several *Enchelyodon* species and lacrymariids with a similar or identical nuclear configuration: all have a different size, shape, and/or oral bulge.

Obliquostoma nov. gen.

Diagnosis: Enchelyidae, as defined by FOISSNER & FOISSNER (1988), with 2 dorsal brush rows and oblique oral bulge containing fibres originating from a ring of minute granules at bulge base. Extrusomes punctate.

Type species: *Obliquostoma enchelyodontides* nov. spec.

Etymology: Composite apposition of the Latin adjective *obliquo* (oblique) and the Greek noun *stoma* (mouth), referring to the oblique oral bulge. Neuter gender.

Comparison with related genera: The Enchelyidae have the oral basket composed of fibres originating from oralized somatic monokinetids at the anterior end of the somatic kineties; a circumoral kinety composed of dikinetids with nematodesmata, so typical for many gymnostomes, is absent (FOISSNER & FOISSNER 1985, 1988). Detailed data are available on several *Enchelys* species showing that all have three dorsal brush rows; a rather inconspicuous, ordinary oral bulge; and rod-shaped extrusomes (FOISSNER 1984, 1987b, 2000a). Thus, the Namibian population, which has two brush rows, an oblique oral bulge, and ellipsoidal extrusomes, is referred to a new genus, *Obliquostoma*.

Certainly, *Obliquostoma* has considerable similarities with → *Sikorops*, especially in possessing distinct bulge fibres. But *Obliquostoma* is unique in that the bulge fibres originate only from a ring of minute, lightly impregnating granules, likely not basal bodies. Such granules and fibres are present also in *Sikorops*, which has, however, an additional fibre originating from the kinetid, likely a dikinetid, at the anterior end of the ciliary rows (cp. Fig.

18j, k). Unfortunately, bulge fibres have not been described in *Enchelys* spp. We re-studied the slides from *E. gasterosteus* and *E. polynucleata*, both described in FOISSNER (1984; note that *E. polynucleata* was wrongly assigned to the genus *Enchelydium* in this study). Neither bulge fibres, nor a lightly impregnated granule ring, so typical for *Obliquostoma*, are recognizable, but transmission electron microscopy shows fibres originating from the anteriormost basal body of each ciliary row (FOISSNER & FOISSNER 1985). Thus, *Obliquostoma* must be considerably different from *Enchelys*. This needs, however, substantiation by electron microscopy.

Obliquostoma enchelyodontides **nov. spec.** (Fig. 18a–j; 304a–i; Table 18)

Diagnosis: Size about 55 × 18 µm in vivo; oblong with oral bulge occupying one quarter of widest trunk region. Macronucleus C-shaped. Micronucleus about 5 µm across, attached to anterior end of macronuclear figure. Ripe extrusomes broadly fusiform, about 2 × 1 µm. On average 16 ciliary rows. Brush row 1 about twice as long as row 2, consists of an average of 11, respectively, 5 dikinetids.

Type location: Soil from the surroundings of the Ameib Guest Farm, Namib Escarpment, Namibia, 21°50'S 15°35'E (site 43 in figure 2 and chapter 2.1.2).

Etymology: Composite of *Enchelyodon* and the Greek suffix *ides* (look like), referring to the similarity with species of the genus *Enchelyodon*.

Description: Size 45–65 × 15–22 µm in vivo, usually near 55 × 18 µm, laterally slightly flattened, up to 20% contractile under mild cover glass pressure. Shape inconspicuous, that is, elongate ovate and slightly asymmetrical (Fig. 18a, e; 304a, c, e; Table 18). Macronucleus on average in posterior body half, usually roughly C-shaped, occasionally tortuous rod-shaped or almost circular, ends often slightly inflated; nucleoli globular, small and numerous. Micronucleus conspicuous because invariably at anterior curve of macronucleus and 4–5 µm across in vivo; with distinct membrane and some indeterminable internal structures (Fig. 18a, f, g; 304d, e). Contractile vacuole in rear end, some excretory pores in posterior pole area. Extrusomes in oral bulge and scattered in cytoplasm, broadly fusiform, 1.7–2.2 × 0.7–1 µm in vivo (Fig. 18a–c; Table 18); ripe organelles do not impregnate with the protargol method used, while two to five cytoplasmic extrusomes, obviously a late (because of similar size and shape as the oral extrusomes) developmental stage, stain rather deeply. Cortex highly flexible, contains pale, minute (≤ 0.3 µm) granules so loosely arranged that rows are hardly recognizable. Cytoplasm colourless, contains many bright fat globules 1–4 µm across and some 6 µm-sized food vacuoles with loose content. Food not known, likely other ciliates. Glides and swims rather rapidly by rotation about main body axis.

Cilia about 8 µm long in vivo, arranged in bipolar, equidistant rows densely ciliated and slightly curved in anterior region; distances between individual kinetids increase distinctly from anterior to posterior. Two kineties differentiated to moderately conspicuous dorsal brush in anterior third. Dikinetidal portion of brush row 1 about twice as long as that of row 2, which has a monokinetidal bristle tail extending to posterior body end; both rows separated by an about 2 µm high crest slightly projecting from body surface when cell is viewed

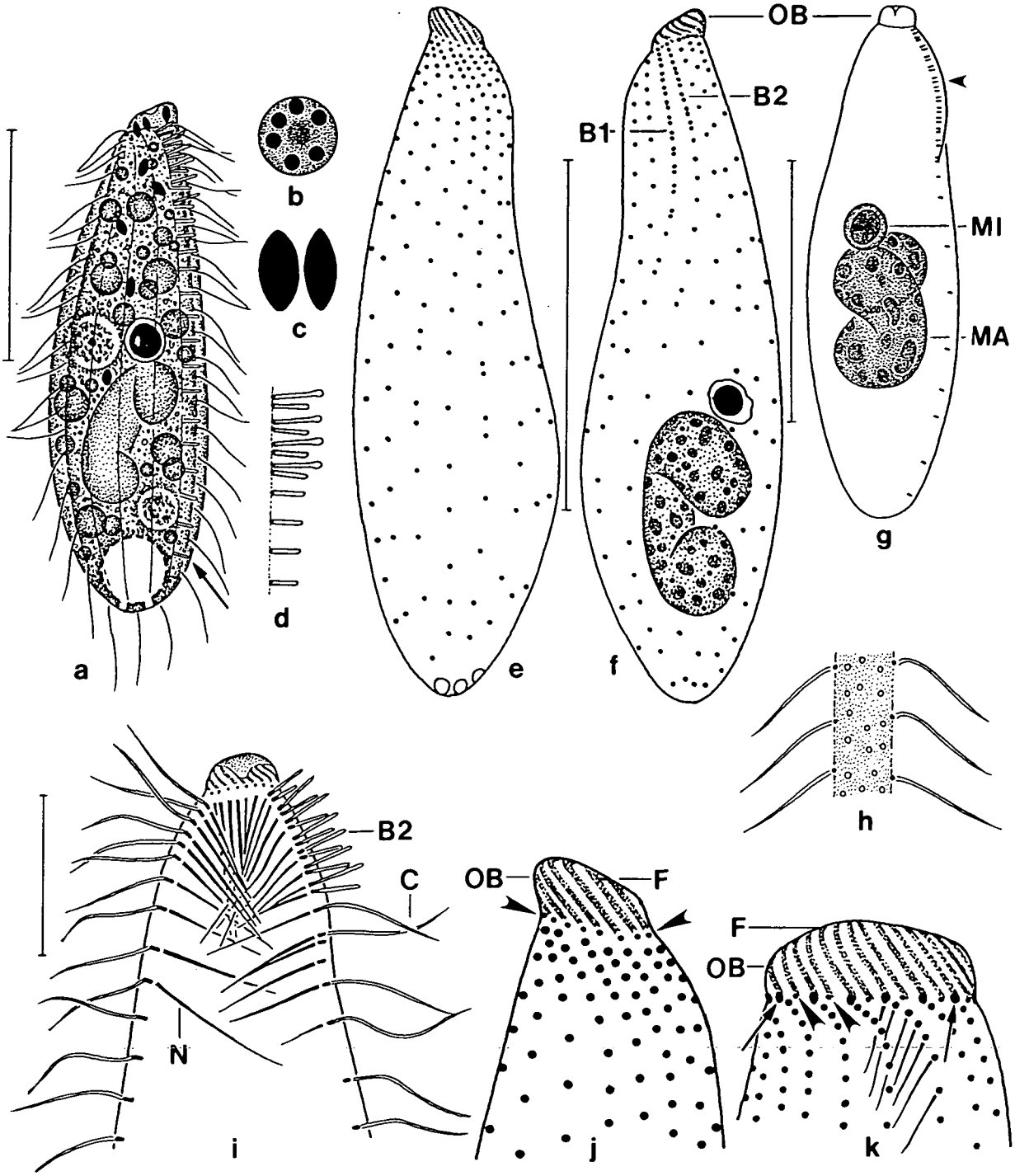

Fig. 18a–j. *Obliquostoma enchelyodontides* from life (a–d, h) and after protargol impregnation (e–g, i, j). **a:** Dorsolateral view of a representative specimen. Arrow marks end of monokinetidal bristle tail of brush row 2. **b:** Frontal view of oral bulge (schematic). **c:** Oral extrusomes from two specimens, length about 2 µm. **d:** Posterior portion of brush row 2. **e, f:** Ciliary pattern of ventral and dorsal side. **g:** Lateral view showing crest (arrowhead) between brush rows. **h:** Surface view showing loose cortical granulation. **i:** Oral fibre system. **j, k:** Oral region of *O. enchelyodontides* and → *Sikorops namibiensis*. Arrowheads mark minute, lightly impregnated granules, which occur in both genera, while enlarged granules (arrows), likely dikinetids, occur only in *Sikorops*. B1, 2 – dorsal brush rows, C – somatic cilia, F – bulge fibres, MA – macronucleus, MI – micronucleus, N – nematodesmata, OB – oral bulge. Scale bars 25 µm.

laterally (Fig. 18g); anterior bristle of pairs about 3 µm long and slightly inflated distally, posterior about 2 µm long and rod-shaped (Fig. 18a, d–g, i, j; 304a–i; Table 18).

Oral bulge 5–7 µm width and up to 4 µm high in vivo, likely slightly contracted in the protargol preparations, higher right than left laterally and thus conspicuously oblique, while button-shaped (symmetrical, enchelyodontid) when viewed laterally; circular to broadly obovate in frontal view, centre slightly depressed. No ordinary circumoral kinety, but a ring of minute (about half the size of ordinary somatic basal bodies), lightly impregnated granules associated with fibres extending spirally to bulge centre. Ciliary rows commence underneath granule ring, likely with a ciliated monokinetid because any indication of a dikinetid is lacking. Oral basket composed of nematodesmata originating from about ten somatic kinetids at anterior end of each ciliary row, including the dorsal brush, where the posterior basal body of a pair usually has a long basket rod; nematodesmata obliquely spread to body midline, forming a rather conspicuous basket (Fig. 18a, b, e–g, i, j; 304d–i; Table 18).

Occurrence and ecology: To date found only at type location, where it was rare in the non-flooded Petri dish culture.

Comparison with related species: *Obliquostoma enchelyodontides* is an inconspicuous ciliate. In spite of this, it is readily identified, both in vivo and silver preparations, by the oblique oral bulge, the curious location of the micronucleus, and the ellipsoidal extrusomes. No species was found in the literature that could be identical to our population. For differences to → *O. namibiense*, see that species.

Table 18. Morphometric data on *Obliquostoma enchelyodontides* (upper line) and *Obliquostoma namibiense* (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	50.4	51.0	3.8	0.9	7.5	43.0	59.0	19
	55.1	55.0	6.1	1.6	11.1	45.0	70.0	15
Body, width	16.4	16.0	1.8	0.4	10.8	14.0	20.0	19
	17.5	17.0	3.7	1.0	21.2	13.0	26.0	15
Body length:width, ratio	3.1	3.1	0.3	0.1	9.6	2.6	3.7	19
	3.3	3.5	0.6	0.2	17.7	2.2	4.1	15
Anterior end to macronucleus, distance	25.6	27.0	3.1	0.7	12.0	21.0	30.0	19
	23.5	23.0	4.8	1.2	20.2	16.0	37.0	15
Macronuclear figure, length	15.2	15.0	2.0	0.5	12.9	11.0	20.0	19
	16.8	16.0	2.6	0.7	15.6	13.0	21.0	15
Macronucleus, length (spread)[b]	23.8	25.0	–	–	–	15.0	30.0	19
	23.4	24.0	–	–	–	15.0	35.0	15
Macronucleus, width	5.7	6.0	1.0	0.2	17.3	4.0	7.0	19
	6.4	6.0	0.7	0.2	11.5	5.0	8.0	15
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Micronucleus, length	3.8	4.0	0.5	0.1	13.8	3.0	5.0	19
	4.2	4.0	0.5	0.1	12.6	3.5	5.0	15
Micronucleus, width	3.6	3.5	0.6	0.1	16.2	2.5	5.0	19
	3.8	4.0	–	–	–	3.0	4.0	15

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Somatic ciliary rows, number	16.1	16.0	1.0	0.2	6.0	14.0	17.0	19
	14.7	15.0	0.6	0.2	4.0	14.0	16.0	15
Ciliated kinetids in a ventral kinety, number	21.0	21.0	4.4	1.0	21.1	13.0	33.0	19
	24.5	25.0	4.2	1.1	17.3	18.0	34.0	15
Fibre granule to last dikinetid of brush row 1, distance [c]	11.7	12.0	1.6	0.4	13.4	10.0	16.0	19
	9.9	10.0	1.9	0.5	19.2	8.0	15.0	15
Dikinetids in brush row 1, number	10.7	11.0	1.0	0.2	9.2	9.0	13.0	19
	9.3	9.0	1.6	0.4	17.0	7.0	13.0	15
Fibre granule to last dikinetid of brush row 2, distance [c]	5.8	5.0	1.5	0.3	25.7	4.0	10.0	19
	4.9	5.0	1.1	0.3	21.8	3.0	7.0	15
Dikinetids in brush row 2	5.5	5.0	0.7	0.2	12.6	5.0	7.0	19
	4.8	5.0	0.8	0.2	16.1	4.0	7.0	15
Dorsal brush rows, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15
Oral bulge, width	4.3	4.0	0.6	0.1	13.6	3.5	5.5	19
	4.7	4.5	0.6	0.2	12.6	4.0	5.5	15
Oral bulge, height	2.4	2.5	–	–	–	2.0	3.5	19
	2.5	2.5	–	–	–	2.0	3.0	15
Cytoplasmic extrusomes, length	2.0	2.0	–	–	–	1.5	2.5	17
			hardly impregnated					
Cytoplasmic extrusomes, width	0.9	1.0	–	–	–	0.7	1.1	17
			hardly impregnated					

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] If curved, artificially spread; values thus approximations.

[c] Row of granules at base of oral bulge.

Obliquostoma namibiense nov. spec. (Fig. 19a–f; 304j, k; Table 18)

Diagnosis: Size about 65 × 20 µm in vivo; oblong with oral bulge occupying one quarter of widest trunk region. Macronucleus C-shaped with micronucleus attached at variable positions and about 5 µm across. Ripe extrusomes amphoriform, about 2 × 1 µm. On average 15 ciliary rows. Brush row 1 about twice as long as row 2, consists of an average of 9, respectively, 5 dikinetids.

Type location: Litter from *Combretum imberbe* (leadwood tree) at foot of the Brandberg, an inselberg at the east margin of the central Namib Desert, Namibia, 21°S 14°35'E (site 48 in figure 2 and chapter 2.1.2).

Etymology: Named after the country discovered.

Description and comparison with related species: This species, as yet found only at type location, is highly similar to *O. enchelyodontides*, except for the extrusomes, which are amphoriform in the former and ellipsoidal in the latter. We consider this as the main feature of *O. namibiense* because extrusome shape hardly varies and is generally an important feature in haptorid gymnostomes.

As *O. namibiense* is highly similar to *O. enchelyodontides*, the reader is referred to the detailed description of this species, the figures, and the morphometric data. The following minor differences occur: (i) *Obliquostoma namibiense* is slightly larger and more distinctly slanted subapically than *O. enchelyodontides*; (ii) the location of the micronucleus varies; (iii) the cytoplasmic extrusomes do not, or only lightly, impregnate; (iv) dorsal brush ridges likely lacking or inconspicuous; (v) dorsal bristles rod-shaped and up to 5 µm long in row 1.

In vivo, *Obliquostoma* spp. are easily confused with several small *Enchelyodon*, *Sikorops*, and *Spathidium* species, especially *Spathidium claviforme* (extrusomes rod-shaped!). Thus, identifications should be checked by protargol impregnation.

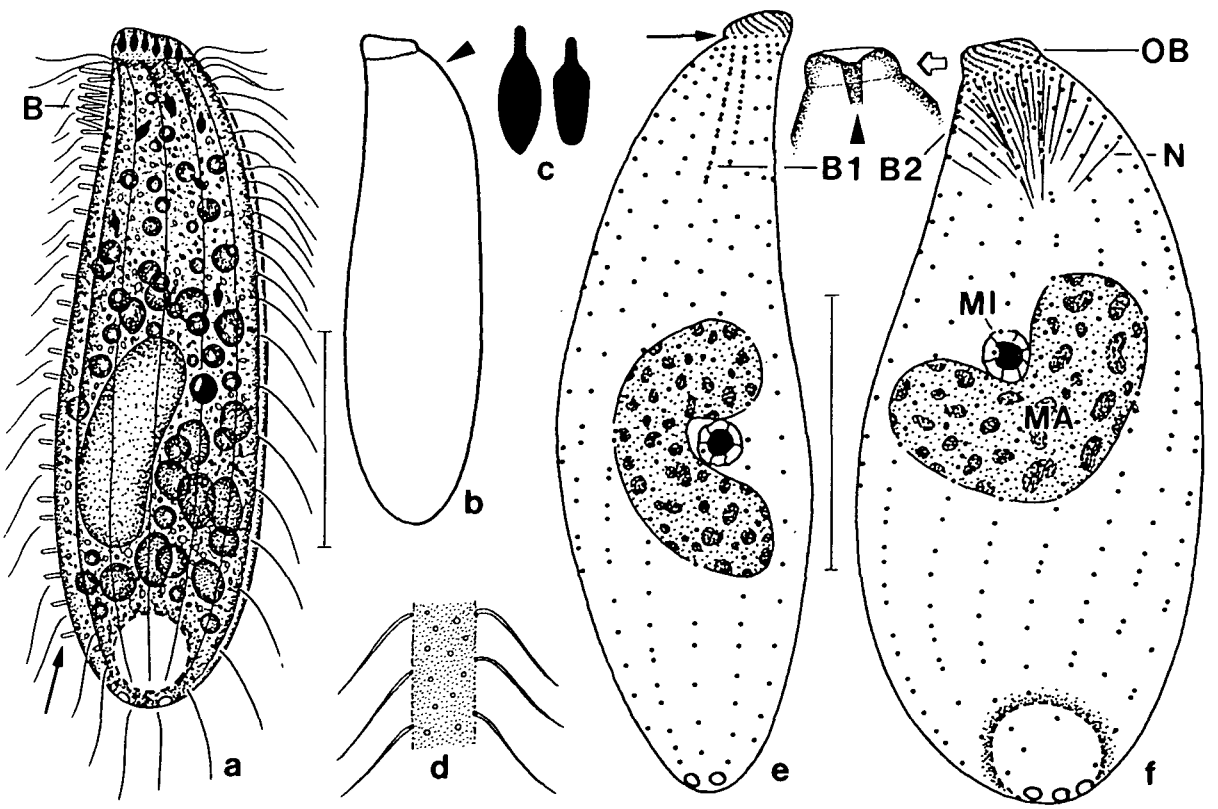

Fig. 19a–f. *Obliquostoma namibiense* from life (a–d) and after protargol impregnation (e, f). **a, b:** Right side views of representative specimens obliquely truncated subapically (arrowhead), producing the impression that half of the oral bulge is lacking. **c:** Oral extrusomes, 2–2.5 × 0.8–1 µm. **d:** Surface view showing loose, inconspicuous cortical granulation. **e:** Ciliary pattern of dorsal side of holotype specimen. Arrow marks a row of minute granules at base of oral bulge. These granules, which are distinctly smaller than ordinary somatic basal bodies, are associated with fibres spiralling to the bulge centre. **f:** Right side view of the fat, darkly impregnated paratype specimen showing nematodesmata (N) originating from oralized somatic monokinetids in the anterior region of the ciliary rows; the figure left shows the distinctly impregnated bulge funnel (arrowhead). B – dorsal brush, B1, 2 – dorsal brush rows, N – nematodesmata, OB – oral bulge. Scale bars 20 µm.

Enchelyodontidae nov. fam.

Diagnosis: Cylindroidal, acontractile Spathidiida with meridionally extending ciliary rows and circular or elliptical circumoral kinety at anterior end. Oral bulge usually conspicuous, hemispherical, cylindroidal, or plate-like. Dorsal brush composed of 3 rows of dikinetids; row 3 with monokinetidal bristle tail.

Type genus: *Enchelyodon* CLAPARÈDE & LACHMANN, 1859.

Remarks: *Enchelyodon* was classified with the Enchelyidae by CORLISS (1979) and the Trachelophyllidae by FOISSNER (1984). However, *Enchelys* has a fundamentally different oral infraciliature, that is, has oralized somatic monokinetids and lacks oral dikinetids (FOISSNER 1984, FOISSNER & FOISSNER 1985[2]). The → Trachelophyllidae are here raised to subordinal rank and restricted to genera with epicortical scales. Thus, the remaining genera are referred to a new family, Enchelyodontidae, as diagnosed above.

The Enchelyodontidae comprise at least two genera: *Enchelyodon* (with hemispherical or plate-like, "closed" oral bulge) and *Enchelydium* (with cylindroidal, "open" oral bulge), as described below.

Enchelydium blattereri nov. spec. (Fig. 20a–t; 305a–z, 306a–o; Table 19)

Diagnosis: Size about 240 × 100 µm in vivo. Macronucleus vermiform. Two size types (30 µm and 50 µm) of rod-shaped extrusomes in oral bulge and posterior body third, where they form about 12 distinct, equidistant bundles. On average 110 ciliary rows. Oral bulge circular, in vivo about 40 µm across and 10 µm high. Resting cysts with conspicuous, hemispherical blisters.

Type location: Soil from Murray River floodplain near Albury at the landside of Ryans road, Australia, 37°S 147°E.

Dedication: Dedicated to Mag. Hubert BLATTERER, a former student of Prof. FOISSNER, who collected the sample and performed the first detailed study on Australian soil ciliates (BLATTERER & FOISSNER 1988).

Description: Size 200–280 × 70–120 µm in vivo, usually around 240 × 100 µm. Bursiform to cylindroidal and slightly curved, resembling a thick, swimming sausage, dorsally often more convex than ventrally and thus slightly asymmetrical. Posterior end broadly rounded, anterior transverse truncate due to thick, cylindroidal oral bulge (Fig. 20a, b; 305k, i; Table 19). Cells opaque and brownish at low magnification (≤ ×100) due to large size and food inclusions. Macronucleus vermiform and tortuous, on average slightly longer than cell, occasionally in two pieces of varying length. About 10 micronuclei along macronucleus,

[2] The *Enchelydium polynucleatum* in this paper belongs to *Enchelys*, as explained in the generic classification of *Enchelydium blattereri*.

in vivo approximately 4 µm across, in protargol preparations difficult to distinguish from similarly sized and impregnated cytoplasmic inclusions (Fig. 20a, k; 305a, c, p). Contractile vacuole in posterior body end, 6–9 pores in unciliated pole centre. Cortex very flexible, bright and 2–3 µm thick due to a dense layer of mucocysts, in protargol preparations separated from cytoplasm by a sharply impregnated sheet, likely the well-developed tela corticalis (Fig. 20a, m; 305a, c). Mucocysts about 2 × 1 µm in vivo, tightly spaced forming bright layer in entire cortex, including outer and inner wall of oral bulge, released when methyl green-pyronin is added, swell to about 5 µm long, irregularly curved rods forming a more of less compact envelope (Fig. 20a, f, g; 305a, c–e). Two size-types of rod-shaped, fine extrusomes (toxicysts) in oral bulge and cytoplasm, where they form about 12 conspicuous, subcortical bundles in posterior body third, produce dense lattice over oral opening when partially extruded, become black and irregularly curved in silver carbonate preparations, while only the proximal, toxin-containing portion impregnates with protargol. Size type I about 50 × 0.6 µm, slightly curved, very numerous and flexible; size type II, possibly only a developmental stage of type I, about 30 × 1 µm, more strongly curved than type I (Fig. 20a, c, e, k; 305a–c, o, w–y, 306n). Cytoplasm packed with fat globules 1–12 µm across, a few large food vacuoles, and some 5–10 µm-sized vacuoles with granular contents (Fig. 20a; 305a). Feeds mainly on medium-sized ciliates (*Meseres corlissi*, *Colpoda lucida*, *Plagiocampa rouxi*), which are ingested whole and move in the food vacuoles for some time; occasionally, flagellates and brown fungal conidia were observed in the food vacuoles, possibly from prey organisms. Movement of field specimens very conspicuous, that is, rapidly and jerkily pushing, giving the impression of intense search for prey; cultivated specimens often swim slowly by rotation about main body axis.

Cilia 10–12 µm long in vivo, closely spaced, especially underneath oral bulge, and thus forming beautiful metachronal waves; arranged in meridional rows at left margin of flat cortical ridges, abut on circumoral kinety, three rows anteriorly differentiated to inconspicuous, dikinetidal dorsal brush. Brush rows in rather deep furrows, respectively, separated by about 1 µm wide ridges, kinetids much more closely spaced than in ordinary ciliary rows; rows 1 and 2 extend with unciliated monokinetids to posterior third of cell, producing an about 3 µm wide, blank stripe (Fig. 305 l). Brush row 1 slightly shorter than row 2, dikinetids with slightly inflated bristles gradually decreasing in length from 6 µm anteriorly to 1 µm posteriorly; posterior bristle of dikinetids only 2 µm long anteriorly and 0.5 µm posteriorly. Row 3 like rows 1 and 2 anteriorly, extends with 3–4 µm long, monokinetidal bristles to posterior third of cell; bristles acicular and straight in vivo, rod-shaped and curved posteriorly in SEM preparations (Fig. 20a, d, k, l; 305 l, p, r–v; Table 19).

Oral apparatus at anterior end of cell and very conspicuous due to the large, cavernous oral bulge making cells appear as if swimming with an open mouth (Fig. 20a, k; 305g–j), as already emphasized by KAHL (1930a, b); cavity, however, covered with pellicle, mouth thus not truly open. Oral bulge cylindroidal because hemispherically or obconically hollowed in centre, as described above; in vivo circular and about 40 µm across and 10 µm high, in protargol slides slightly widened (Table 19), while shrunken to about 30 µm (15–25 µm in the small, cultivated specimens) in SEM preparations; can contract and extend by about half of its ordinary width to become higher, respectively, flatter; consists of a lamellar, anastomosing material and contains anterior end of extrusomes and fine fibres forming an inner basket (Fig. 19n; 305m, n, w, x). Circumoral kinety at base of oral bulge, composed of very closely spaced kinetids (likely dikinetids) with about 10 µm long cilia. Oral basket conspicuous because

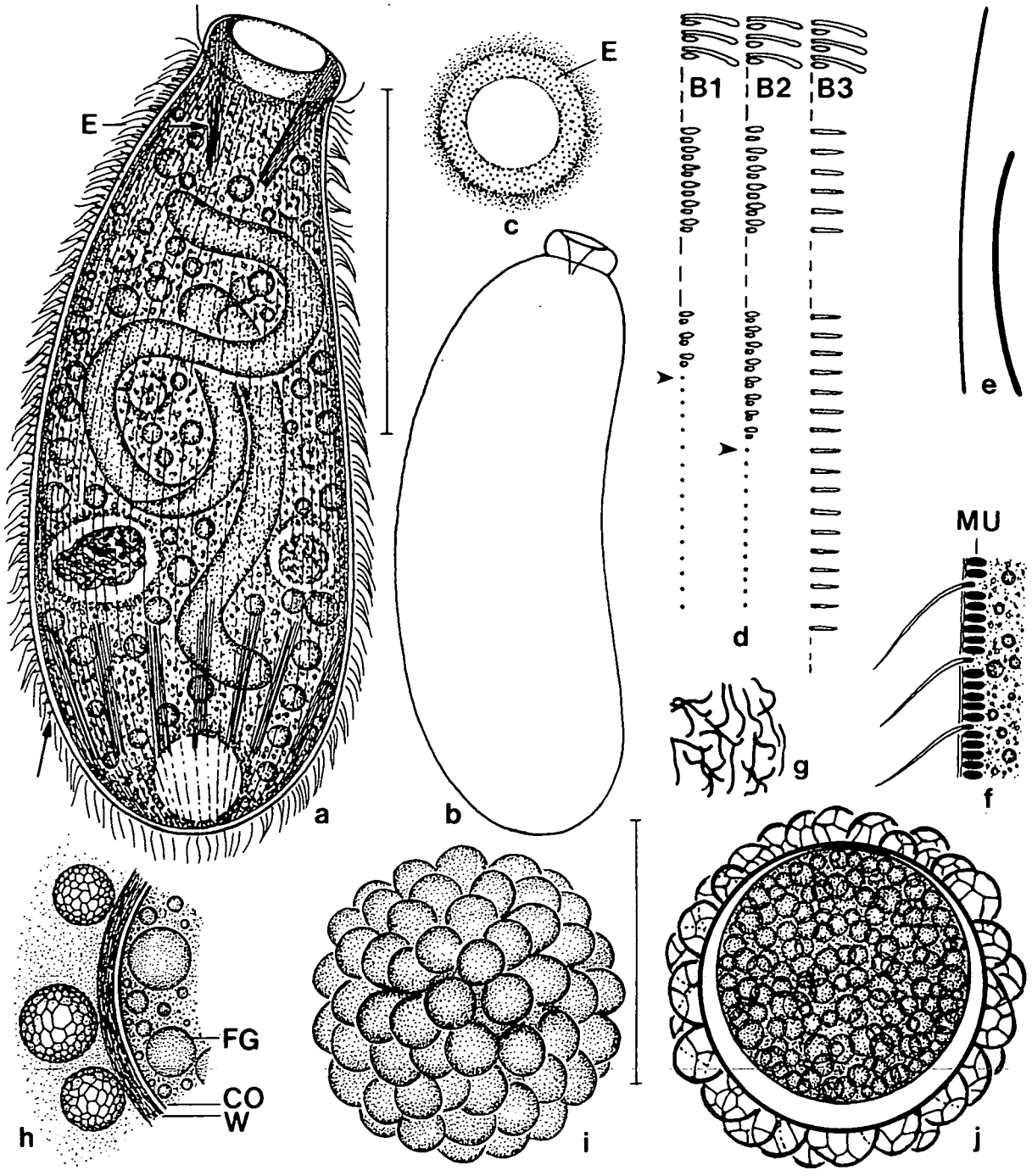

Fig. 20a–j. *Enchelydium blattereri* from life (a–f, h–j) and after methyl green-pyronin staining (g). **a:** Right lateral view of a representative, bursiform specimen. Arrow marks posterior end of dorsal brush row 3. **b:** The cylindroidal shape variant looks like a swimming sausage. **c:** Frontal view of the ring-shaped oral bulge, which is packed with extrusomes. **d:** Fine structure of dorsal brush, which consists of three dikinetidal rows anteriorly. Rows 1 and 2 extend with unciliated monokinetids (arrowheads) to posterior third of cell, while the monokinetids of row 3 bear acicular bristles. **e:** *Enchelydium blattereri* has two size-types (50 × 0.6 µm, 30 × 1 µm) of curved, rod-shaped toxicysts. **f, g:** The mucocysts form a conspicuous layer and are released when dye is added, extending to about 5 µm long rods. **h:** Forming resting cyst with faceted spheres on wall. **i, j:** Surface view and optical section of a ripe resting cyst. B1-3 – dorsal brush rows, CO – cortex of encysted cell, E – extrusomes, FG – fat globules, MU – mucocysts, W – cyst wall. Scale bars 100 µm.

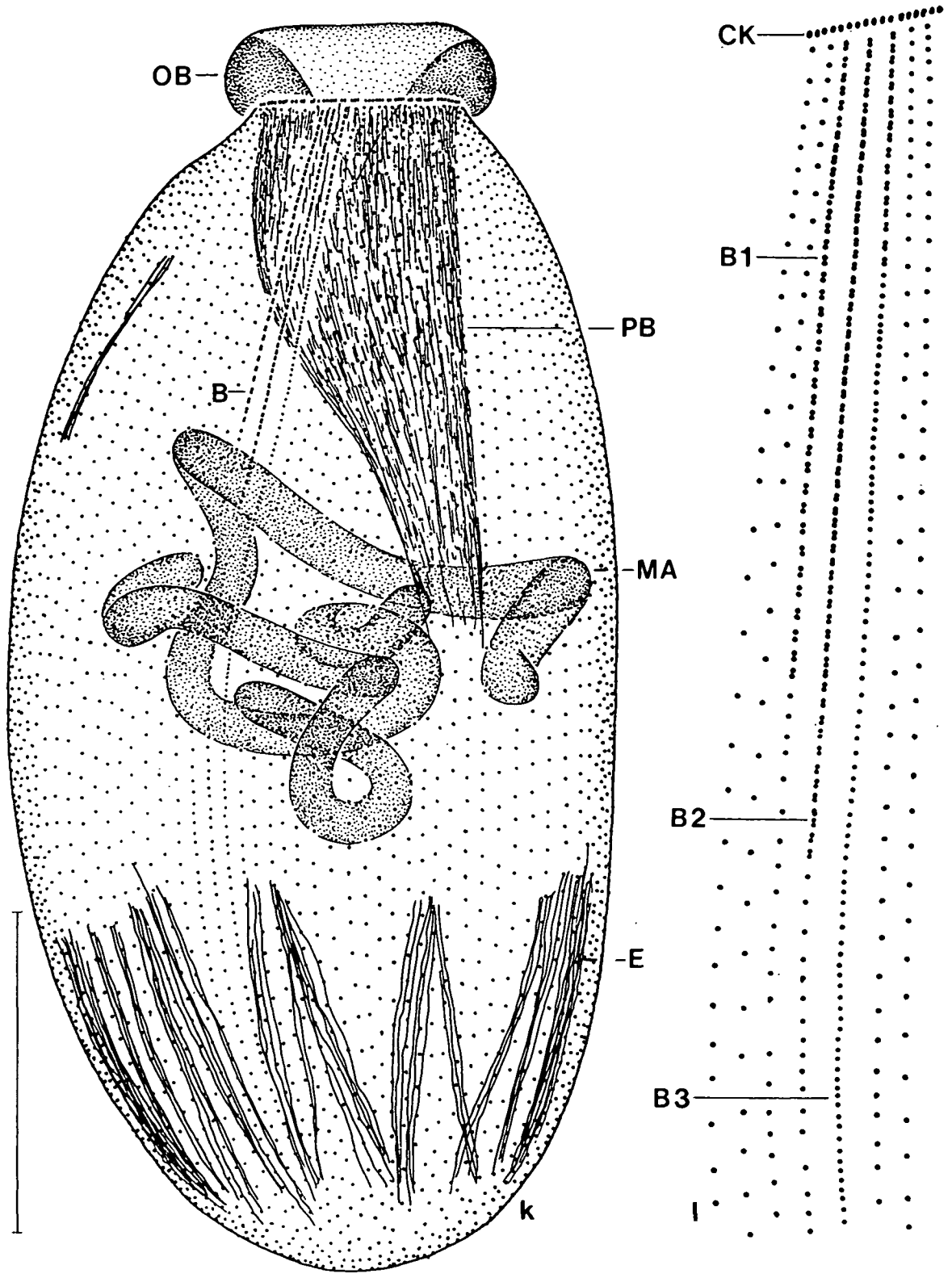

Fig. 20k, l. *Enchelydium blattereri*, dorsal view of holotype specimen after protargol impregnation. B – dorsal brush, B1-3 – dorsal brush rows, CK – circumoral kinety, E – subcortical extrusome bundles, OB – oral bulge, PB – pharyngeal basket. Scale bar 50 µm.

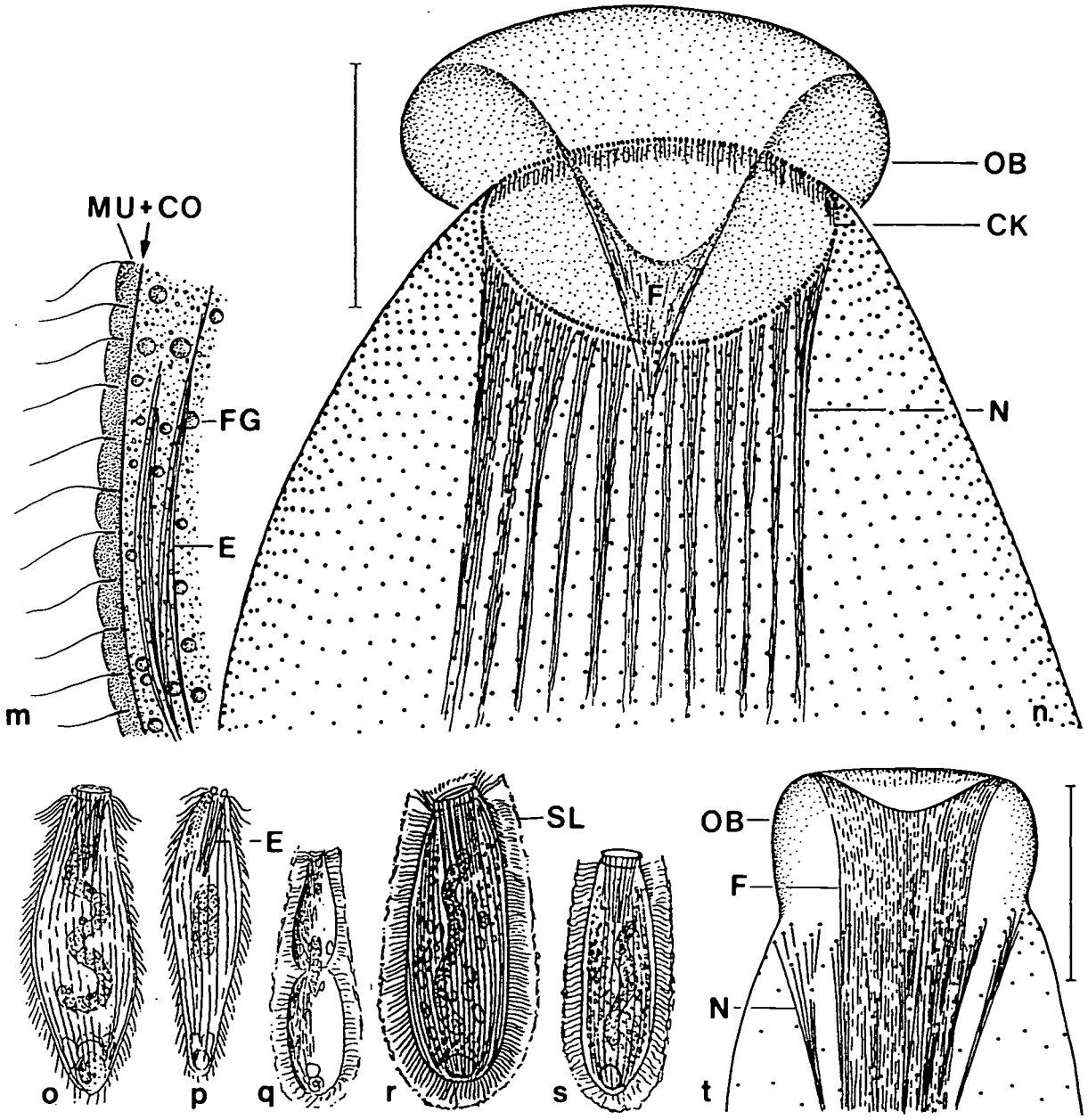

Fig. 20m–t. *Enchelydium blattereri* (m, n), *Enchelydium thecatum* (o–s; from KAHL 1926, 1930a, b), and *Enchelys gasterosteus* (t; from FOISSNER 1984) from life (o–s) and after protargol impregnation (m, n, t). **m:** Optical section of cell periphery. The cortex and the mucocysts form an about 2 µm thick, opaque layer, which is separated from the cytoplasm by a sharply impregnated sheet (arrow), likely the strongly developed, microfibrillar tela corticalis. **n, t:** Ventral views of oral region showing the main differences between *Enchelydium* (family Enchelyodontidae) and *Enchelys* (Enchelyidae). The nematodesmata of *Enchelydium* originate from a circumoral kinety, while those of *Enchelys* originate from the anterior basal bodies of the somatic ciliary rows. The oral bulge of *Enchelydium* is ring-shaped, that is, has a conspicuous central opening (Fig. 305g–j), while that of *Enchelys* is only slightly depressed and closed (Fig. 305z). **o–s:** *Enchelydium thecatum* differs from *E. blattereri* mainly by body size (100–130 µm vs. 200–280 µm), the oral bulge (cleft-like vs. cylindroidal), and the mucilaginous envelope, which is lacking in *E. blattereri*. KAHL (1926, 1930a, b) studied *E. thecatum* several times and provided figures from each observation. CK – circumoral kinety composed of dikinetids, CO – cortex, E – extrusome bundles in oral bulge (p) and posterior body portion (m), F – fibres which form an inner oral basket, FG – fat globules, MU – mucocysts, N – nematodesmata form the outer oral basket, OB – oral bulge, SL – mucilaginous envelope. Scale bars 20 µm (n) and 10 µm (t).

extending to mid-body and composed of fine, bundled nematodesmata originating from circumoral kinetids (Fig. 20k, l, n; 305n–q; Table 19).

Resting cysts from cultivated specimens in vivo 128–152 µm across and conspicuously mulberry-shaped because covered with hemispherical blisters originating from spherical, polygonally faceted precursors released during cyst formation (Fig. 20h; 306o; Table 19). Blisters brownish and foam-like, that is, consisting of a large, central vacuole surrounded by about 10 smaller vacuoles (306d, f, h); blister wall about 0.5 µm thick and composed of fibrous material with numerous, scattered pores, very much like filter paper (306k–m); individual blisters on average 14 µm high and connected by star-like extensions of wall fibres (306i, j; Table 19). Cyst wall proper about 1 µm thick, brownish, flexible. Encysted cell often separated from cyst wall by a more or less wide, hyaline zone and packed with fat globules 1–10 µm across.

Table 19. Morphometric data on *Enchelydium blattereri*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body (with oral bulge), length	215.9	215.0	24.0	5.2	11.1	173.0	250.0	21
Body, width	101.4	98.0	15.9	3.5	15.6	71.0	130.0	21
Body, width at circumoral kinety	31.1	31.0	4.3	0.9	13.9	23.0	40.0	21
Oral bulge, width	43.4	44.0	6.0	1.3	13.9	33.0	53.0	21
Oral bulge, height	10.7	10.0	1.4	0.3	12.6	7.0	13.0	21
Brush row 1, length [b]	56.7	60.0	9.0	3.0	15.9	40.0	65.0	9
Brush row 2, length [b]	70.6	70.0	13.6	4.5	19.2	45.0	90.0	9
Brush row 3, length [b, c]	21.2	20.0	2.5	0.8	11.7	18.0	25.0	9
Macronucleus, length [d]	271.0	260.0	–	–	–	180.0	390.0	21
Macronucleus, diameter	10.1	10.0	1.3	0.3	12.5	9.0	15.0	21
Somatic ciliary rows, number [e]	109.2	110.0	3.7	1.5	3.4	105.0	113.0	6
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	12
Resting cysts, length (with blisters) [f]	138.5	136.0	8.2	2.1	5.9	128.0	152.0	15
Resting cysts, width (with blisters) [f]	137.3	136.0	7.7	2.0	5.6	128.0	152.0	15
Resting cysts, length (without blisters) [f]	109.1	109.0	6.8	1.8	6.3	100.0	120.0	15
Resting cysts, width (without blisters) [f]	109.1	109.0	6.8	1.8	6.3	100.0	120.0	15
Resting cysts, length (encysted cell) [f]	98.5	96.0	6.1	1.6	6.2	88.0	114.0	15
Resting cysts, width (encysted cell) [f]	98.5	96.0	6.1	1.6	6.2	88.0	114.0	15

[a] Data based, if not otherwise stated, on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Distance from circumoral kinety to last dikinetid.

[c] Dikinetidal portion only; see description for monokinetidal tail.

[d] Rough data, i. e., from uncoiled (spread) nucleus.

[e] From silver carbonate-impregnated specimens.

[f] In vivo; cultivated specimens.

Occurrence and ecology: To date found only at type location. The sample was a mixture of leaf litter (mainly from red gum trees and dried *Myriophyllum*) and light brown soil, pH 5.2. It contained a very rich (about 80 species) mixture of limnetic and euedaphic ciliate species.

Enchelydium blattereri could be cultivated in Eau de Volvic with *Colpoda lucida* and *Meseres corlissi* as food source. However, cultures did not grow well and specimens became smaller (150–200 µm) and died out after about two months. *Tetrahymena mobilis*, *Paramecium aurelia*, and *Blepharisma americanum* were not ingested.

The peculiar resting cysts could help to escape the strong sedimentation common in floodplain environments. The large blisters might increase buoyancy of the cyst and facilitate distribution of the species by floatation.

Comparison with related species: Few *Enchelydium* species have been described since KAHL (1930a), and most very likely belong to other genera (see below). All species are small (length < 100 µm) and have one or two macronuclear nodules, except for *E. thecatum* KAHL, 1926, which is 100–130 µm long and has, like *E. blattereri*, a vermiform macronucleus (Fig. 20o–s). KAHL (1926, 1930a, b) studied two populations of *E. thecatum*. Both were distinctly smaller than *E. blattereri*, had an elongate-ellipsoidal oral bulge, and produced a mucilaginous case. A case was not observed in *E. blattereri*, not even in cultures, where specimens moved incessantly; however, when cells were irritated, they released their mucocysts producing a more or less voluminous cover (305c–f), indicating that they were not fundamentally different from *E. thecatum* in this respect. Thus, the considerable size difference (100–130 µm vs. 200–300 µm) and the shape of the oral bulge (elongate ellipsoidal vs. circular) are the main distinguishing features of *E. thecatum* and *E. blattereri* at the present state of knowledge; very likely, the number of ciliary rows is highly different, too. Furthermore, *E. thecatum* apparently lacks the terminal extrusome bundles, which are so conspicuous in *E. blattereri* (Fig. 20a, o–s; 305n).

Generic classification: The Australian ciliate perfectly matches the genus *Enchelydium*, as defined by KAHL (1930a, b), that is, has a very conspicuous, ring-shaped oral bulge making specimens look as if swimming with an open mouth (Fig. 20a; 305g, h, k). The infraciliature, described here for the first time, is simple and very similar to that of *Enchelyodon*, as shown by FOISSNER (1984). Thus, the oral bulge (ring-shaped vs. button-shaped or plate-like) is the sole distinguishing feature. Both genera belong to the spathidiids, as already proposed by KAHL (1930a, b), and are fundamentally different from *Enchelys*, which lacks oral dikinetids (see introduction to family and Fig. 20t).

The "open mouth" of *Enchelydium*, although being very conspicuous, is difficult to imagine without appropriate scanning electron micrographs (305g–j). Thus, and because details of the infraciliature of *Enchelydium* were unknown, FOISSNER (1984) misclassified an *Enchelys* species in *Enchelydium*: *Enchelys polynucleata* (FOISSNER, 1984) nov. comb. (basionym: *Enchelydium polynucleatum* FOISSNER, 1984). *Spathidium piliforme* KAHL, 1930b, as redescribed and transferred to *Enchelydium* by FOISSNER (1984), either belongs to *Enchelys* or *Sikorops* FOISSNER, 1999b. Likewise, *Enchelydium alpinum* FOISSNER, 1980d and *E. simile* FOISSNER, 1980d belong to *Enchelys* or *Spathidium*. However, a definite assignment of these taxa should await more detailed data on the infraciliature.

Enchelyodon kenyaensis nov. spec. (Fig. 21a, b, e–j; Table 20)

Diagnosis: Size about 130 × 20 µm in vivo; obclavate to cylindroidal. Macronucleus a long strand. Extrusomes rod-shaped, about 10 µm long. About 16 ciliary rows. Brush kinety 3 composed of few dikinetids and a monokinetidal bristle extending to mid-body.

Type location: Highly saline, alkaline (pH 8.5) soil from the Buffalo Springs National Reserve, Kenya, 00°40'S 27°30'E.

Etymology: Named after the country discovered.

Description: This species is difficult to study because the cortical granules usually impregnate and hide the infraciliature. Thus, morphometry is incomplete.

Size 80–160 × 15–30 µm in vivo, usually near 130 × 20 µm, length:width ratio 3–7.5:1, on average 5:1 in protargol preparations; up to 2:1 flattened. Claviform to almost cylindroidal, oral bulge distinctly set off from body proper (Fig. 21a, b, e, f; Table 20). Very flexible and up to 20% contractile under slight cover glass pressure. Macronucleus a long, slightly tortuous strand with inflated ends and many small nucleoli, usually in posterior body thirds, occasionally constricted in mid-region. Several globular micronuclei along and near macronucleus. Contractile vacuole in posterior body end, likely with single excretory pore in pole centre. Extrusomes attached to oral bulge and scattered in cytoplasm, rod-shaped and slightly curved, about 10 µm long (Fig. 21j). Cortex very flexible, distinctly furrowed by ciliary rows, contains rows of minute (≤ 0.5 µm) granules that usually impregnate with the protargol method used. Cytoplasm colourless, contains some fat globules 2–4 µm across and large food vacuoles likely with ciliate remnants. Swims and glides moderately rapidly showing worm-like flexibility.

Cilia about 8 µm long in vivo, arranged in about 16 meridional, equidistant rows slightly more densely ciliated in posterior than anterior half of cell. Three rows anteriorly differentiated to short, inconspicuous dorsal brush composed of dikinetids bearing about 4 µm long bristles. Brush row 1 slightly shorter than row 2, each composed of at least 10 dikinetids, row 3 consists of only two anterior dikinetids followed by a monokinetidal tail with about 3 µm long bristles; tail extends to second third of body, where it changes to an ordinary somatic kinety (Fig. 21a, f–i).

Oral bulge occupies anterior body end, distinctly set off from body proper and thus conspicuous, slightly obliquely truncate anteriorly, contains anterior end of extrusomes. Circumoral kinety at base of oral bulge, distinctly set off from somatic ciliary rows, composed of oblique dikinetids each associated with a cilium and an oral basket rod. Oral basket obconical, extends to second third of body, hardly recognizable in live specimens (Fig. 21a, b, f–h).

Occurrence and ecology: To date found only at type location, where it was rare in the non-flooded Petri dish culture.

Comparison with related species: See → *Enchelyodon armatides*. Briefly, *E. kenyaensis* and *E. armatides* differ in the shape of the extrusomes (rod-shaped vs. acicular).

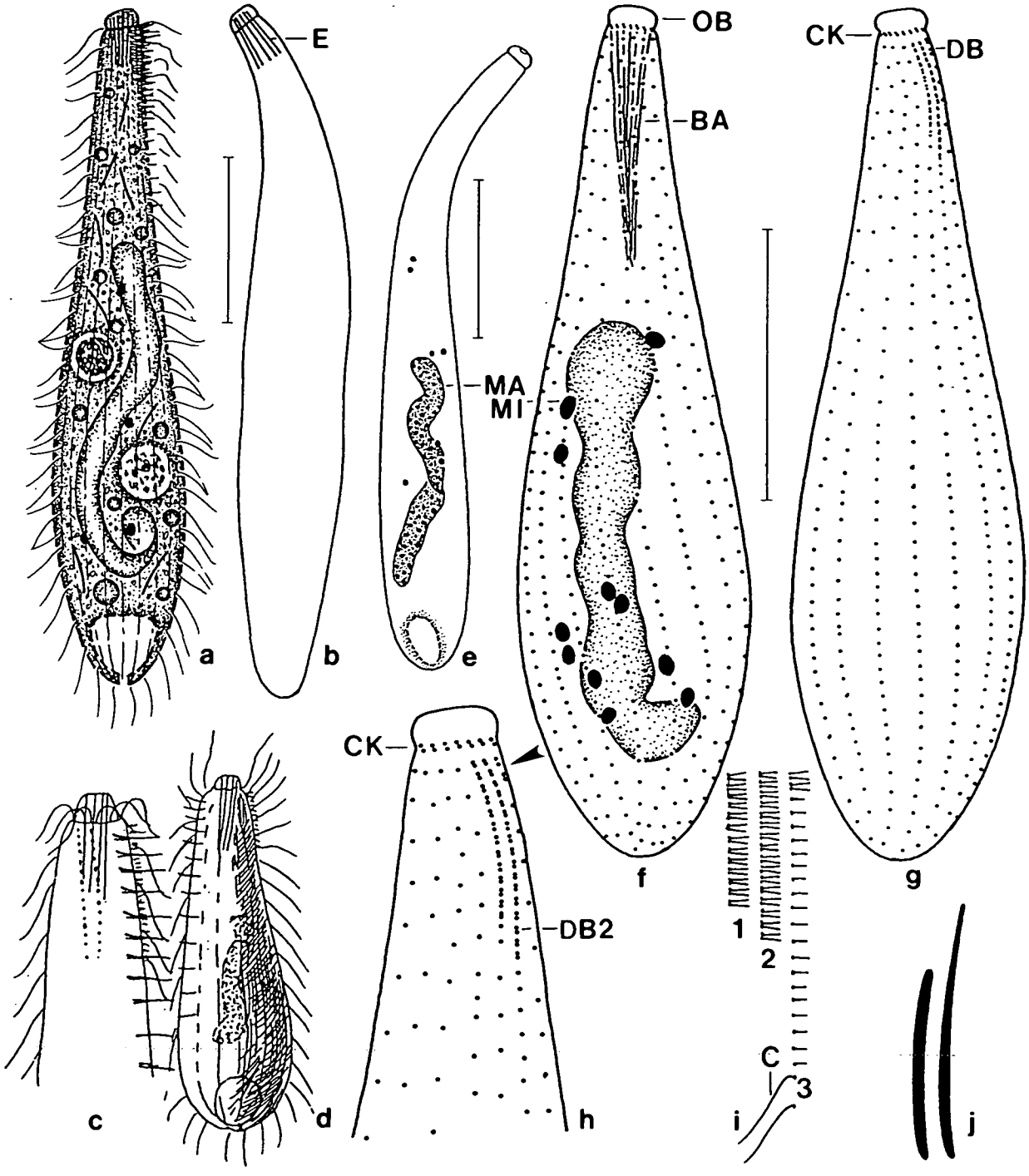

Fig. 21a–j. *Enchelyodon armatus* (c, d) and *E. kenyaensis* (a, b, e–j) from life (a–d, i, j) and after protargol impregnation (f–h). **a, b:** Lateral and dorsal view of a representative, slightly flattened specimen. **c, d:** *Enchelyodon armatus*, length about 100 µm (from KAHL 1926). KAHL illustrated dorsal brush rows 1+2 and 3 on opposite sides of the cell in (d). **e:** One of the slenderest specimens found in the protargol preparations. **f–h:** Ciliary pattern and nuclear apparatus of holotype specimen. Arrowhead (h) marks the two dikinetids at anterior end of brush row 3. **i:** Dorsal brush. Row 3 continues with monokinetidal bristles to second third of cell. **j:** Comparison of extrusomes of *E. kenyaensis* (left; length 10 µm) and → *E. armatides* (right; length 13 µm) from Namibian site (1). BA – oral basket, C – somatic cilium, CK – circumoral kinety, DB, DB2 – dorsal brush (kineties), E – extrusomes, MA – macronucleus, MI – micronucleus, OB – oral bulge. Scale bars 30 µm.

Table 20. Morphometric data on *Enchelyodon kenyaensis*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	114.2	110.0	23.9	6.4	20.9	76.0	155.0	14
Body, width	23.7	24.0	5.0	1.3	21.3	17.0	36.0	14
Body length:width, ratio	5.1	5.0	1.3	0.3	25.6	3.0	7.5	14
Oral bulge, width	6.1	6.0	0.8	0.2	13.7	5.0	8.0	14
Nuclear figure, length	55.4	51.0	14.4	3.8	25.9	36.0	90.0	14
Macronucleus, width	6.6	6.5	0.9	0.2	13.0	5.0	3.0	14
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	14
Micronuclei, length	2.3	2.1	0.5	0.1	23.4	1.8	3.0	4
Micronuclei, width	2.0	2.0	2.0	0.1	8.2	1.8	2.2	4
Micronuclei, number	6.3	5.0	2.5	1.0	40.8	4.0	11.0	7
Ciliary rows, number	17.0	16.0	–	–	–	16.0	19.0	3

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Enchelyodon armatides nov. spec. (Fig. 22a–n, 23a–l; 307c–f; Table 21)

Diagnosis: Size about 160 × 30 µm in vivo; obclavate to almost cylindroidal. Macronucleus a long, tortuous strand. Extrusomes acicular, about 18 µm long. On average 15 ciliary rows, 3 anteriorly modified to dorsal brush: rows 1 and 2 of about same length, each consisting of about 15 dikinetids; row 3 composed of only about 4 dikinetids, but with monokinetidal bristle tail extending to mid-body.

Type location: Litter from *Combretum imberbe* (leadwood tree) at foot of the Brandberg, an inselberg at the east margin of the central Namib Desert, Namibia, 21°S 14°35'E (site 48 in figure 2 and chapter 2.1.2).

Etymology: Composite of the Latin adjective *armatus* (armed) and the Latin suffix *ides* (similar), meaning a ciliate similar to *Enchelyodon armatus* KAHL.

Description: Although the populations studied match well in all main features, the diagnosis contains only the Namibian population, mainly because the other specimens are from different biogeographic regions. The few differences found are mentioned in the description and/or are recognizable in table 21. Generally, the species is highly similar to → *E. kenyaensis*, differing mainly in the shape of the extrusomes (acicular vs. rod-like).

Size 120–200 × 25–40 µm, usually near 160 × 30 µm, length:width ratio 3.5–6.8:1, on average 5.2:1 in protargol preparations; size and shape of Australian specimens similar to those of Namibian type material in vivo, while considerably smaller (109 × 24 µm vs. 143 × 28 µm) and stouter (4.3:1 vs. 5.2:1) in the protargol preparations (Table 21), likely because they are more contractile than the Namibian cells. Australian specimens flattened up to 2:1

and about 30% contracted when removed from the culture and transferred on the microscope slide, slowly extend to become cylindroidal during the next 10 min (Fig. 22f–h). Shape similar in both populations, viz., obclavate to almost cylindroidal and often slightly curved; inconspicuously inflated subapically, where the thick portion of the extrusomes is located (Fig. 22a, f–j, n). Macronucleus usually in posterior two thirds of cell, filiform and tortuous, ends frequently slightly inflated and/or coiled; nucleoli globular to lobate. Micronuclei along and near macronucleus, broadly ellipsoidal about 3 μm in size, often difficult to discern because of many similarly sized and impregnated cytoplasmic inclusions. Contractile vacuole in posterior end, excretory pores not recognizable in the protargol preparations. Ripe extrusomes form a conspicuous bundle attached to the oral bulge, individual toxicysts acicular and rather distinctly curved, about 18 μm (Namibian specimen), respectively, 10–13 μm long (Australian specimens), do not impregnate with protargol, while a certain cytoplasmic developmental stage impregnates deeply (Fig. 22a, c, d; 307c, d). Cortex very flexible, contains about 10 rows of minute, colourless granules between each two kineties. Cytoplasm colourless, usually packed with fat globules up to 7 μm across in posterior body half. Feeds on heterotrophic flagellates and small ciliates, digested rapidly because food vacuoles are rarely seen. Swims and glides rather rapidly showing great flexibility.

Cilia 6 μm long (8–10 μm in Australian specimens) in vivo, arranged in an average of 15 (16 in Australian specimens) meridional, equidistant rows loosely ciliated in anterior third. Three rows anteriorly differentiated to short, inconspicuous dorsal brush composed of dikinetids bearing up to 4 μm long, distally slightly inflated bristles. Brush rows 1 and 2 of about same length, each composed of about 15 dikinetids (18 in Australian specimens); row 3 consists of only four anterior dikinetids followed by a monokinetidal tail extending to mid-body with about 2 μm long, tongue-shaped bristles (Fig. 22a, b, k, m, n; 307e, f; Table 21).

Oral bulge occupies anterior body end, conspicuous because comparatively large (6–8 × 3–4 μm in vivo) and distinctly set off from body proper, appearing button-like at low (×100) magnification, contains anterior end of extrusomes and an x-shaped, fibrillar structure extending into the oral basket. Circumoral kinety at base of oral bulge, distinctly set off from somatic ciliary rows, composed of oblique dikinetids each associated with a cilium and an oral basket rod. Oral basket obconical, extends in anterior fifth of body, hardly recognizable in live specimens (Fig. 22a, f–m; 307c, e, f; Table 21).

Occurrence and ecology: To date found at type location and in Australia (soil from Botanical Garden in Darwin, Northern Territory); associated with *Spathidium aciculare* at both sites. *Enchelyodon armatides* is a slender species and thus well adapted to live in soil.

Comparison with related species: This and the following species show considerable similarity to *Trachelophyllum* s. l., especially in body and extrusome shape and size, the slight contractility, and the almost complete reduction of dorsal brush row 3. However, the nuclear pattern is different and epicortical scales are lacking, indicating that the similarities evolved convergently or are plesiomorphies.

Enchelyodon armatides is very similar to *E. kenyaensis*, differing only by the shape of the extrusomes (acicular vs. rod-shaped). However, extrusome shape is fairly constant in haptorid gymnostomes and thus an important species character. Further, there exists another similar species with rod-shaped extrusomes but many macronuclear nodules. Thus, the acicular extrusome type likely represents a different evolutionary line and species.

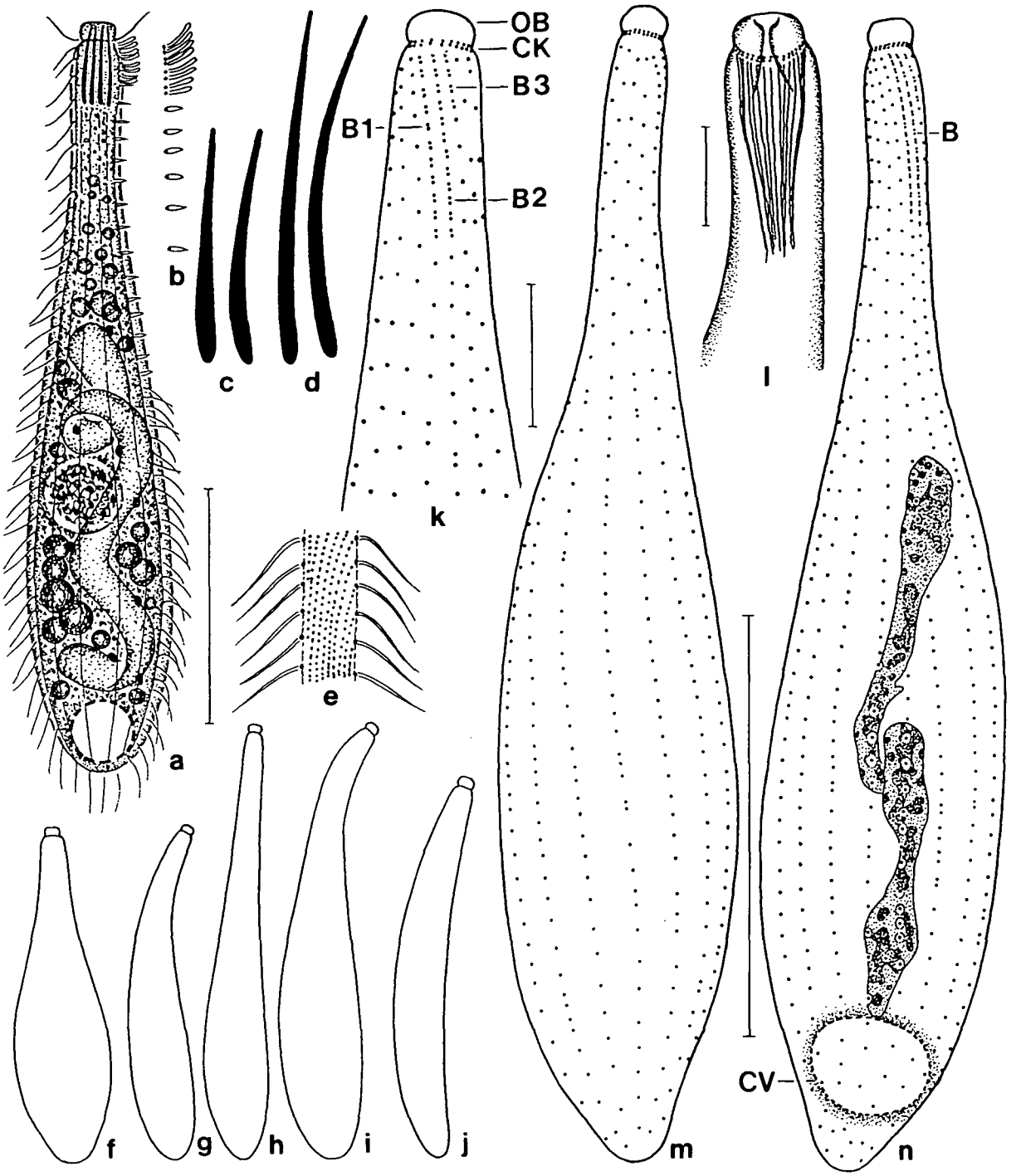

Fig. 22a–n. *Enchelyodon armatides* from life (a–j) and after protargol impregnation (k–n). **a:** Right side view of a representative specimen. **b:** Anterior portion of dorsal brush row 3. **c, d:** Acicular extrusomes of Australian (length 10–13 µm) and Namibian (18 µm) specimens, drawn to scale. **e:** Surface view showing cortical granulation. **f–h:** An Australian specimen: when taken from the culture, it was slightly contracted (f) and flattened (g), but after 10 min it had extended and become cylindroidal (h). **i, j:** Shape variants. **k:** Anterior dorsal region. **l:** Oral fibre system consisting of a diverging bundle in the oral bulge and the pharyngeal funnel made by nematodesmata originating from the circumoral dikinetids. **m, n:** Ciliary pattern of ventral and dorsal side and nuclear apparatus of holotype specimen. B1, 2, 3 – dorsal brush rows, CK – circumoral kinety, CK – contractile vacuole. OB – oral bulge. Scale bars 50 µm (a, m, n) and 10 µm (k, l).

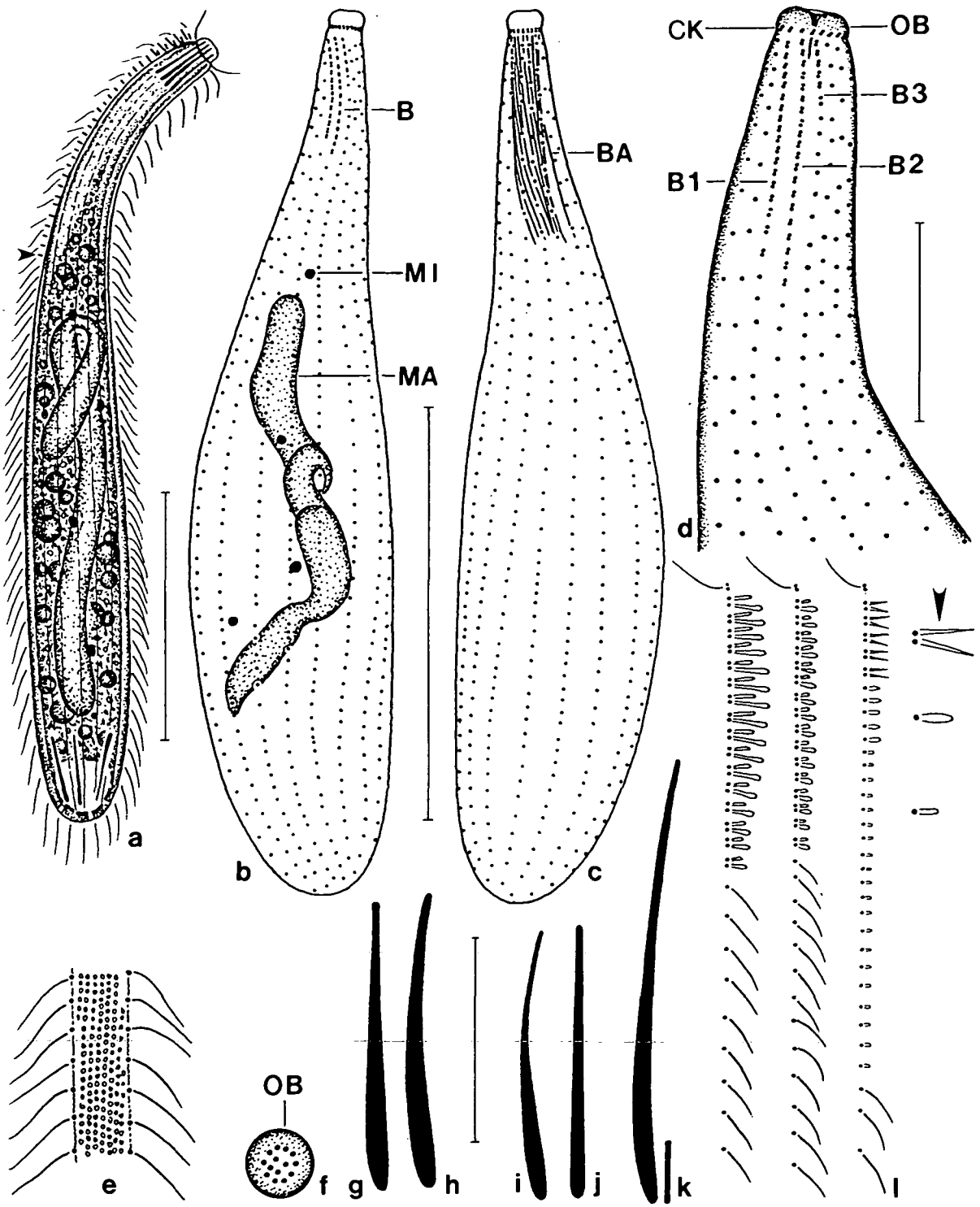

Fig. 23a–l. Tenerife (a–f, h, l) and other (g, i–k) populations of *Enchelyodon armatides* from life (a, e–l) and after protargol impregnation (b–d). **a:** Right side view. Arrow marks end of bristle tail of brush row 3. **b–d:** Ciliary pattern. **e:** Cortical granulation. **f:** Frontal view showing extrusome tips in bulge centre. **g–k:** Extrusomes of specimens from Spain, Tenerife, Namibian site (49), South Africa, and Colombia. Drawn to scale, 10 µm. **l:** Fine structure of dorsal brush, with bristles of row 3 shown at higher magnification (arrowhead). B1–3 – dorsal brush (rows), BA – oral basket, CK – circumoral kinety, MA – macronucleus, MI – micronucleus, OB – oral bulge. Scale bars 50 µm (a, b, c) and 10 µm (d, g–k).

Table 21. Morphometric data on *Enchelyodon armatides* from Namibian type location (NA), Australia (AU) and Tenerife (TE), and on *Enchelyodon kenyaensis* (KE).

Characteristics [a]	Pop	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	NA	143.5	143.0	16.7	3.8	11.6	108.0	176.0	19
	AU	108.6	105.0	16.6	4.4	15.2	87.0	145.0	14
	TE	133.3	130.0	27.8	8.4	20.9	93.0	190.0	11
	KE	114.2	110.0	23.9	6.4	20.9	76.0	155.0	14
Body, width	NA	27.9	27.0	3.8	0.9	13.6	23.0	37.0	19
	AU	25.9	26.0	2.9	0.8	11.0	20.0	30.0	14
	TE	25.9	26.0	2.8	0.9	10.8	20.0	30.0	11
	KE	23.7	24.0	5.0	1.3	21.3	17.0	36.0	14
Body length:width, ratio	NA	5.2	5.3	0.9	0.2	16.3	3.5	6.8	19
	AU	4.3	4.0	0.9	0.2	20.2	3.0	5.9	14
	TE	5.1	4.8	1.2	0.4	24.2	3.2	7.5	11
	KE	5.1	5.0	1.3	0.3	25.6	3.0	7.5	14
Oral bulge, width	NA	6.7	7.0	0.6	0.1	8.3	6.0	8.0	19
	AU	4.9	5.0	0.3	0.1	6.3	4.0	5.0	14
	TE	4.6	5.0	–	–	–	4.0	5.0	11
	KE	6.1	6.0	0.8	0.2	13.7	5.0	8.0	14
Oral bulge, height	NA	3.2	3.0	–	–	–	3.0	4.0	19
	AU	2.7	2.8	–	–	–	2.0	3.5	14
	TE	2.6	2.5	–	–	–	2.0	3.0	11
Anterior body end to macronucleus, distance	NA	47.4	48.0	4.2	1.0	8.8	38.0	53.0	19
	AU	38.0	37.0	8.6	2.3	22.5	24.0	55.0	14
Nuclear figure, length	NA	74.2	70.0	13.3	3.1	18.0	50.0	98.0	19
	AU	54.9	55.0	9.6	2.6	17.4	40.0	77.0	14
	TE	73.6	74.0	20.7	6.3	28.2	40.0	105.0	11
	KE	55.4	51.0	14.4	3.8	25.9	36.0	90.0	14
Macronucleus, length (spread) [b]	NA	93.8	92.0	–	–	–	68.0	140.0	19
	AU	73.6	70.0	–	–	–	60.0	90.0	14
Macronucleus, width	NA	5.5	6.0	1.2	0.3	21.4	3.0	8.0	19
	AU	5.6	5.0	1.5	0.4	27.0	3.0	9.0	14
	TE	4.9	5.0	–	–	–	4.0	5.0	11
	KE	6.6	6.5	0.9	0.2	13.0	5.0	8.0	14
Macronucleus, number	NA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
	AU	1.0	1.0	0.0	0.0	0.0	1.0	1.0	14
	KE	1.0	1.0	0.0	0.0	0.0	1.0	1.0	14
Micronuclei, length	NA	2.3	2.0	–	–	–	2.0	3.0	4
	TE	2.4	2.2	–	–	–	2.0	3.0	8
	KE	2.3	2.1	–	–	–	1.8	3.0	4
Micronuclei, width	NA	1.8	1.9	–	–	–	1.5	2.0	4
	TE	2.1	2.1	–	–	–	2.0	2.5	8
	KE	2.0	2.0	–	–	–	1.8	2.2	4
Micronuclei, number	several in all populations								
Somatic kineties, number	NA	14.9	15.0	1.1	0.2	7.0	14.0	17.0	19
	AU	16.0	16.0	1.0	0.3	6.5	14.0	18.0	14
	TE	16.7	17.0	1.2	0.4	7.1	14.0	19.0	11
	KE	17.0	16.0	–	–	–	16.0	19.0	3

(continued)

Characteristics [a]	Pop	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Ciliated kinetids in a ventral kinety, number	NA	46.6	48.0	8.9	2.1	19.2	30.0	61.0	19
	AU	66.4	61.0	12.6	3.4	18.9	50.0	90.0	14
	TE	59.6	56.0	14.6	4.4	24.5	30.0	80.0	11
Circumoral kinety to last dikinetid of brush row 1, distance	NA	17.0	17.0	2.5	0.6	14.5	13.0	22.0	19
	AU	17.6	18.0	3.5	0.9	19.9	12.0	25.0	14
	TE	14.5	15.0	2.6	0.8	18.1	9.0	20.0	11
Dikinetids in brush row 1, number	NA	14.7	14.0	2.6	0.6	17.8	11.0	20.0	19
	AU	18.9	19.0	2.6	6.7	13.8	14.0	23.0	14
	TE	16.2	16.0	2.7	0.8	16.8	11.0	20.0	11
Circumoral kinety to last dikinetid of brush row 2, distance	NA	17.6	18.0	2.6	0.6	14.7	13.0	22.0	19
	AU	17.5	18.0	3.5	0.9	19.8	12.0	25.0	14
	TE	15.1	15.0	3.1	1.0	20.8	9.0	21.0	11
Dikinetids in brush row 2, number	NA	15.6	16.0	3.0	0.7	19.0	10.0	21.0	19
	AU	17.9	18.0	2.5	0.7	14.1	13.0	23.0	14
	TE	16.5	16.0	2.6	0.8	15.9	11.0	21.0	11
Circumoral kinety to last dikinetid of brush row 3, distance	NA	4.7	5.0	0.8	0.2	17.5	3.0	7.0	19
	AU	4.5	4.5	0.8	0.2	16.9	3.0	6.0	14
	TE	4.4	4.0	0.9	0.3	21.2	3.0	6.0	11
Dikinetids in brush row 3, number	NA	4.1	4.0	0.7	0.2	18.0	2.0	5.0	19
	AU	4.0	4.0	0.6	0.2	13.9	3.0	5.0	14
	TE	4.6	5.0	–	–	–	4.0	5.0	11

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Approximations.

Both *Enchelyodon armatides* and *E. kenyaensis* are rather similar to *E. armatus* (KAHL, 1926), KAHL, 1930a, of which KAHL once found large numbers in a road ditch near Hamburg, Germany. However, KAHL's organism is considerably smaller (100 µm vs. 120–160 µm) and stouter (3:1 vs. 4.3–5.2:1, on average) than our species, and the monokinetidal bristle tail of brush row 3 extends above mid-body (Fig. 21c, d → *E. kenyaensis*); furthermore, it is from a limnetic habitat. Thus, it appears justified to separate the terrestrial populations as distinct species.

Further similar species: *Enchelyodon vorax* (PENARD, 1922) KAHL, 1930a, b (length 200–360 µm vs. 150–200 µm, length:width ratio 3.3:1 vs. 4.3–5.2:1); *Enchelyodon nodosus* BERGER et al., 1984 (extrusomes 30 µm vs. 10–18 µm, 76 vs. 16 ciliary rows); and *E. tratzi* FOISSNER, 1987b (highly similar, but macronucleus in 20 scattered nodules). Beginners may also confuse *E. armatides* and *E. kenyaensis* with *Trachelophyllum* s. l.; these, however, invariably have two macronuclear nodules.

Description of a population from Tenerife: Some months after we had finished the description, we recognized that this species occurs in soils globally, except of Antarctica. The notes made show that *E. armatides* invariably has an average size of between

150 µm and 200 µm and acicular extrusomes. The observations on the extrusomes will be reported in some detail because we consider them as an important feature in alpha-taxonomy of haptorid gymnostomes. Spain: acicular, 12–17 × 0.8–1 µm (Fig. 23h); Namibian site 49: acicular, 15 × 0.8–1 µm (Fig. 23i); Tenerife: acicular, 15 × 1 µm (Fig. 23g); Saudi Arabia: acicular, length 17–21 µm; Republic of South Africa: only slightly acicular, 15 µm long (Fig. 23j); Colombia (South America): acicular, 20–30 µm long; additionally 3 µm long, rod-shaped extrusomes occur, as in many haptorids (Fig. 23k). Obviously, extrusome shape is very similar in all populations (see also specimens from Namibia and Australia described above!), while length varies from 10–20 (30) µm; the Colombian population might be a distinct species or subspecies, and the extrusomes of the South African specimens are rather similar to those of *E. kenyaensis*.

The Tenerife *E. armatides* matches the Namibian and Australian specimens, as evident from a comparison of the figures (Fig. 22a–n, 23a–l) and the morphometric data (Table 21). Thus, conspecificity is beyond reasonable doubt. The following additional observations were made: (i) length usually near 150 µm; (ii) contractile by up to 30% and thus often stouter in preparations than in vivo; (iii) macronucleus rarely strongly tortuous, ends not inflated; (i) several excretory pores in posterior pole area; (v) extrusomes acicular, about 15 × 1 µm, found not only in oral bulge but also in rear end (Fig. 23a, h); (vi) cortex distinctly furrowed by ciliary rows; (vii) creeps slowly, worm-like; (viii) cilia about 7 µm long; (ix) dorsal brush highly differentiated, especially row 3, with up to 6 µm long bristles (Fig. 23 l); (x) oral and neck area hyaline, oral bulge distinctly set off from body proper.

Enchelyodon minutus **nov. spec.** (Fig. 24a–h; Table 22)

Diagnosis: Size about 60 × 15 µm in vivo; cylindroidal with distinct oral bulge. Macronucleus reniform. Oral extrusomes rod-shaped and fine, about 3 µm long. On average 10 somatic kineties with cilia very loosely spaced and approximately 14 µm long in vivo; 3 rows anteriorly modified to dorsal brush having up to 8 µm long bristles; rows 1 and 2 each composed of seven dikinetids, row 3 of three.

Type location: Mud from granitic rock-pools in a stream of the Daan Viljoen Game Park near Windhoek, Namibia, 22°35'S 17°05'E (site 73 in figure 2 and chapter 2.1.2).

Etymology: The Latin adjective *minuta* (small) refers to the small size of the organism.

Description: Size 45–90 × 12–20 µm in vivo, length:width ratio 3.1–5.6:1, on average 4:1 in protargol preparations. Shape cylindroidal to more or less distinctly clavate, both ends moderately broadly rounded (Fig. 24a, c, f, h; Table 22); unflattened and acontractile. Macronucleus in mid-body on average, ellipsoidal or reniform, rarely C-shaped. Micronucleus broadly ellipsoidal, usually attached to concave side of macronucleus. Contractile vacuole in rear body end, with single excretory pore in pole centre. Extrusomes attached to oral bulge, rod-shaped, about 3–4 × 0.2–0.3 µm in size; do not impregnate with protargol, except of posterior third, which is occasionally black (Fig. 24a, e, f). Cortex very flexible and thin, apparently without granules. Cytoplasm colourless, usually packed with fat globules up to 5 µm across, indicating a predatory mode of life. Swims rather rapidly by rotation about main body axis.

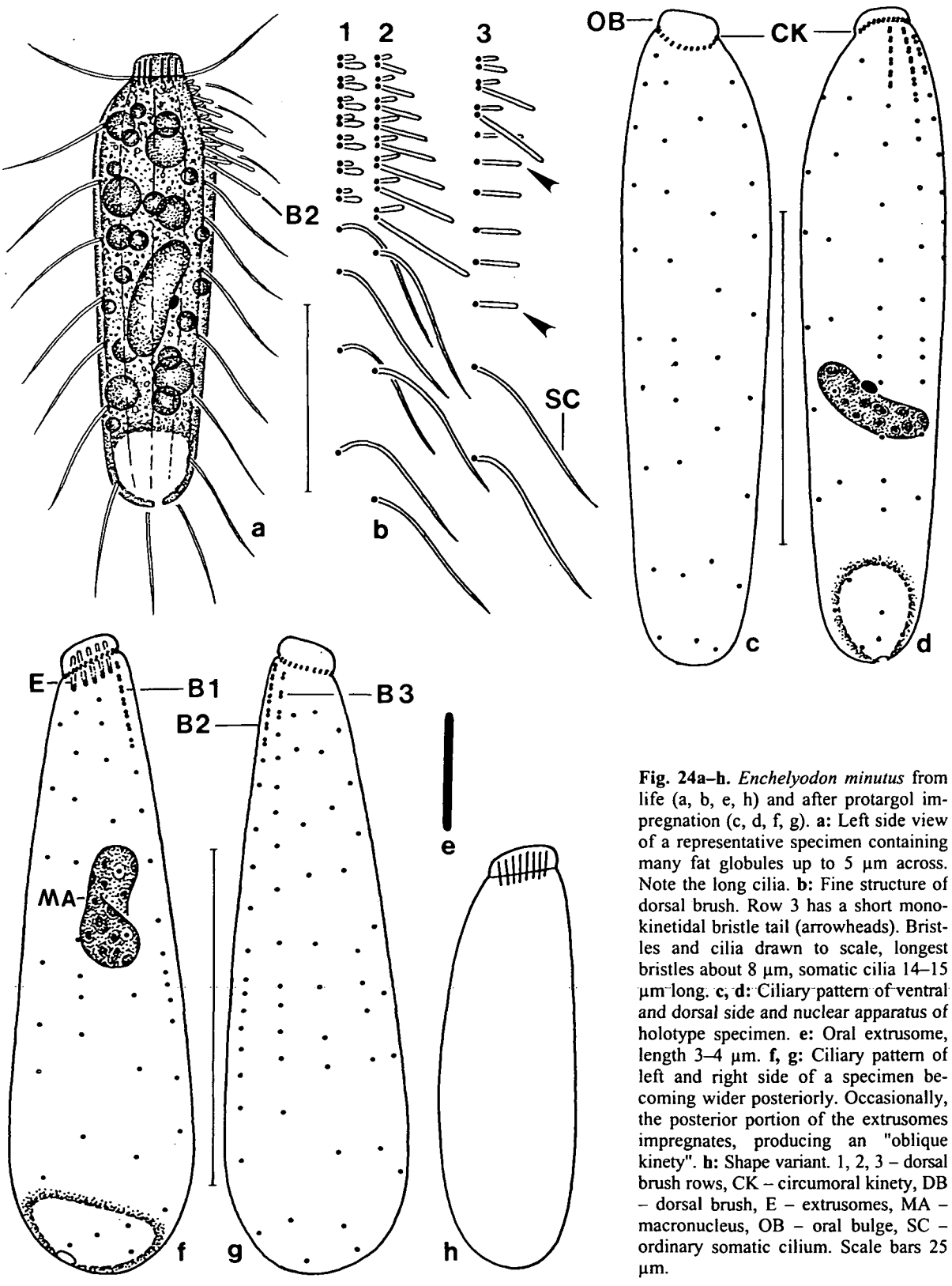

Fig. 24a–h. *Enchelyodon minutus* from life (a, b, e, h) and after protargol impregnation (c, d, f, g). **a:** Left side view of a representative specimen containing many fat globules up to 5 µm across. Note the long cilia. **b:** Fine structure of dorsal brush. Row 3 has a short monokinetidal bristle tail (arrowheads). Bristles and cilia drawn to scale, longest bristles about 8 µm, somatic cilia 14–15 µm long. **c, d:** Ciliary pattern of ventral and dorsal side and nuclear apparatus of holotype specimen. **e:** Oral extrusome, length 3–4 µm. **f, g:** Ciliary pattern of left and right side of a specimen becoming wider posteriorly. Occasionally, the posterior portion of the extrusomes impregnates, producing an "oblique kinety". **h:** Shape variant. 1, 2, 3 – dorsal brush rows, CK – circumoral kinety, DB – dorsal brush, E – extrusomes, MA – macronucleus, OB – oral bulge, SC – ordinary somatic cilium. Scale bars 25 µm.

Cilia very widely spaced (6–7 µm) and long, namely, 14–15 µm in vivo and 9–11 µm in protargol-impregnated cells (Fig. 24a); arranged in an average of ten equidistant, meridional rows distinctly shortened anteriorly, except of brush rows, which abut to the circumoral kinety; some unciliated kinetids interspersed. Dorsal brush three-rowed, although minute rather conspicuous because bristles up to 8 µm long; each row of different fine structure (Fig. 24a, b, d): row 1 composed of an average of seven dikinetids having 1 µm (anterior bristle) or 2 µm (posterior) long, inflated bristles; row 2 composed of an average of seven dikinetids having rod-shaped bristles gradually increasing in length from 2 µm anteriorly to 8 µm posteriorly; row 3 composed of only three dikinetids with bristles that also lengthen posteriorly, continues to mid-body with a monokinetidal tail composed of 3 µm long bristles.

Oral bulge rather conspicuous in vivo because about 6 µm wide and 3 µm high, slightly oblique, contains extrusomes as described above. Circumoral kinety at base of oral bulge, continuous, that is, composed of closely spaced dikinetids each with one basal body ciliated. Oral basket not recognizable either in vivo or protargol preparations (Fig. 24a, c, f; Table 22).

Table 22. Morphometric data on *Enchelyodon minutus*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body length	53.8	53.0	10.5	2.3	20.0	40.0	84.0	21
Body, width	13.7	13.0	2.0	0.4	14.7	11.0	17.0	21
Body length:width, ratio	4.0	3.9	0.6	0.1	15.7	3.1	5.6	21
Oral bulge, width	5.2	5.0	0.6	0.1	12.3	4.0	6.0	21
Oral bulge, height	2.3	2.5	–	–	–	2.0	3.0	21
Anterior body end to macronucleus, distance	21.8	21.0	8.1	1.8	36.9	9.0	42.0	21
Macronucleus, length	12.9	13.0	2.2	0.5	17.0	10.0	17.0	21
Macronucleus, width	4.7	5.0	0.6	0.1	12.4	4.0	6.0	21
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Micronucleus, length	2.1	2.0	–	–	–	1.5	2.5	9
Micronucleus, width	1.6	1.5	–	–	–	1.0	2.0	9
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	9
Somatic ciliary rows, number	10.1	10.0	0.8	0.2	8.0	9.0	12.0	21
Kinetids in a ventral kinety, number	8.4	8.0	1.6	0.4	19.4	6.0	11.0	21
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Circumoral kinety to end of brush row 1, distance	8.0	8.0	1.0	2.0	12.9	6.0	10.0	21
Dikinetids in dorsal brush row 1, number	6.7	7.0	0.6	0.1	8.7	5.0	7.0	21
Circumoral kinety to end of brush row 2, distance	8.1	8.0	1.5	0.3	19.0	6.0	11.0	21
Dikinetids in dorsal brush row 2, number	7.1	7.0	0.7	0.1	9.2	6.0	8.0	21
Circumoral kinety to end of brush row 3, distance	4.1	4.0	0.7	0.2	17.6	3.0	6.0	21
Dikinetids in dorsal brush row 3, number	3.1	3.0	–	–	–	3.0	4.0	21

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Occurrence and ecology: To date found only at type location, where it was rare in the non-flooded Petri dish culture. The biological meaning of the long cilia is obscure.

Generic classification and comparison with related specimen: This population is difficult to classify. It belongs either to *Enchelyodon*, → *Spathidium*, or *Rhopalophrya*. An enchelyodontid relationship is indicated by the general appearance, specifically, the button-shaped oral bulge on a cylindroidal trunk with meridional ciliary rows. However, the oral bulge is slightly oblique and the ciliary rows do not abut to the circumoral kinety, suggesting that our species is a highly modified *Spathidium/Arcuospathidium*. Three similar *Spathidium* species are mentioned in KAHL (1930a): *Spathidium lagyniforme* (length 100 µm; infraciliature distinctly different, according to the redescription by FOISSNER 1984); *Spathidium vermiculus* (matches almost perfectly, except for the cilia, which are short and numerous); and *Spathidium cylindricum* (also rather similar, but cortex distinctly and spirally furrowed and extrusomes 6 µm long).

Our species also resembles *Rhopalophrya crassa* KAHL, 1926, a poorly known genus and species, which, however, has a globular macronucleus and a more distinct shoulder under the oral bulge. Actually, there are many more small ciliates resembling *Enchelyodon minutus*; most are poorly known, and thus any identification is difficult. Thus, we emphasize the extraordinarily long cilia, compared to body size, a feature not shared with any other species.

***Enchelyodon megastoma* nov. spec.** (Fig. 25a–g; Table 23)

Diagnosis: Size about 200 × 100 µm in vivo; ellipsoidal to slightly dumb-bell-shaped. Macronucleus almost twice as long as cell and tortuous. Two size types (25 µm, 12 µm) of fine, rod-shaped oral extrusomes. About 130 ciliary rows, 3 differentiated to dorsal brush extending to mid-body. Oral basket broadly conical, distal diameter about 70 µm in vivo.

Type location: Mud and soil from road puddles in the Bambatsi Guest Farm, Namibia, 20°10'S 15°25'E (site 49 in figure 2 and chapter 2.1.2).

Etymology: Apposition of the Greek prefix *mega* (very large) and the Greek noun *stoma* (mouth), referring to the extraordinarily large oral basket.

Description: Size 150–260 × 65–150 µm in vivo, usually near 200 × 100 µm; length:width ratio rather stable, that is, about 2:1 both in vivo and protargol preparations (Table 23). Cells opaque and brownish at low magnification (≤ ×100). Outline slightly dumb-bell-shaped to elliptical, with anterior region usually slightly broader than posterior; unflattened, acontractile (Fig. 25a, e). Macronucleus conspicuous because almost twice as long as cell and strongly tortuous; rarely in two tortuous pieces of unequal length. Micronuclei 2–3 µm across, attached and near macronucleus, exact number difficult to count because of many similar-sized and impregnated cytoplasmic inclusions. Contractile vacuole in rear body end. Two size types of rod-shaped, fine extrusomes in oral basket and cytoplasm, do not impregnate with protargol, except of certain cytoplasmic developmental stages (Fig. 25a, b): type I slightly curved and about 20–30 × 0.4 µm in size; type II straight with pointed ends, about 12 × 0.4 µm in size. Cortex flexible, contains countless moderately refractive, about 1 × 0.4 µm-

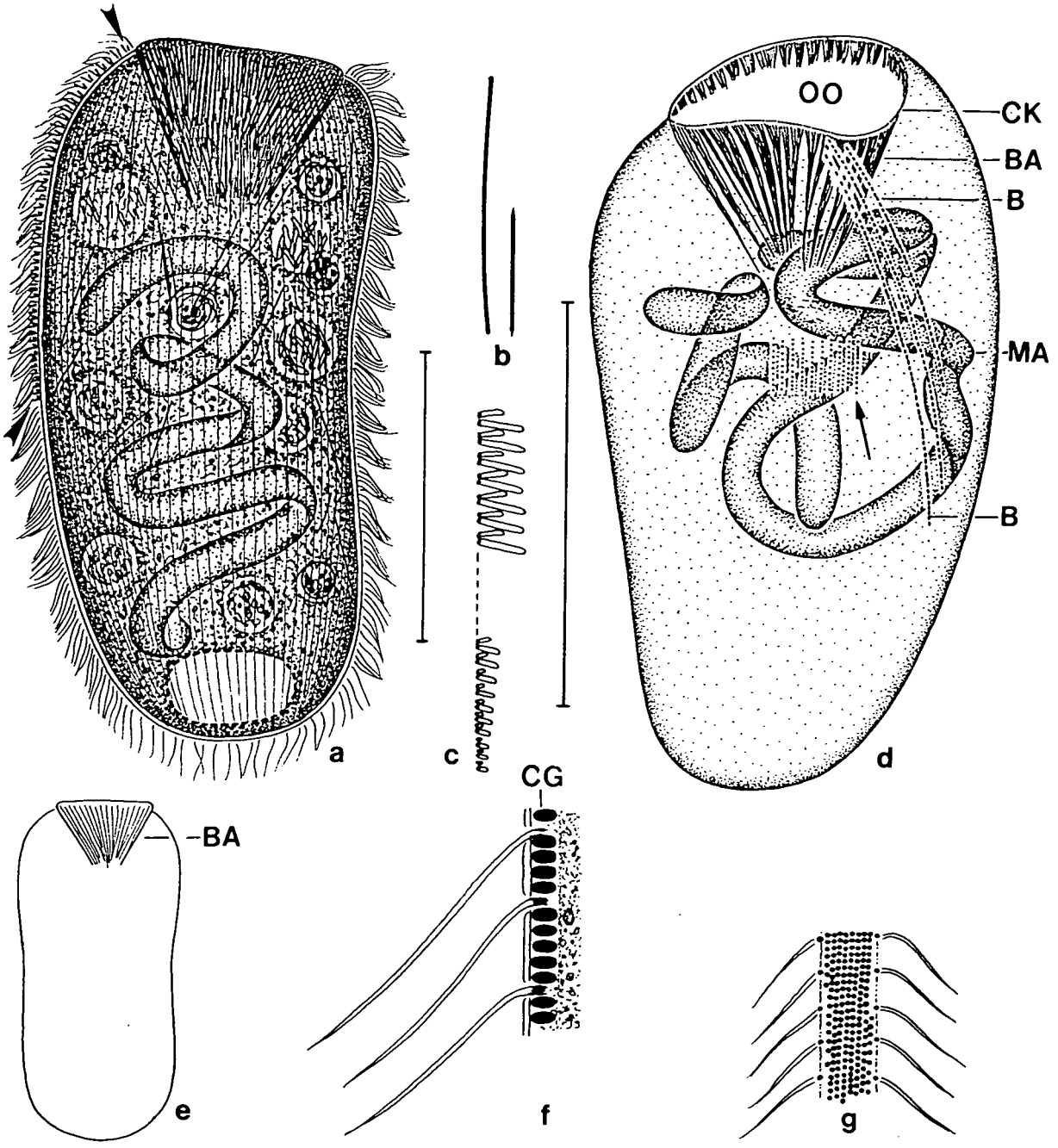

Fig. 25a–g. *Enchelyodon megastoma* from life (a–c, e–g) and after protargol impregnation (d). **a:** Right side view of a representative specimen with a size of about 200 × 100 µm; a very large oral basket; and a long, tortuous macronucleus. Note the dorsal brush which extends to mid-body (arrowheads). **b:** Oral extrusomes, length 24 µm and 12 µm. **c:** A dorsal brush row with bristles decreasing in length from 5 µm anteriorly to 1 µm posteriorly. **d:** Dorsal view showing the three long, dikinetidal dorsal brush rows; the large oral opening; and the tortuous macronucleus, which is composed of two pieces in this specimen. Arrow marks part of somatic ciliary pattern. **e:** Shape variant. **f, g:** Optical section and surface view showing the conspicuous cortical granules so narrowly spaced that a plate-like layer results. Individual granules have a size of about 1 × 0.4 µm. B – dorsal brush, BA – oral basket, CG – cortical granules, CK – circumoral kinety, MA – macronucleus, OO – oral opening. Scale bars 80 µm.

sized granules, likely mucocysts, so densely spaced that a plate-like structure results, which appears as a conspicuously bright, approximately 2 µm thick fringe under bright field illumination (Fig. 25a, f, g). Cytoplasm rather opaque due to many granules 0.2–3 µm across and 10–25 µm-sized food vacuoles containing remnants from bacteria and heterotrophic flagellates (*Polytomella*); interestingly, ciliates were not observed in the food vacuoles neither in vivo or protargol preparations. Movement conspicuous because jerky and rather quick.

As the species was rare, the infraciliature could be studied only in 10 poorly impregnated specimens. Accordingly, data are incomplete, especially morphometrics. Cilia about 12 µm long in vivo, narrowly spaced and thus forming nice metachronal waves, arranged in an average of approximately 130 meridional, equidistantly spaced rows abutting to circumoral kinety; three rows differentiated to a long dorsal brush extending from circumoral kinety to mid-body. Dorsal brush of ordinary structure, row 3 likely with a monokinetidal tail, anterior bristles of dikinetids shorter than posterior ones, bristles decrease in length from about 5 µm anteriorly to 1 µm posteriorly (Fig. 25a, c, d; Table 23).

Oral basket occupies anterior body end, highly conspicuous because extraordinarily large and strongly refractive due to the many extrusomes contained, which form a short, but very distinct, broadly conical assemblage (Fig. 25a, d; Table 23). Oral bulge in vivo circular and about 70 µm (!) across, but rather inconspicuous because flat and only 2–3 µm high. Circumoral kinety composed of narrowly spaced granules, likely dikinetids, each associated with an about 45 µm long nematodesma; neighbouring nematodesmata form conspicuous bundles producing a comparatively short, broadly conical oral basket (Fig. 25a, d).

Occurrence and ecology: To date found only at type location, where it was very rare and present only a few days in the non-flooded Petri dish culture. The blunt shape indicates that *E. megastoma* is a limnetic species.

Table 23. Morphometric data on *Enchelyodon megastoma*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	175.9	183.5	33.4	10.6	19.0	125.0	230.0	10
Body, width	98.8	95.5	20.7	6.5	20.9	65.0	140.0	10
Body length:width, ratio	1.9	1.9	0.2	0.1	10.8	1.6	2.2	10
Oral entrance, diameter	60.6	65.0	10.8	3.4	17.8	40.0	77.0	10
Oral basket, length (~)	44.0	40.0	–	–	–	35.0	70.0	10
Macronuclear figure, length	97.0	95.0	23.3	7.4	24.1	55.0	135.0	10
Macronucleus, length (spread; approximate)	320.0	325.0	–	–	–	200.0	500.0	10
Macronucleus, width	9.2	9.0	0.8	0.2	8.6	8.0	10.0	10
Distance between kineties in mid-body	2.4	2.5	–	–	–	2.0	2.5	6
Somatic kineties, number [b]	133.3	128.5	–	–	–	88.0	189.0	10

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Calculated from average kinety distance and diameter of individual specimens.

Generic classification and comparison with related species: *Enchelyodon megastoma* looks like a large prostomatid, e.g., *Holophrya teres*. However, the structure of the oral basket, the oral extrusomes, and the dorsal brush show that it belongs to the haptorid gymnostomes. Within that group, the Namibian population looks like an undescribed genus, if compared to "ordinary" *Enchelyodon* species, such as → *E. armatides* and → *E. minutus*. However, the structure of the oral bulge and dorsal brush basically match *Enchelyodon*. Indeed, *E. megastoma* looks highly similar to → *Enchelydium blattereri*, except of the flat oral bulge. A spathidiid relationship is excluded by the circular oral opening and the somatic kineties, which are not curved anteriorly.

Enchelyodon megastoma is a highly characteristic species and thus easy to identify. We did not find a similar species in the literature. On superficial observation, it may be confused with → *Holophrya salinarum* and other prostomatids.

Trachelophyllina novus subordo

Diagnosis: Spathidiida FOISSNER & FOISSNER, 1988 with epicortical scales.

Type family: Trachelophyllidae KENT, 1881.

Remarks: There are several genera, described below, with epicortical scales, which are such an extraordinary feature that separation seems warrantable at subordinal level. The oral apparatus is, as concerns the fine structural details, very similar to that of the Spathidiina (FOISSNER & FOISSNER 1988, LYNN & NICHOLLS 1985). A close relationship with spathidiids is also indicated by the brush structure, especially the monokinetidal tail of row 3.

As yet, the suborder is monotypic. There are, however, several gymnostomatids from various families and genera with a distinct mucilaginous layer. Reinvestigation with modern methods might show that they are related to the trachelophyllids, but distinct at family level. Representative examples are *Enchelys vestita* (KAHL, 1927b) and *Ileonema simplex* PENARD, 1922, which have a distinct mucilaginous envelope composed of rod-shaped, serpentine scales (Fig. 308a–e). Very likely, they represent a new trachelophylline family. Recent observations indicate that *Enchelyotricha* FOISSNER, 1987b also has a thin mucilaginous layer. Thus, this genus, which has a highly differentiated dorsal brush, might also belong, as another new family, to the Trachelophyllina.

Family Trachelophyllidae KENT, 1881

Improved diagnosis: Slender (> 5:1) and often highly contractile Trachelophyllina with three-rowed dorsal brush; brush rows 1 and 2 dikinetidal, row 3 monokinetidal.

Type genus: *Trachelophyllum* CLAPARÈDE & LACHMANN, 1859.

Remarks: In contrast to FOISSNER (1984), we assign to this family only genera with epicortical scales. Other genera are referred to a new family, → Enchelyodontidae, diagnosed above. The dorsal brush of the trachelophyllids is not composed of two rows, as stated by FOISSNER (1984), GROLIERE (1977), NICHOLLS & LYNN (1984), and SONG (1994), but of three rows as evident from our scanning electron micrographs and refined live observation with differential interference contrast optics. However, row 3, already clearly recognized by BLOCHMANN (1895) and GELEI (1933), is monokinetidal and thus difficult to distinguish from the ordinary somatic ciliary rows in silver preparations.

Here we describe and redescribe several *Trachelophyllum* species, whose ciliary pattern is very similar, while the epicortical scales are highly different, suggesting separation at genus level (Fig. 26). The epicortical scales are recognizable, albeit not easily, in all species with phase-contrast or differential interference contrast optics and after protargol impregnation (FOISSNER's method). Even some of the species-specific features are discernible, provided one knows them from the scanning electron microscope. Thus, these features are also described in detail because they may help in light microscopic species identification. Generally, however, light microscopy is insufficient for scale analysis, especially in new or supposedly new species.

The epicortical scales are rather fragile and thus subject to various preparation artifacts, such as insufficient chemical preservation and/or too high sputter energy (Fig. 309a–d). Usually, however, the species-specific pattern is recognizable even in mediocre preparations, at least in some specimens or at certain sites of individual specimens. Often, the scales are slightly smaller in the oral and neck region. Rarely, they are partially or almost completely lost in SEM-preparations, especially in a still undescribed species from South America.

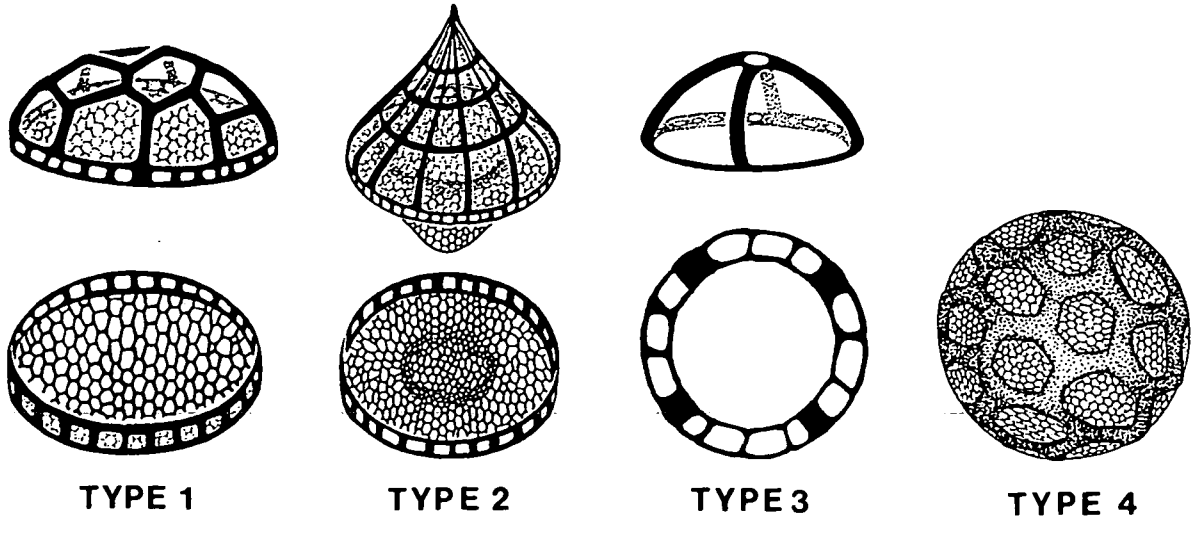

Fig. 26. Oblique lateral and baseplate views of trachelophyllid epicortical scale types (diagrammatically after scanning electron micrographs). **Type I:** Occurs in → *Trachelophyllum* and → *Bilamellophrya* and has a finely perforated, dish-shaped, ellipsoidal baseplate from which a polygonally faceted, dome-shaped superstructure emerges. **Type II:** Occurs in → *Bilamellophrya* and has a finely perforated, broadly obconical, circular baseplate from which several arcs emerge to form a conical, more or less distinctly faceted superstructure. **Type III:** Occurs in → *Epitholiolus* and has a finely perforated, flat, ring-shaped baseplate from which few, tiny arcs emerge to form a dome-shaped superstructure. **Type IV:** Occurs in *Spetazoon* FOISSNER, 1994c and is spherical with a finely perforated baseplate to which a widely-faceted, polygonal superstructure is attached.

We shall describe the epicortical scales of two known and six new species. Two other species have been described previously (FOISSNER 1994c, NICHOLLS & LYNN 1984). Thus, the scales of nine species are known. Possibly, formerly most of these species would have been classified in two or three species! However, the scales are so different that species status of the nine populations is beyond any doubt. Indeed, only two of the populations investigated with the scanning electron microscope have very similar scales (→ *Trachelophyllum costaricanum*), indicating a high diversity of the group. Very likely, trachelophyllids are an excellent model for exploring ciliate diversity, which is controversialy discussed (see chapter 3.1.6.1).

Trachelophyllum CLAPARÈDE & LACHMANN, 1859

1859 *Trachelophyllum* CLAPARÈDE & LACHMANN, Mém. Inst. natn. génev., 6: 306.
1984 *Lepidotrachelophyllum* n. g. NICHOLLS & LYNN, J. Protozool., 3: 418 (new synonym).

Improved diagnosis: Trachelophyllidae KENT, 1881 with type I scales (a polygonally faceted, dome-shaped superstructure emerges from the flat, ellipsoidal baseplate).

Type species (subsequently designated by KENT, 1881): *Trachelius apiculatus* PERTY, 1852.

Remarks: Fortunately, we rediscovered and could study in detail the type species. This showed that the genus *Lepidotrachelophyllum* NICHOLLS & LYNN, 1984 is a junior synonym because it possesses the same scale type and ciliary pattern as → *T. apiculatum*.

As mentioned above, the ciliary pattern and general appearance are very similar in all trachelophyllids investigated so far; and there are many other, not yet described, similar-looking species (→ *Trachelophyllum africanum* and *Bilamellophrya* spp.). The epicortical scales and extrusomes, in contrast, are highly different. As both have not been studied previously, it will never be possible to be sure about the identity of the species described in the old literature. We can only assign them more or less arbitrarily and must neotypify the species with the scale and extrusome data now available. This may cause problems with article 70 of the ICZN (1999) in cases where the generic type species are concerned. If later authors reach different conclusions, the case must be referred to the Commission.

Even if SEM scale data are available, a few "classic" features must also be studied for a reliable species identification, viz. the nuclear apparatus (single nodule; two widely separated nodules; two abutting nodules with a micronucleus in between) and the extrusomes (size and shape, presence/absence), which must be investigated in live specimens because they usually do not impregnate with protargol and/or change size and shape significantly in preparations. In our experience, most species are definitely assignable only by their cortical scales and extrusomes!

The taxonomic value of several other features, such as details of the dorsal brush (bristles in parallel or V-like spread), the shape of the body and oral bulge, and the extent of body

contractility, is unknown. Nonetheless, they should be described because they might become important in future.

Trachelophyllum apiculatum (PERTY, 1852) CLAPARÈDE & LACHMANN, 1859 (Fig. 27a–y; 310a–t; Tables 24, 25)

1852 *Trachelius apiculatus* PERTY, Zur Kenntniss kleinster Lebensformen, p. 151.
1859 *Trachelophyllum apiculatum* (PERTY) — CLAPARÈDE & LACHMANN, Mém. Inst. natn. génev., 6: 306.
1922 *Trachelophyllum apiculatum* (PERTY) CLAP. et LACHM. (1859) — PENARD, Études Infusoires, p. 51 (redescription from life).
1930 *Trachelophyllum apiculatum* PERTY, 1852 — KAHL, Tierwelt Dtl., 18: 115 (revision).
1983 *Trachelophyllum apiculatum* PERTY, 1852 — FOISSNER, Annln naturh. Mus. Wien, 84/B: 69 (redescription from life and after protargol impregnation).
1984 *Trachelophyllum apiculatum* (PERTY, 1852) — FOISSNER, Stapfia, 12: 50 (redescription form life and after protargol impregnation).
1995 *Trachelophyllum apiculatum* (PERTY, 1852) CLAPARÈDE & LACHMANN, 1859 — FOISSNER, BERGER, BLATTERER & KOHMANN, Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft, 1/95: 180 (review on taxonomy and ecology).

Neotype material: Neotypified from soil of a small salt pan in the Morrocoy National Park at the north coast of Venezuela (11°N 68°W), according to reasons 1–6 given in chapter 2.4.2. The very flat pan, which was dry when the sample was taken, was about 500 m inshore and covered with halophytes. Soil moist, brownish, with many fine roots, highly saline, pH 7.3. The sample from the top 0–5 cm layer included surface plant litter and algal crusts and contained 60 ciliate species, of which several were new. The second population, which was not studied in detail because it matched the redescriptions by FOISSNER (1983b, 1984), occurred in a soil sample from a rice field near Tsukuba, Japan.

Improved diagnosis (mainly based on Venezuelan neotype population): Size in vivo usually 100–200 × 15–30 µm, contractile by up to 50% of body length; slenderly claviform. 2 ellipsoidal, widely distant macronuclear nodules with a micronucleus each. Extrusomes rod-shaped, 10–20 µm long. Usually 10–15 ciliary rows. Epicortical scales about 1.3 × 0.8 µm and with an average of 11 polygons in hemispherical superstructure.

Description of Venezuelan neotype population (Fig. 27a–j, l, q, t; 310f–t): Size of extended specimens 130–200 × 20–30 µm in vivo; length:width ratio about 7:1, in protargol preparations 3–9:1, on average 5.7:1 (Table 25); up to 2:1 flattened dorsoventrally. Slenderly clavate to fusiform with neck slightly widened in oral region and gradually merging into broadened trunk; anterior end (oral bulge) cylindroidal, posterior narrowly rounded (Fig. 27a, b, l; 310f–i, k). Cells very flexible and contractile by up to 50% of body length, especially in neck region; partially contracted specimens clavate (Fig. 310f); contracts and extends slowly, preserved specimens thus of similar size and shape as live ones. Nuclear apparatus in trunk. Macronuclear nodules globular to slenderly ellipsoidal (3:1), on average 1.7:1, stand out as bright blisters from granulated cytoplasm, usually distinctly apart and connected by a fine strand, very rarely abutting or only a single nodule (in 6 out of 290 specimens analyzed); nucleoli scattered, minute, globular to elongate. Micronuclei usually

attached to, rarely distant from macronuclear nodules, globular to ellipsoidal (Fig. 27a, l; 310h). Contractile vacuole in rear end, a conspicuous pore in pole centre. Oral bulge extrusomes about 10 × 0.3 µm in vivo, rod-shaped and slightly curved, do not impregnate with protargol, become acicular just before release and up to 30 µm long when exploded (Fig. 27a, d–f; 310j); developing extrusomes usually darkly impregnated, acicular or fusiform and 7–9 µm long (Fig. 27c; 310 l). Cytoplasm and movement without peculiarities. Probably feeds on ciliates and flagellates.

Cortex thin and flexible, contains scattered, colourless granules about 0.3 µm across and faintly impregnated fibres (microtubule ribbons?) obliquely extending from basal bodies anteriorly and posteriorly, forming two rather distinct bundles between each two ciliary rows; furthermore, a short fibre (kinetodesma?) extends right-laterally from each ciliated kinetid (Fig. 27q). Mucilaginous layer inconspicuous because very hyaline and only 1–2.5 µm thick both in vivo and protargol preparations, produces tuberculate body surface because composed of two to three layers of hemispherical epicortical scales (Fig. 27a, j, l; 310 l, m, q). Scales broadly (1.5:1) to slenderly (2.5:1) ellipsoidal, on average 1.3 × 0.8 µm, hemispherical superstructure composed of an average of 11 widely faceted polygons; baseplate dish-shaped, finely faceted, including dish margin, central area slightly to distinctly convex (Fig. 27t; 310k, n–p, r–t; Table 23).

Cilia in vivo 10–12 µm long, rather widely spaced, many unciliated granules (kinetids?) in line with ciliated ones. Ciliary rows meridionally and equidistantly arranged, three of them differentiated to dorsal brush rows anteriorly (Fig. 27a, h, i, l; 310g, n; Table 25). Brush row 1 about one quarter (four dikinetids on average) shorter than row 2, composed of fairly widely spaced dikinetids bearing acicular, V-like spread, immobile bristles about 3 µm long in vivo and about 5 µm in protargol preparations; bristles obliquely attached to body surface and thus entirely covered by epicortical scale layer and not recognizable in the scanning electron microscope (Fig. 310n). Brush row 2 like row 1. Brush row 3 extends to mid-body, composed of monokinetids having about 3 µm long, acicular (rod-shaped in SEM micrographs), immobile bristles projecting at right angles from body proper and piercing scale layer; thus recognizable in scanning electron micrographs (Fig. 310n). All brush rows continue posteriorly as ordinary somatic ciliary rows.

Oral bulge rather inconspicuous, about 4 × 4 µm, distinctly set off from body proper, in vivo cylindrical, in protargol preparations conical in about 50% of specimens, not covered by epicortical scales. Circumoral kinety at base of oral bulge, composed of about 12 rather widely spaced dikinetids, each bearing a single cilium; gives rise to delicate fibres extending anteriorly and to fine nematodesmata forming conical, ventricose basket (Fig. 27a, b, g, l; 310g–i, k).

Occurrence and ecology: *Trachelophyllum apiculatum* has been recorded from soils world-wide (FOISSNER 1998a) and from many freshwater and brackish habitats (FOISSNER et al. 1995). However, many records and autecological data, which were comprehensively reviewed by FOISSNER et al. (1995), are possibly based on misidentifications, as explained in the genus discussion above. However, the species is likely the most frequent one of the genus, according to our experience; but the varying thickness and distinctiveness of the epicortical scale layer indicate that it might be a species complex.

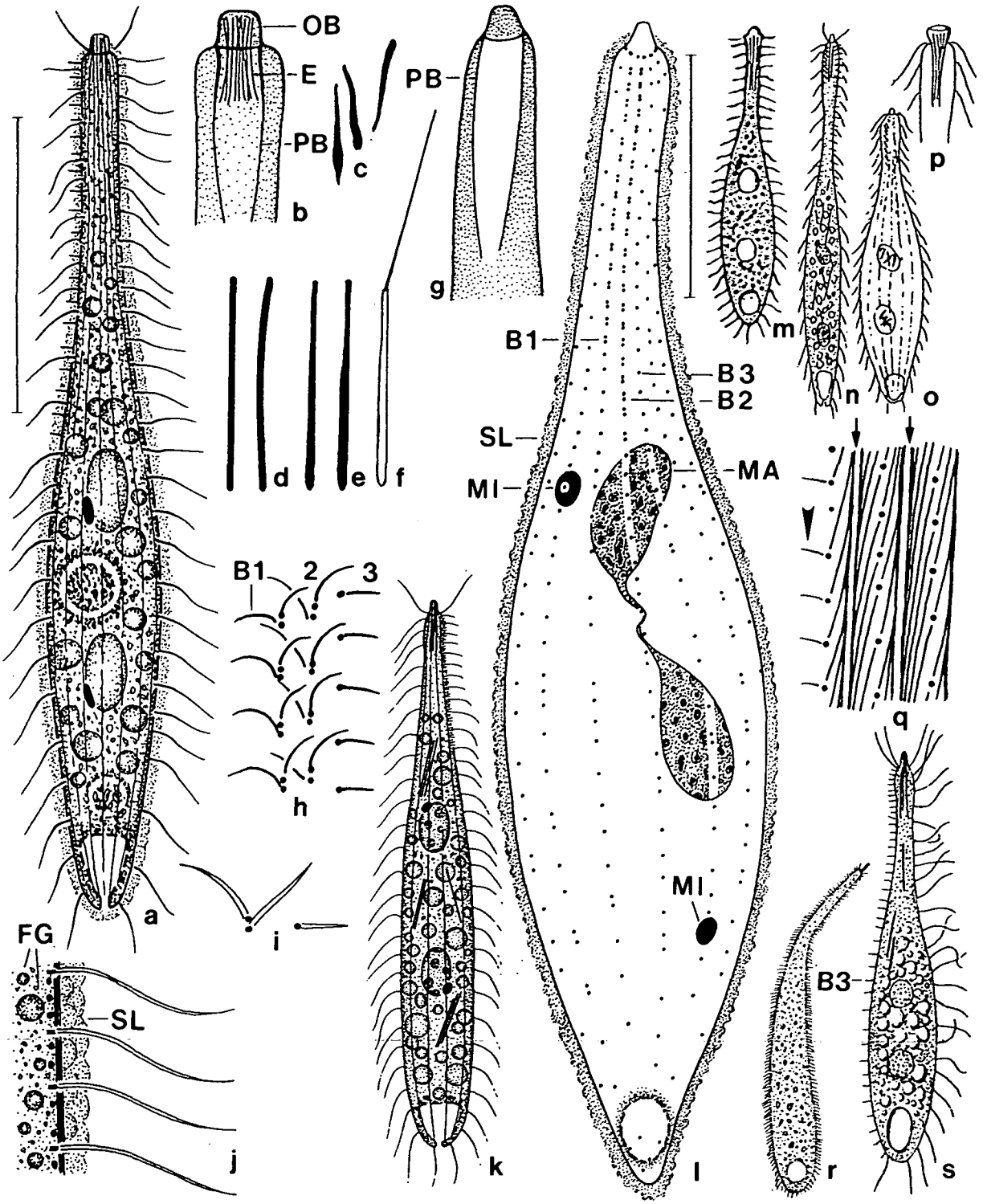

Fig. 27a–s. *Trachelophyllum apiculatum*, Venezuelan neotype population (a–j, l, q) and other populations (k, m–p, r, s) from life (a, b, d–f, i–k, m–p, r, s) and after protargol impregnation (c, g, h, l, q). **a:** Right lateral view of an extended, representative specimen with a thin and very hyaline epicortical slime (scale) layer. **b, g:** Oral area at higher magnification in vivo and after protargol impregnation. Note different shape of oral bulge. **c:** Developing extrusomes are acicular and impregnate with protargol. **d:** Fully developed, resting extrusomes are 10 µm long, curved rods, which do not impregnate with protargol. **e:** Extrusomes are slightly acicular just before exploding. **f:** Exploded toxicyst. (Continued on opposite page.)

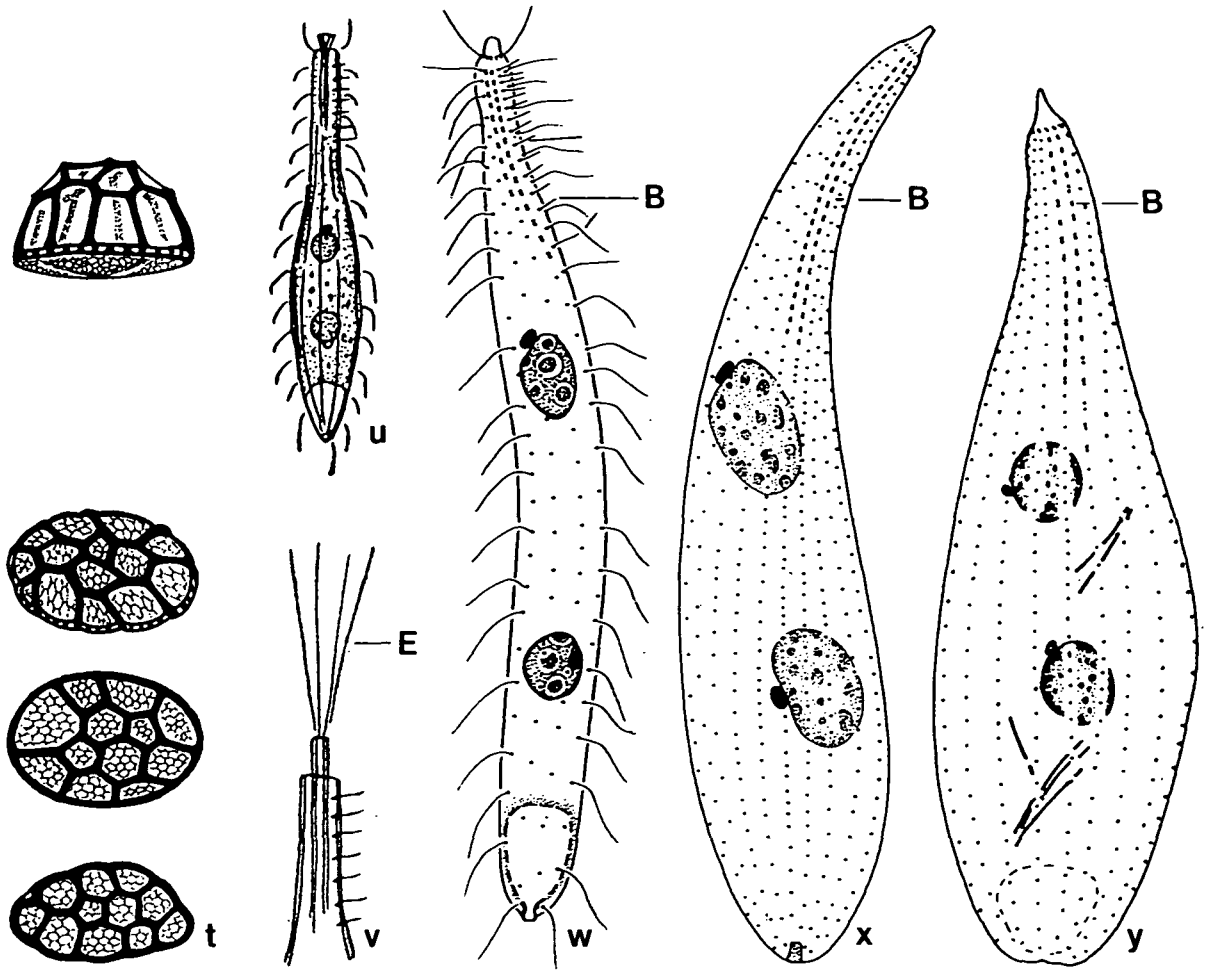

Fig. 27t–y. *Trachelophyllum apiculatum* in the scanning electron microscope (t), from life (u, v), and after protargol impregnation (w–y). **t:** Lateral and surface views of epicortical scales of Venezuelan neotype population, scale size about 1.3 × 0.8 × 0.8 µm. **u, v:** Specimens studied by PENARD (1922), 125 µm when contracted, up to 280 µm when extended. **w:** Ciliary pattern of dorsal side of the Austrian soil population studied by FOISSNER (1984), length 110 µm (life aspect shown in figure 27k). **x:** Ciliary pattern of dorsal side of a population from a pond in Salzburg, Austria, length 105 µm (from FOISSNER 1984). **y:** Ciliary pattern of dorsal side of the Chinese soil population investigated by SONG (1994), length 75 µm.

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h, i: Ciliature of dorsal brush (cp. figure 310g). **j:** Optical section of cell periphery. The mucilaginous layer is tuberculate by the dome-shaped epicortical scales. **k:** Representative specimen from a soil in Austria, length 140 µm (from FOISSNER 1984). **l:** Ciliary pattern of dorsal side of neotype specimen. **m:** *Trachelophyllum tachyblastum*, a supposed junior synonym of *T. apiculatum*, length 127–152 µm (from STOKES 1884). **n–p:** Various populations studied by KAHL (1926), length 100–350 µm. **q:** Cortical fibre system. Arrows mark bundles formed by overlapping individual fibres. Arrowhead marks a short, right-laterally extending fibre, possibly the kinetodesma. **r:** Type specimen, length 170 µm (from PERTY 1852). It is highly similar to the Venezuelan neotype specimen shown in Fig. 310e. **s:** Dorsal brush row 3 extends to posterior body end in the population studied by BLOCHMANN (1895). B1-3 – dorsal brush rows, E – extrusomes, FG – fat globules, MA – macronuclear nodules, MI – micronuclei, OB – oral bulge, PB – pharyngeal basket, SL – scale (slime) layer. Scale bars 30 µm.

Table 24. Main morphometrics of *Trachelophyllum apiculatum* populations.

Author	Body, length in vivo (µm)	Extrusomes, length (µm)	Ciliary rows, number	Habitat
PENARD (1922)	125–280	~40	~10	freshwater
DRAGESCO (1966)	200	~20	16–20	freshwater
CZAPIK & JORDAN (1976a)	130–150	~20	16–18	brackish water
FOISSNER (1983b)	90–110	13	8–11	freshwater
FOISSNER (1984), pop. I	120–150	14	11–12	soil
FOISSNER (1984), pop. II	100–170	21	22–25	freshwater
SONG (1994)	50–80 [1]	12–18	19–22	soil
Venezuelan neotype	130–200	10	12–16	soil

[1] Possibly from prepared specimens.

Identification: The Venezuelan population largely corresponds to *T. apiculatum* as redescribed by BLOCHMANN (1895; Fig. 27s), PENARD (1922; Fig. 27u, v), KAHL (1926; Fig. 27n–p), DRAGESCO (1966), CZAPIK & JORDAN (1976a), FOISSNER (1983b, 1984; Fig. 27k, w, x), and SONG (1994; Fig. 27y). It is also similar to the synonym proposed by KAHL (1930a), viz., *Trachelophyllum tachyblastum* STOKES, 1884 (Fig. 27m), and to the original description (Fig. 27r), which is, however, too incomplete for a definite identification[3]. On the other hand, considerable differences are evident between some of the populations listed in table 24, indicating confusion of at least two species (one with about 10–15 and another with about 15–25 ciliary rows). Furthermore, the shape of the oral bulge and the distinctiveness of the mucilaginous layer seem to be different in some populations. However, the mucilaginous layer is very hyaline in this species and hardly recognizable without interference contrast optics, and the bulge shape is fragile in general. Accordingly, these features must not be over-interpreted and are of hardly any use for a subsequent assignment of populations. In this situation, improved characterization by the epicortical scales and neotypification are the only way to bring some order to the chaos.

Table 25. Morphometric data on *Trachelophyllum apiculatum* (Venezuelan neotype population, upper line) and *T. africanum* from type location (middle line) and Namibian site (30; lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	148.2	145.0	23.9	5.2	16.1	92.0	180.0	21
	151.0	150.0	25.1	7.6	16.6	120.0	207.0	11
	120.0	116.0	18.4	5.3	15.3	91.0	157.0	12

(continued)

[3] Translation of PERTY's original description (from German; Fig. 27r): "Slender, gradually tapering anteriorly ending in a rounded nib. Length about 170 µm. Near Bern, Switzerland. Colourless, with scattered vacuoles and globules. Anterior region finely striated by ciliary rows; cilia very fine and thus hardly recognizable. Body flattened. Contractile vacuole in posterior end. Moves slowly and gropingly".

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, width [b]	25.9	25.0	6.4	1.4	24.8	18.0	47.0	21
	20.0	20.0	3.7	1.1	18.5	15.0	26.0	11
	26.3	26.0	5.2	1.5	19.6	19.0	34.0	12
Oral bulge, height	3.7	4.0	–	–	–	3.0	5.0	21
	2.9	3.0	–	–	–	2.5	3.0	11
	2.9	3.0	–	–	–	2.0	3.0	12
Oral bulge, maximum diameter	3.9	4.0	–	–	–	3.0	5.0	21
	4.1	4.0	–	–	–	3.5	5.0	11
	4.0	4.0	–	–	–	3.0	4.0	12
Anterior body end to first macronuclear	53.5	53.0	11.5	2.5	21.5	30.0	74.0	21
nodule, distance	60.8	58.0	10.8	3.2	17.7	45.0	78.0	11
	53.2	49.0	13.2	3.8	24.8	37.0	80.0	12
Circumoral kinety to last dikinetid of brush	37.9	36.0	9.4	2.0	24.7	23.0	65.0	21
row 1, distance	34.8	34.0	9.6	2.9	27.5	23.0	53.0	11
	35.3	35.5	6.0	1.7	17.0	23.0	45.0	12
Brush row 1, number of dikinetids	18.3	18.0	3.3	0.7	17.9	10.0	24.0	21
	11.3	11.0	1.8	0.5	15.9	9.0	14.0	11
	18.1	17.0	3.4	1.0	18.6	15.0	27.0	12
Circumoral kinety to last dikinetid of brush	43.8	45.0	9.4	2.1	21.5	30.0	75.0	21
row 2, distance	42.7	45.0	11.9	3.6	27.8	25.0	63.0	11
	34.1	35.0	6.6	1.9	19.4	23.0	47.0	12
Brush row 2, number of dikinetids	21.8	22.0	2.3	0.5	10.5	17.0	26.0	21
	16.3	17.0	3.8	1.1	23.2	10.0	22.0	11
	17.9	18.0	4.3	1.3	24.2	12.0	29.0	12
Anterior macronuclear nodule, length [c]	14.8	15.0	2.7	0.6	18.3	11.0	20.0	21
	17.6	18.0	2.3	0.7	13.3	14.0	20.0	11
	13.5	13.5	3.3	1.0	24.6	9.0	20.0	12
Anterior macronuclear nodule, width [c]	8.4	8.0	1.4	0.3	16.6	7.0	11.0	21
	6.6	7.0	0.8	0.2	12.5	5.0	8.0	11
	7.9	8.0	1.4	0.4	17.5	6.0	10.0	12
Macronuclear nodules, distance in	16.8	15.0	8.8	1.9	52.4	0.0	35.0	21
between	20.3	17.0	9.0	2.7	44.6	9.0	37.0	11
	15.2	15.5	8.5	2.5	56.0	0.0	28.0	12
Macronuclear nodules, number [d]	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	12
Micronuclei, length	4.5	5.0	0.8	0.2	16.9	3.0	6.0	21
	5.3	5.0	–	–	–	5.0	6.0	11
	3.9	4.0	0.8	0.3	21.3	3.0	5.0	11
Micronuclei, width	3.1	3.0	0.6	0.1	18.1	2.0	4.0	21
	2.5	3.0	–	–	–	2.0	3.0	11
	2.3	2.0	0.3	0.1	15.1	2.0	3.0	11
Micronuclei, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
	1.7	2.0	–	–	–	1.0	2.0	10
Somatic ciliary rows, number	13.3	13.0	1.1	0.2	8.0	12.0	16.0	21
	13.5	13.0	1.1	0.3	8.4	12.0	15.0	11
	13.0	13.0	1.3	0.4	9.8	11.0	15.0	12

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Kinetids in a ventral kinety, number [c]	39.5	40.0	8.8	1.9	22.4	25.0	61.0	21
	36.0	38.0	6.8	2.0	18.8	23.0	45.0	11
	39.0	40.0	7.5	2.3	19.3	20.0	50.0	11
Dikinetidal brush rows, number [f]	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	12
Mucilaginous layer, thickness	1.8	2.0	–	–	–	1.0	3.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
Epicortical scales, length [g, h]	1.3	1.3	0.2	0.02	11.7	1.0	1.6	38
	1.0	1.0	0.2	0.01	15.6	0.8	1.6	34
Epicortical scales, width [g, h]	0.8	0.8	0.1	0.01	10.0	0.6	0.9	38
	0.6	0.6	0.1	0.02	15.0	0.5	0.8	34
Epicortical scales, number of polygons in superstructure [g, h]	10.6	11.0	1.2	0.2	11.3	8.0	13.0	38
	12.4	12.0	3.9	1.7	31.2	7.0	21.0	34

[a] Data based, if not otherwise stated, on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Without mucilaginous (scale) layer.

[c] From specimens with two macronuclear nodules.

[d] Of 290 specimens analyzed, 284 have two macronuclear nodules, 6 have only one nodule.

[e] Ciliated and unciliated kinetids were counted.

[f] Row 3 is monokinetidal (see description).

[g] From SEM micrographs.

[h] Upper line: *Trachelophyllum apiculatum*, Venezuelan neotype population. Lower line: *Trachelophyllum africanum*, Venezuelan population.

Trachelophyllum africanum nov. spec. (Fig. 28a–n; 311a–m; Table 25)

Diagnosis: Size about 200 × 25 µm in vivo, contractile by up to 50% of body length; slenderly claviform. 2 ellipsoidal, widely distant macronuclear nodules with a micronucleus each. Extrusomes narrowly lanceolate, about 3.5 µm long. On average 13 ciliary rows. Epicortical scales of a Venezuelan population about 1 × 0.6 µm and with an average of 12 polygons in hemispherical superstructure.

Type location: Soil from margin of Sirkelsvlei, a small lake in the centre of the Cape of Good Hope Nature Reserve, Republic of South Africa, 34°15'S 18°25'E.

Etymology: Named after the continent discovered.

Description: Three likely conspecific populations were studied. However, the diagnosis contains only the population from the Republic of South Africa, except for the fine structure

of the epicortical scales.

Extended specimens 150–250 × 20–30 µm in vivo; length:width ratio about 8:1, in protargol preparations 6:1-14:1, on average 7.5:1 (Table 25); slightly to up to 2:1 flattened dorsoventrally. Slenderly clavate with neck slightly widened in oral region and gradually merging into broadened trunk, anterior end (oral bulge) cylindroidal, posterior rounded (Fig. 28a–c; 311a). Cells very flexible and contractile by up to 50% of body length, showing *Euglena*-like convulsions under slight cover glass pressure; contracts and extends slowly, preserved specimens thus of similar size and shape as live ones. Nuclear apparatus in trunk, of 30 specimens analyzed, 27 had two macronuclear nodules, 2 had three, and 1 possessed only a single nodule. Macronuclear nodules ellipsoidal (2:1) to elongate ellipsoidal (3:1), on average 2.7:1, stand out as bright blisters from granulated cytoplasm, usually distinctly apart and connected by a fine strand. Micronuclei usually attached to macronuclear nodules, ellipsoidal to elongate ellipsoidal. Contractile vacuole in posterior end, with conspicuous pore in pole centre. Oral bulge extrusomes sparse, that is, bulge contains 2–5 organelles only, narrowly lanceolate and 3–4 µm long in vivo and protargol preparations, distinctly clavate and 8–10 µm long when exploded (Fig. 28a–e, h, i; 311b, c). Cytoplasm and movement without peculiarities. Feeds on resting cysts of *Vorticella* and very likely also on medium-sized active ciliates and flagellates.

Cortex thin and flexible, contains scattered, colourless granules and a fibre system as described in → *T. apiculatum*. Mucilaginous layer very hyaline and 2–3 µm thick in vivo, produces tuberculate body surface because composed of hemispherical scales, whose faceted superstructure causes minute, granular condensations on surface of scale layer (Fig. 28a, b, e, g; 311d); becomes more distinct in almost desiccated specimens (Fig. 311f). Epicortical scales of a Venezuelan population 0.8–1.6 × 0.5–0.8 µm in size and with 7–21 polygons in hemispherical superstructure (Fig. 311g–m).

Cilia about 12 µm long in vivo, rather widely spaced, many unciliated granules (kinetids?) in line with ciliated ones. Ciliary rows meridionally and equidistantly arranged, three of them differentiated to dorsal brush rows anteriorly (Fig. 28a, b, e, f; 311a, c). Brush row 1 about a quarter (six dikinetids on average) shorter than row 2, composed of widely spaced dikinetids bearing acicular, V-like spread bristles; anterior bristle about 1 µm long, posterior about 4 µm. Brush row 2 similar to row 1, anterior bristle of dikinetids about 2.5 µm long, posterior about 6 µm. Brush row 3 extends to mid-body, composed of monokinetids having about 3 µm long bristles projecting at right angles from body proper. All brush rows continue posteriorly as ordinary somatic ciliary rows.

Oral bulge in vivo cylindroidal, about 4 × 4 µm, very fragile becoming conical at even the slightest cover glass pressure (Fig. 28h, i) and in preserved specimens (Fig. 311b). Circumoral kinety at base of oral bulge, composed of about 12 rather widely spaced dikinetids each bearing a single cilium; give rise to delicate fibres extending anteriorly and to fine nematodesmata forming conical, ventricose basket (Fig. 28c, e, h, i; 311b, c).

Observations from other populations: A similar population occurred at Namibian site 30 (Fig. 28j–n; 311e, f; Table 25). It matches *T. africanum* in habitat and most morphological and morphometrical features, except for the following details: size (about 150 × 16 µm vs. 200 × 25 µm in vivo), dorsal brush (rows 1 and 2 of same length vs. row 1 slightly longer than row 2), and shape and size of the extrusomes (rod-shaped and only about 1 µm long vs. elongate lanceolate and 3.5 µm long). These inconspicuous differences indicate

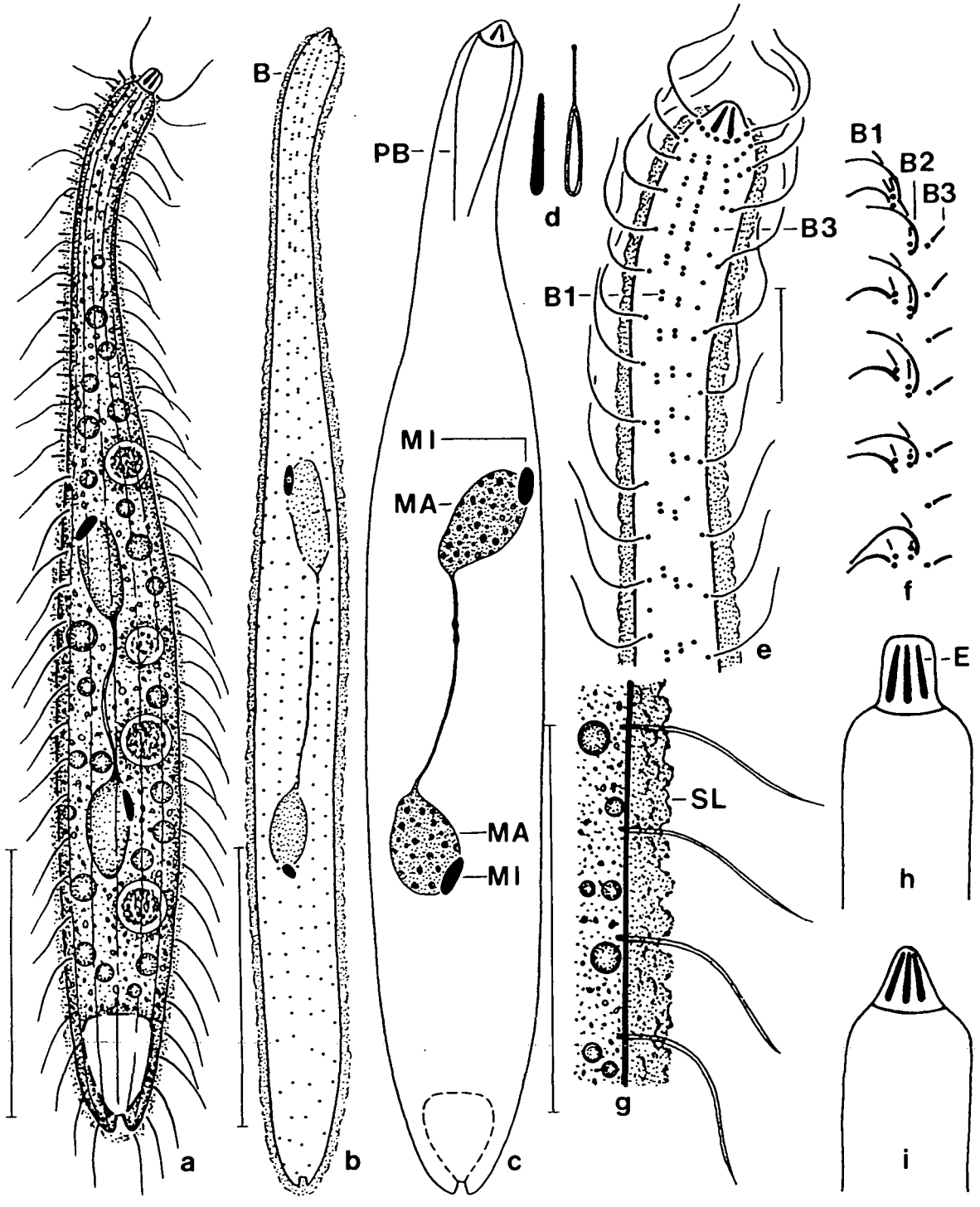

Fig. 28a–i. *Trachelophyllum africanum* from life (a, d, h, i) and after protargol impregnation (b, c, e–g). **a:** Dorsolateral view of a representative specimen. **b, c, e:** Ciliary pattern and nuclear apparatus of a very slender and a moderately broad specimen. **d:** Resting (3.5 µm) and exploded (8 µm) oral bulge extrusome. **f:** Ciliature of dorsal brush, longest bristles 6 µm. **g:** Optical section showing tuberculate mucilaginous layer. **h, i:** Anterior body end of same specimen, undisturbed and disturbed. B1-3 – dorsal brush rows, E – extrusomes, MA – macronuclear nodules, MI – micronuclei, PB – pharyngeal basket, SL – epicortical scale layer. Scale bars 50 µm (a–c) and 10 µm (e).

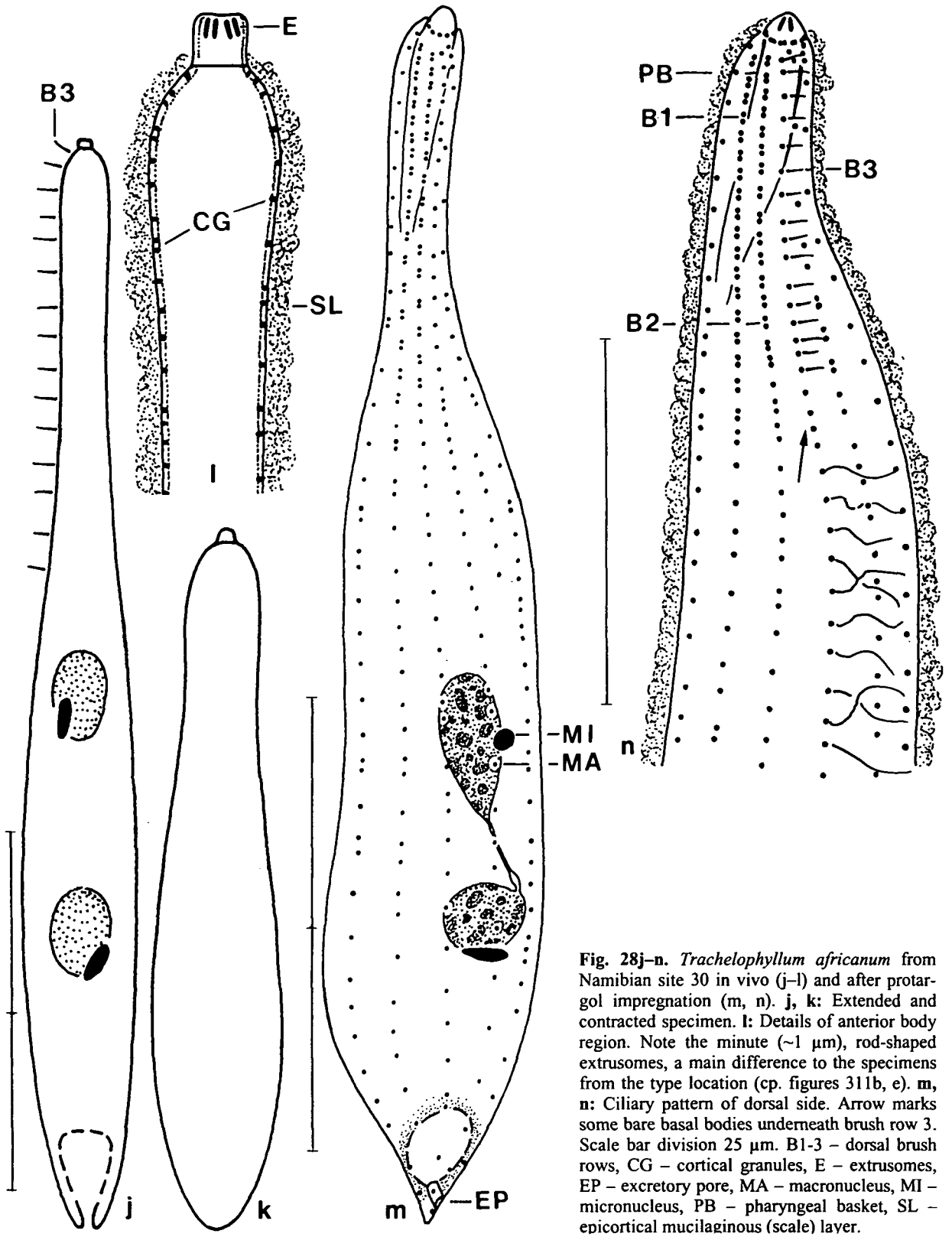

Fig. 28j–n. *Trachelophyllum africanum* from Namibian site 30 in vivo (j–l) and after protargol impregnation (m, n). **j, k:** Extended and contracted specimen. **l:** Details of anterior body region. Note the minute (~1 µm), rod-shaped extrusomes, a main difference to the specimens from the type location (cp. figures 311b, e). **m, n:** Ciliary pattern of dorsal side. Arrow marks some bare basal bodies underneath brush row 3. Scale bar division 25 µm. B1-3 – dorsal brush rows, CG – cortical granules, E – extrusomes, EP – excretory pore, MA – macronucleus, MI – micronucleus, PB – pharyngeal basket, SL – epicortical mucilaginous (scale) layer.

conspecificity, which is supported by the epicortical scale layer, which appears very similar in the light microscope. On the other hand, the differences in the extrusomes, which occurred also in the population from the Hluhluwe Game Reserve, South Africa, might justify subspecies rank. However, in the absence of detailed scale data, we prefer to lump all populations in a single species, *T. africanum*.

Very recently, we found a population with extrusomes like the Namibian site (30) specimens in Venezuela, South America, about 200 km north of Puerto Ayacucho. The epicortical scales form two layers and are very similar to those of *T. apiculatum* (Fig. 311g–m; Table 25).

Occurrence and ecology: To date found at type location, that is, in soil from the margin of a small lake, and possibly at Namibian site (30), which is a similar biotope. The type location is covered with grass and small sedges and very likely flooded during wet periods. The soil is sandy, wet, and contains many fine roots, pH 5.4. The sample, taken from the top 5 cm on 18.02.1995, contained about 50 ciliate species, including two new genera and four new species. Other populations were observed in soil from a forest in the Hluhluwe Game Reserve (picnic site at crocodile pool), South Africa, and in Venezuela, as mentioned above.

Comparison with related species and generic classification: The general appearance of *T. africanum* is very similar to members of the → *T. apiculatum* group. The extrusomes, in contrast, are almost unique by their small size and lanceolate shape. Such extrusomes occur only in one other species, namely → *Bilamellophrya etoschensis*. This species is similar to *T. africanum* also in many other respects, especially when the population from the Galàpagos Islands is included in the variation range. Thus, these two species are easily confused. Nonetheless, the light microscopical appearance of the mucilaginous (scale) layer is different, indicating that they belong to different genera: tuberculate by dome-shaped type I scales in *T. africanum* (Fig. 28g; 311d, f), serrate by conical type II scales in → *B. etoschensis*. Furthermore, the extrusomes are different: narrowly lanceolate and protargol-affine in *T. africanum* (Fig. 28d, h, i; 311b, e), while rod-shaped and unstained in → *B. etoschensis* (Fig. 34b, d; 316c). The different generic classification of *T. africanum* and → *B. etoschensis* is sustained by the SEM investigation of the Venezuelan population, showing that this type of trachelophyllids belongs to *Trachelophyllum* (Fig. 311g–m).

Trachelophyllum pannonicum **nov. spec.** (Fig. 29a–j; 312a–j; Table 26)

Diagnosis: Size about 200 × 20 µm in vivo, slightly contractile; slenderly fusiform. 2 ellipsoidal, widely distant macronuclear nodules with a micronucleus each. Two types of extrusomes: type I acicular and 9 µm long; type II rod-shaped, inconspicuous because fine and only 2 µm long. On average 11 ciliary rows. Epicortical scales about 1.5 × 1 µm and with an average of 46 polygons in hemispherical superstructure.

Type location: Saline grassland soil from margin of the Neusiedlersee, a soda lake in the "hell" region near Illmitz, Burgenland, Austria, 47°45'N 16°48'E.

Etymology: Adjective of *Pannonia* (Latin), that is, the region at the Austrian-Hungarian borderline, where the species was discovered.

Description: All observations are from specimens grown in a raw culture set up with some ml soil percolate containing the indigenous organism community, Eau de Volvic (French table water), and two crushed wheat grains to stimulate growth of food organisms (bacteria, flagellates, small ciliates). *Trachelophyllum pannonicum* and some other ciliates grew well in this culture for some time.

Size of extended specimens 140–250 × 18–25 μm in vivo, usually about 200 × 20 μm (width without mucilaginous layer), length:width ratio about 10:1, in protargol preparations 7–14:1, on average 9.5:1 (Table 26); flattened up to 2:1 dorsoventrally, depending on nutrition. Slenderly fusiform to clavate with neck slightly widened in oral region and gradually merging into broadened trunk, anterior end (oral bulge) cylindroidal, posterior invariably narrowed to short, sharp tip, occasionally forming indistinct tail in protargol preparations (Fig. 29a–c, f; 312e). Cells very flexible but only slightly (< 30%) contractile, mainly in neck region, preserved specimens thus of similar size and shape as live ones (Fig. 312e, f). Nuclear apparatus in trunk. Macronuclear nodules globular to slenderly ellipsoidal (3:1), on average 2:1, stand out as bright blisters from granulated cytoplasm, usually distinctly apart and connected by a fine strand, very rarely almost abutting; of 90 specimens analyzed, 5 had only one macronuclear nodule, 80 had two nodules, 4 had three and 1 even four nodules; nucleoli numerous, minute, irregularly globular. Micronuclei usually attached or near to, rarely distant from macronuclear nodules, globular to slightly ellipsoidal. Contractile vacuole in posterior end, obconical, no excretory pore could be found, not even in many excellently or over-impregnated specimens. Two types of extrusomes, which impregnate with silver carbonate but not with protargol, in oral bulge and cytoplasm (Fig. 29a, d, e; 312a, b): type I conspicuous because 8–10 × 0.5 μm, that is, composed of a thick, cylindroidal proximal half and a thin, slightly curved, distally nippled rod, does not form bundles in cytoplasm; type II rod-shaped and inconspicuous because very fine (< 0.3 μm) and only about 2 μm long, mainly attached to bulge surface. Cytoplasm colourless often containing several food vacuoles with *Halteria grandinella* and many globular and irregular fat inclusions 1–10 μm across. Glides rather rapidly on microscope slide and swims by rotation about main body axis.

Cortex thin and flexible, contains fibres as described in → *T. apiculatum* after protargol impregnation. Furthermore, three argyrophilic structures (fibres?) are associated with each kinetid after silver carbonate impregnation (Fig. 312a): (i) an about 3 μm long (kinetodesmal fibre?) structure extending obliquely anteriad at the right side of the basal body, (ii) an about 1 μm long structure extending obliquely anteriad at the left side of the kinetid, and (iii) an about 2 μm long structure extending posteriorly. Mucilaginous layer much more inconspicuous and thinner in vivo (1–2 μm) than in protargol preparations (2–3 μm), where the epicortical scales appear globular or hemispherical, producing a tuberculate body surface (Fig. 29a, d, f–h; 312c–f). Epicortical scales stacked in two to three layers on body surface, highly variable in size and number of polygons composing superstructure, those near oral bulge usually distinctly smaller than those on rest of cell. Individual scales circular to elliptical (2:1), on average 1.5 × 1 μm, hemispherical superstructure composed of 46 polygons on average, those abutting on baseplate usually distinctly larger than those in central area, which form a rather regular, honey-comb pattern; baseplate dish-shaped, finely faceted, including dish margin, central area slightly to distinctly convex (Fig. 29i, j; 312g–j).

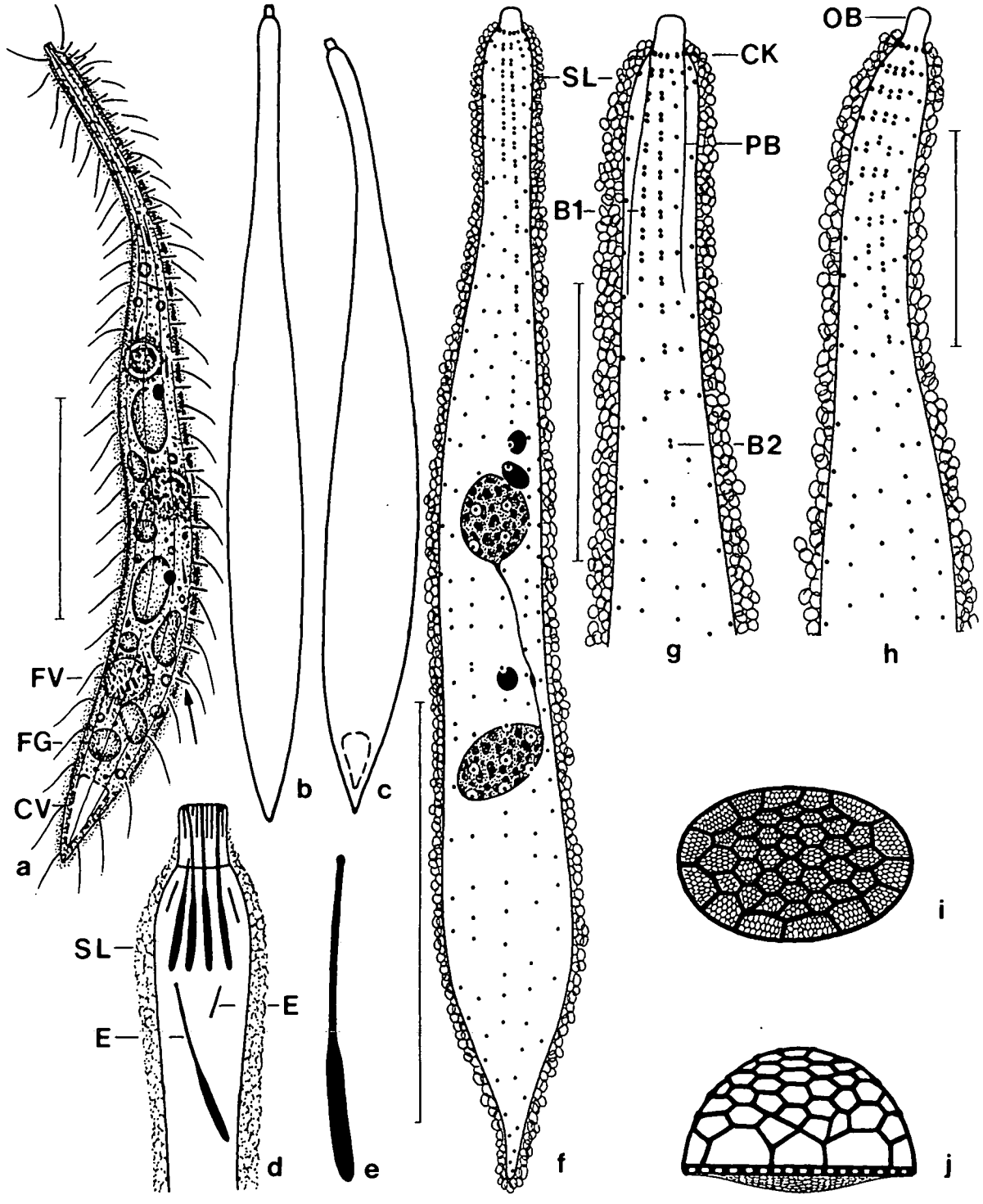

Fig. 29a–j. *Trachelophyllum pannonicum* from life (a–e), after protargol impregnation (f–h), and in the SEM (i, j). **a:** Dorsolateral view of a representative specimen. Arrow marks end of brush row 3. **b, c:** Shape variants. **d:** Details of anterior body region. **e:** Extrusome, length 10 µm. **f, g:** Ciliary pattern of dorsal side. **h:** Anterior dorsal portion of a specimen with three dikinetidal brush rows. **i, j:** Vertical projection and lateral view of an epicortical scale, size about 1.5 × 1 × 1 µm. B1, 2 – dorsal brush rows, CK – circumoral kinety, CV – contractile vacuole, E – extrusomes, FG – fat globule, FV – food vacuole, OB – oral bulge, PB – pharyngeal basket, SL – epicortical slime layer. Scale bars 50 µm (a, f) and 25 µm (g, h).

Table 26. Morphometric data on *Trachelophyllum pannonicum* (upper line) and *T. costaricanum* (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	155.9	156.0	22.5	4.9	14.4	115.0	210.0	21
	157.7	160.0	20.6	4.5	13.1	115.0	187.0	21
Body, width [b]	16.4	16.0	3.1	0.7	19.0	12.0	25.0	21
	14.4	15.0	1.8	0.4	12.3	11.0	20.0	21
Oral bulge, height	4.1	4.0	–	–	–	4.0	5.0	21
	3.5	3.5	–	–	–	3.0	5.0	21
Oral bulge, maximum diameter	3.2	3.0	–	–	–	3.0	4.0	21
	2.9	3.0	–	–	–	2.0	3.0	21
Anterior body end to first macronuclear	63.7	61.0	14.4	3.1	22.6	38.0	100.0	21
nodule, distance	53.5	55.0	10.8	2.4	20.2	30.0	72.0	21
Circumoral kinety to last dikinetid of brush	17.6	18.0	2.6	0.6	15.0	12.0	22.0	21
row 1, distance	14.5	14.0	2.2	0.5	15.5	11.0	20.0	21
Brush row 1, number of dikinetids	8.2	8.0	0.8	0.2	9.9	6.0	9.0	21
	7.7	8.0	0.9	0.2	11.1	6.0	9.0	21
Circumoral kinety to last dikinetid of brush	35.6	35.0	5.7	1.3	16.1	27.0	46.0	21
row 2, distance	32.9	33.0	5.0	1.1	15.2	21.0	42.0	21
Brush row 2, number of dikinetids	14.1	14.0	1.2	0.3	8.5	12.0	16.0	21
	16.3	17.0	1.6	0.4	9.9	13.0	18.0	21
Anterior macronuclear nodule, length [c]	15.5	15.0	2.8	0.6	18.2	12.0	21.0	21
	12.2	12.0	1.5	0.3	12.7	8.0	15.0	21
Anterior macronuclear nodule, width [c]	8.0	8.0	1.4	0.3	17.2	6.0	11.0	21
	8.0	8.0	0.7	0.1	8.4	7.0	9.0	21
Macronuclear nodules, distance in	19.3	19.0	9.2	2.0	47.8	6.0	37.0	21
between	27.2	28.0	9.3	2.0	34.3	9.0	45.0	21
Macronuclear nodules, number [d]	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Micronuclei, length	3.1	3.0	–	–	–	3.0	4.0	21
	4.0	4.0	–	–	–	4.0	5.0	21
Micronuclei, width	3.0	3.0	–	–	–	3.0	4.0	21
	3.1	3.0	–	–	–	3.0	4.0	21
Micronuclei, number	2.1	2.0	0.5	0.1	25.7	1.0	3.0	21
	1.2	2.0	1.1	0.2	94.7	0.0	3.0	21
Somatic ciliary rows, number	11.5	11.0	0.9	0.2	8.1	10.0	14.0	21
	9.2	9.0	0.5	0.1	5.9	8.0	10.0	21
Kinetids in a ventral kinety, number [e]	not investigated							
	34.5	36.0	5.8	1.3	16.9	25.0	43.0	21
Dikinetidal brush rows, number [f]	2.1	2.0	–	–	–	2.0	3.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Mucilaginous layer, thickness	2.3	2.0	–	–	–	2.0	3.0	21
	1.6	2.0	–	–	–	1.0	2.0	21
Epicortical scales, length [g]	1.5	1.5	0.2	0.04	13.4	1.2	1.9	33
	1.3	1.3	0.2	0.02	11.8	1.0	1.6	49
Epicortical scales, width [g]	1.0	1.0	0.2	0.03	16.9	0.7	1.4	33
	1.0	1.0	0.1	0.02	14.2	0.8	1.4	49
Epicortical scales, height [g]	0.9	1.0	0.1	0.03	10.7	0.8	1.1	14

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	0.9	0.9	0.1	0.04	15.7	0.6	1.0	10
Epicortical scales, number of polygons in	46.8	45.0	21.8	3.90	46.6	16.0	95.0	32
superstructure [g]	13.2	13.0	3.2	0.44	24.1	7.0	20.0	52

[a] Data based, if not otherwise stated, on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a pure culture (*T. pannonicum*) or a non-flooded Petri dish culture (*T. costaricanum*). Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Without mucilaginous (scale) layer.

[c] From specimens with two macronuclear nodules.

[d] Of 90 *T. pannonicum* specimens analyzed, 5 have one macronuclear nodule, 80 have two nodules, 4 have three and 1 has four nodules.

[e] Ciliated and unciliated kinetids were counted.

[f] Row 3 is monokinetidal (see description).

[g] From SEM micrographs. The small scales near the oral bulge of *T. pannonicum* were excluded.

Cilia about 12 µm long in vivo, rather widely spaced, some unciliated granules (kinetids?) in line with ciliated ones. Ciliary rows meridionally and equidistantly arranged, three (rarely four) of them differentiated to dorsal brush rows anteriorly (Fig. 29a, f–h; Table 26). Brush row 1 about half as long as row 2, composed of fairly widely spaced dikinetids bearing about 4 µm long, parallel bristles (not spread V-like as in some other species) obliquely attached to body surface and thus usually not recognizable in the scanning electron microscope because covered by the epicortical scale layer. Brush row 2 like row 1, bristles, however, only about 3 µm long. Brush row 3 extends to near posterior body end, composed of monokinetids having about 4 µm long, immobile bristles projecting at right angles from body proper and piercing scale layer. Brush rows 1 and 2 continue posteriorly as ordinary somatic kineties.

Oral bulge rather conspicuous because distinctly set off from body proper and refractive due to the extrusomes contained; cylindrical, rarely bluntly conical, 3– 5µm high and 3–4 µm across, not covered by epicortical scales, bulge surface flat and smooth in the scanning electron microscope. Circumoral kinety composed of about 10 rather widely spaced dikinetids each bearing a single cilium; gives rise to delicate fibres extending anteriorly, as in → *Epitholiolus chilensis*, and to fine nematodesmata forming an inconspicuous, slightly conical oral basket (Fig. 29a–d, f–h; 312e).

Occurrence and ecology: To date found only at type location, that is, in a rather saline, dark brown grassland soil with pH 7.9.

Comparison with related species: The epicortical scales of *T. pannonicum* are unique in having a high number and specific arrangement of polygons in the hemispherical superstructure (Fig. 29i, j; 312g–j). Thus, species status is beyond reasonable doubt. However, all other main features of *T. pannonicum*, such as body size and shape, nuclear apparatus, number of ciliary rows, and shape and size of the extrusomes, are highly similar to those of → *T. costaricanum* and → *Bilamellophrya hawaiiensis*. Indeed, these species are

hardly separable by conventional features, although they differ slightly in some details, such as the shape of the micronucleus (globular in *T. pannonicum*, ellipsoidal in → *T. costaricanum* and → *B. hawaiiensis*) and the extrusomes (all belong, however, to the acicular type), the excretory pore of the contractile vacuole (distinct only in → *B. hawaiiensis*), and several morphometric features (length ratio of brush rows 1 and 2). However, the taxonomic value of these sophisticated features is doubtful because of the lack of data on variability among populations. Accordingly, unequivocal identification of *T. pannonicum*, → *T. costaricanum*, and → *B. hawaiiensis* requires scanning electron microscopy of the epicortical scales.

Trachelophyllum costaricanum nov. spec. (Fig. 30a–v; 313a–m; Table 26)

Diagnosis: Size about 180 × 15 µm in vivo, slightly contractile; slenderly fusiform. 2 ellipsoidal, widely distant macronuclear nodules with a micronucleus each. Two types of extrusomes: type I acicular to obclavate and 12 µm long; type II rod-shaped, inconspicuous because fine and only 2 µm long. On average 9 ciliary rows. Epicortical scales about 1.3 × 0.9 µm and with an average of 13 rather regularly arranged hexagons in truncate cone-shaped superstructure.

Type location: Soil from coastal swamp near Punta Cocles, Caribbean coast of Costa Rica, Central America, 09°40'N 82°40'W.

Etymology: Named after the country discovered.

Description: Size of extended specimens 140–220 × 13–20 µm in vivo, usually about 180 × 15 µm (width without mucilaginous layer); length:width ratio in vivo about 12:1, in protargol preparations 7–17:1, on average 11:1 (Table 26); flattened up to 2:1 dorsoventrally, depending on nutrition state. Slenderly fusiform to clavate with neck slightly widened in oral region and gradually merging into broadened trunk, anterior (oral) region cylindroidal, posterior narrowed and bluntly pointed (Fig. 30a, g, i, j, m). Cells very flexible, but only about 30% of body length contractile, mainly in neck region (Fig. 30g, h), preserved specimens thus of similar size and shape as live ones. Nuclear apparatus in middle third of cell, micronuclei lacking or not impregnated in about half of specimens. Macronuclear nodules globular to ellipsoidal (2:1), on average 1.5:1, stand out as bright blisters from granulated cytoplasm, usually distinctly apart and connected by a fine strand in about 70% of specimens; nucleoli globular and of usual size. Micronuclei attached to or rather distant from macronuclear nodules, broadly ellipsoidal (Fig. 30a, j, m; 313a). Contractile vacuole subterminal, globular, no excretory pore could be found, not even in excellently or over-impregnated specimens. Two types of extrusomes in oral bulge and cytoplasm (Fig. 30a, b, d–f; 313b, c). Type I extrusomes conspicuous because about 12 × 1.2 µm and acicular to obclavate, does not form bundles in cytoplasm, those attached to oral bulge do not impregnate with protargol, while those in the cytoplasm stain lightly and have various shapes, possibly representing developmental stages (Fig. 30o); when exploding, the thinner, distal half elongates to an up to 40 µm long thread, and some toxin droplets remain in the proximal half (Fig. 30d; 313c). Type II extrusomes rod-shaped and inconspicuous because fine (< 0.3 µm across) and only about 2 µm long, do not impregnate with protargol. Cytoplasm colourless,

contains some fat globules up to 3 µm across and food vacuoles with various protozoans, mainly medium-sized ciliates, such as *Gonostomum affine* and *Vorticella astyliformis*; prey is ingested whole, often deforming the predator and dislocating the nuclear apparatus (Fig. 30a, m; 313a). Glides rather rapidly on microscope slide.

Cortex about 1 µm thick and very flexible, contains scattered, colourless granules about 0.5 µm across and a faintly impregnated fibre system very similar to that described in → *T. apiculatum*; however, fibre extending anteriorly at left side of kinetids shorter than in → *T. apiculatum* and thus not bundled with fibres from more anteriorly located kinetids (Fig. 30b, c). Mucilaginous layer about 3 µm thick in vivo, but very hyaline and thus difficult to recognize, composed of 1–2 layers of rather loosely adhering epicortical scales (Fig. 30a, b; 313a, d, e, h). Individual scales in vivo about 2 µm across, in protargol preparations approximately 1.5 µm, and in scanning electron micrographs only about 1 µm, indicating strong shrinkage due to the preparation procedures (Table 26). Size and structure of scales rather constant, baseplate broadly ellipsoidal, superstructure uniquely forms truncate cone producing pentagonal outline of scales in side view, recognizable even in protargol preparations (Fig. 30p–v; 313d–l; Table 26). Superstructure composed of an average of 13 rather regularly arranged hexagons separated by broad bridges, that is, a ring of elongated hexagons extends anteriorly from the margin of the baseplate and abuts on one or two rows of ordinary hexagons in the slightly convex central area of the distal, truncate cone surface. Baseplate dish-shaped, finely faceted, including dish margin, central area slightly to distinctly convex (Fig. 30q; 313f, g, m).

Cilia in vivo about 12 µm long and rather widely spaced because irregularly alternating with slightly smaller, bare basal bodies (Fig. 30c). Ciliary rows meridionally and equidistantly arranged, three of them differentiated to dorsal brush rows anteriorly (Fig. 30a, b, j, k, n; Table 26). Brush row 1 on average slightly less than half as long as row 2, composed of fairly widely spaced dikinetids bearing about 4 µm long, parallel bristles (not spread V-like as in some other species) obliquely attached to body surface and thus usually not recognizable in the scanning electron microscope because covered by the epicortical scale layer (Fig. 313d). Brush row 2 like row 1, bristles, however, about 5 µm long. Brush row 3 extends to posterior body end, composed of monokinetids having about 5 µm long, immobile bristles projecting at right angles from body proper and thus piercing scale layer (Fig. 313d). Brush rows 1 and 2 continue posteriorly as ordinary somatic ciliary rows.

Oral bulge rather conspicuous because distinctly set off from body proper and refractive due to the extrusomes contained; cylindroidal to indistinctly conical, about 4 µm high and 3 µm wide in vivo, not covered by epicortical scales. Circumoral kinety composed of about 12 rather widely spaced dikinetids each bearing a single cilium; gives rise to delicate fibres extending anteriorly, as in → *Epitholiolus chilensis*, and to fine nematodesmata forming an inconspicuous oral basket (Fig. 30a, b, j–l; 313d). Interestingly, the oral basket of *T. costaricanum* appears in two forms: slightly conical, as in all other species described (Fig. 30k), and obconical (funnel-shaped; Fig. 30l). We could not clarify the reason.

Occurrence and ecology: To date found at type location (dark swamp soil from coastal rain forest about 20 m inshore of the Caribbean Sea coast; pH 6.0) and, probably (see below), in a paddy field from Japan. Two other populations were found in soils from the Republic of South Africa. However, identification is doubtful because entirely based on live observations, mainly shape and size of the body and extrusomes.

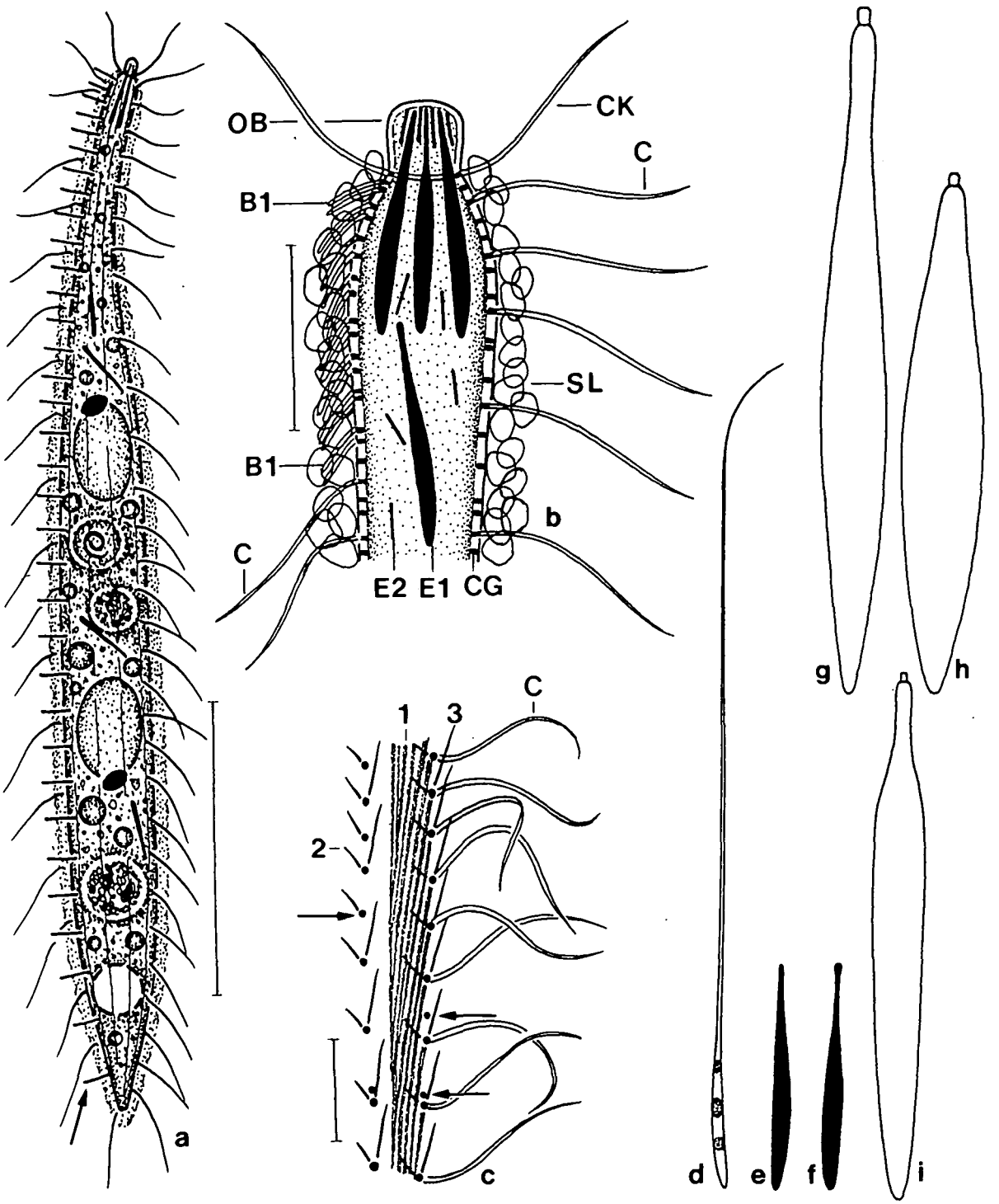

Fig. 30a–i. *Trachelophyllum costaricanum* from life (a, b, d–i) and after protargol impregnation (c). **a:** Dorsolateral view of a representative specimen. Arrow marks end of brush row 3. **b:** Details of anterior body portion. **c:** Cortical fibre system. Numbers mark different fibres. Arrows denote unciliated granules (basal bodies?) partially without fibres. **d:** Extruded type I extrusome, length 40 µm. **e, f:** Resting type I extrusomes, length 12 µm. **g, h:** Same specimen extended and contracted. **i:** Shape variant. B3 – dorsal brush row 3, C –somatic cilia, CG – cortical granules, CK – circumoral kinety, E1, 2 – type I and II extrusomes, OB – oral bulge, SL – scale layer. Scale bars 10 µm (b, c) and 50 µm (a).

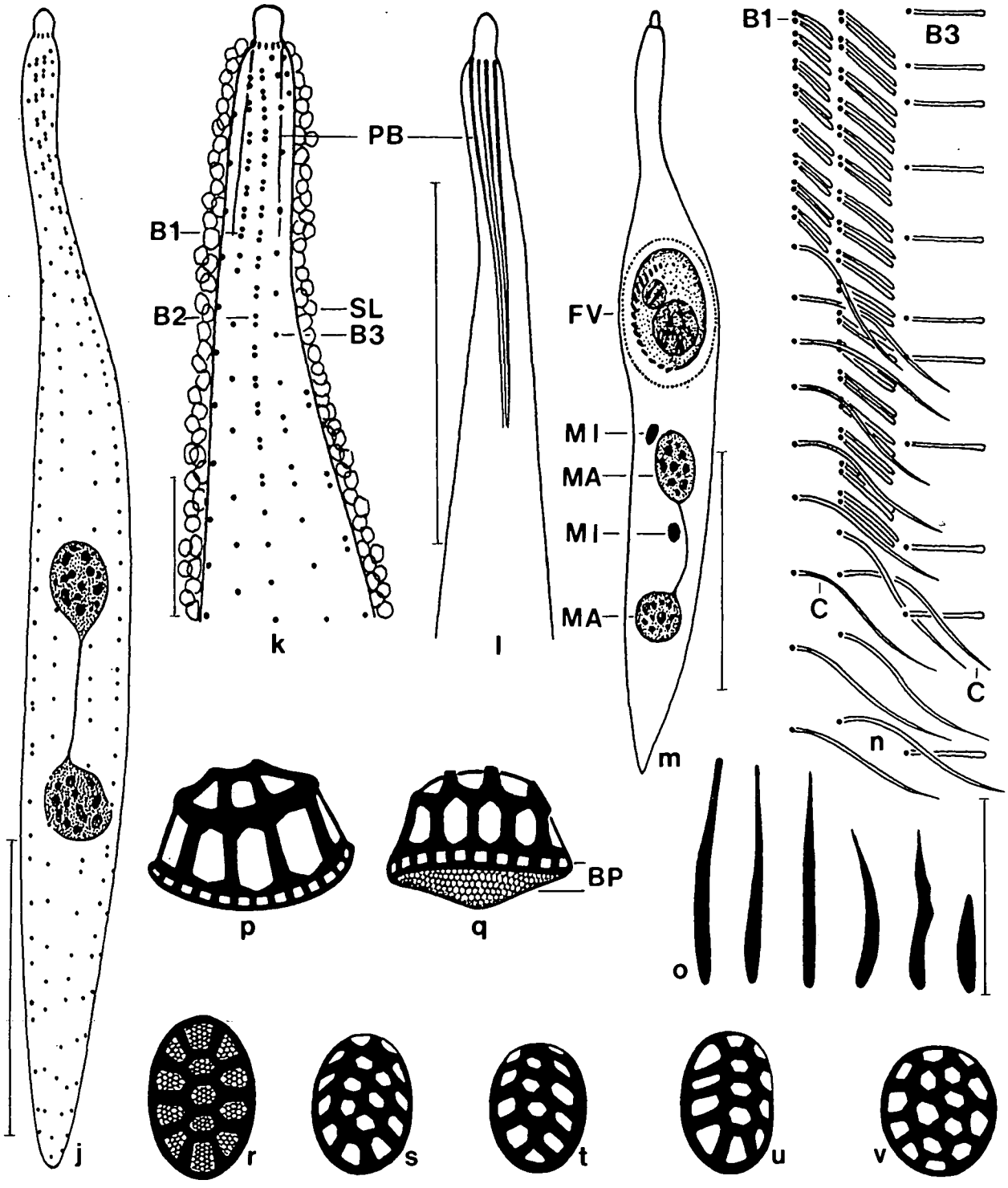

Fig. 30j–v. *Trachelophyllum costaricanum* from life (n), after protargol impregnation (j–m, o), and in the SEM (p–v). **j, k:** Infraciliature of dorsal side of holotype specimen. **l:** Specimen with funnel-shaped oral basket. **m:** A just ingested *Gonostomum affine* bulges the predator. **n:** Details of dorsal brush. Row 3 extends to body end (Fig. 30a). **o:** Cytoplasmic extrusomes, drawn to scale. **p, q, s–v:** Epicortical scales in oblique lateral and surface views, size about 1 µm. **r:** Vertical projection of a scale. B1-3 – dorsal brush rows, BP – baseplate, C – cilia, FV – food vacuoles, MA – macronuclear nodules, MI – micronuclei, PB – pharyngeal basket, SL – scale layer. Scale bars 10 µm (k, o) and 40 µm (j, l, m).

Comparison with related species: The epicortical scales of *T. costaricanum* are rather similar to those of → *T. apiculatum* (Fig. 313n–q); uniquely, the superstructure is truncate cone-shaped, providing the scales with a highly characteristic pentagonal outline in side view (Fig. 30p, q; 313f–h). Similar scales were observed in a Japanese *Trachelophyllum* (Fig. 313n–p), which, unfortunately, was insufficiently studied in vivo. Thus, conspecificity is uncertain. The scales of the Japanese population have thinner bridges between the facets and usually possess a circular field of small hexagons in the centre of the superstructure. While the thickness of the bridges may vary with preparation conditions, the pentagonal (rarely hexagonal) shape of the basal facets and the circular field of hexagons in the centre of the superstructure indicate that it is a different species.

The unique shape of the epicortical scales defines *T. costaricanum* as a distinct species. All other main features highly resemble those of → *T. pannonicum* and → *Bilamellophrya hawaiiensis*. See *T. pannonicum* for detailed discussion.

Epitholiolus nov. gen.

Diagnosis: Trachelophyllidae KENT, 1881 with type III scales (some tiny arcs, which form a dome-shaped superstructure, emerge from a ring-shaped baseplate).

Type species: *Lacrimaria chilensis* BÜRGER, 1906.

Etymology: Composite of the Greek preposition *epi* (upon), the Latin plural noun *tholi* (domes, cupolae), and the Latin diminutive suffix *olus*, referring to the minute domes covering the cell. Masculine gender.

Comparison with related genera and species assignable: KAHL (1930a) transferred *Lacrymaria chilensis* BÜRGER, 1906 to *Trachelophyllum*, recognizing the similarities with that genus. This is supported by our investigations, which show that the ciliary pattern of *L. chilensis* is very similar to classic members of the genus *Trachelophyllum* CLAPARÈDE & LACHMANN, 1859, as redescribed by FOISSNER (1984) and SONG (1994). Here, the species is referred to a new genus, *Epitholiolus*, which differs from the other genera of the family not only by the unique structure of the epicortical scales (see introduction to family), but also by the nuclear apparatus (abutting vs. widely distant macronuclear nodules) and the mode of conjugation (by lateral fusion [Fig. 31g] vs. polar fusion [KAHL 1930a]). Whether these features are of generic significance needs further investigation.

We assign to *Epitholiolus* also *Trachelophyllum attenuatum* FOISSNER, 1983b because it has, like → *E. chilensis*, an inconspicuous mucilaginous (scale) layer and two abutting macronuclear nodules with a micronucleus in between (Fig. 31p, q): *Epitholiolus attenuatus* (FOISSNER, 1983) nov. comb. *Epitholiolus attenuatus*, as redescribed by FOISSNER (1984), differs from → *E. chilensis* in body shape (ellipsoidal vs. slenderly claviform; Fig. 31a, p) and number of ciliary rows (14 vs. 9 on average). Furthermore, *E. attenuatus* has rod-shaped extrusomes (FOISSNER 1983b, 1984). However, in protargol-impregnated specimens they may be acicular like those of → *E. chilensis*. We checked the original notes on *E. attenuatus*. The extrusomes were measured and drawn, but their exact shape was not definitely stated. Thus, they might be acicular as in → *E. chilensis*.

Epitholiolus chilensis (BÜRGER, 1906) **nov. comb.** (Fig. 31a–z; 314a–y; Table 27)

1906 *Lacrimaria chilensis* nov. spec., BÜRGER, An. Univ. Chile, 117: 427.
1930 *Trachelophyllum* (*Lacrymaria*) *chilense* BÜRGER, 1906 — KAHL, Tierwelt Dtl., 18: 115.

Neotype material: Neotypified from Namibian site (26) population, according to reasons 1, 2, 4, 6 given in chapter 2.4.2.

Improved diagnosis: Size about 95 × 10 µm in vivo, contractile by up to 40% of body length; slenderly claviform to almost cylindrical. Micronucleus usually in corners formed by two abutting, globular macronuclear nodules. Two types of extrusomes: type I acicular and 9 µm long; type II flask-shaped and 2 µm long. On average 9 ciliary rows. Epicortical scales about 0.6 µm across and with an average of 4 arcs forming hemispherical superstructure.

Description of Namibian neotype population: Size of extended specimens 70–130 × 9–11 µm in vivo; unflattened. Slenderly clavate, fusiform or cylindroidal, length:width ratio in vivo 7–13:1, after protargol impregnation about 8:1 (Table 27). Anterior end narrowly cylindrical and refractive due to the extrusomes contained, posterior narrowly rounded to slightly tapered (Fig. 31a, k–m; 314a, e, k–m). Cells very flexible and contractile by up to 40% of body length, fully contracted specimens about 65 × 20 µm and rather broadly claviform, highly resembling ordinary specimens of *E. attenuatus* (cp. Fig. 31k–p; 314r); contracts and extends slowly, preserved specimens thus of almost same length as live ones. Nuclear apparatus in centre of cell on average, occasionally however, considerably anterior or posterior of mid-body, consists of one to two, usually two macronuclear nodules and one to two, usually one micronucleus often difficult to distinguish from similarly sized and impregnated cytoplasmic inclusions. Macronuclear nodules globular to slightly ellipsoidal, in vivo 6–8 µm across, stand out as bright blisters from granulated cytoplasm, usually tightly abutting; nucleoli minute and globular. Micronucleus usually in corners formed by abutting macronuclear nodules, rarely in between or attached to other sites of nodules, disc-shaped and slightly ellipsoidal (Fig. 31a, k, m, s; 314a–c, f, g, k–m); rarely up to 7 µm across and reticular (Fig. 31c). Contractile vacuole in posterior body end, with single excretory pore about 2.5 µm across. Two types of extrusomes, both heavily impregnated by silver carbonate, in oral dome and cytoplasm (Fig. 31a, b; 314d, g, i, j, l, n): type I conspicuous because 8–10 × 0.8 µm and highly refractive, acicular and slightly curved, those developing in cytoplasm slightly shorter (6–8 µm) and occasionally impregnated by protargol (Fig. 31d, s; 314 l, n); type II inconspicuous because only 2 × 0.5 µm, mainly in oral region, flask-shaped, especially after silver carbonate impregnation, does not stain with protargol. Cytoplasm colourless, contains many globular and irregular fat inclusions 1–6 µm across and some 3–4 µm-sized food vacuoles with remnants of ciliates, mainly *Protocyclidium muscicola*. Glides slowly on microscope slide and serpentinely between organic debris.

Cortex thin and flexible, contains minute (about 0.2 µm), colourless granules forming posteriorly broadening stripes within ciliary rows (Fig. 31j; 314h); covered with an about 0.4 µm thick, mucilaginous layer of epicortical scales producing tuberculate body surface both in vivo and protargol preparations (Fig. 31a, v; 314p). Scales tightly spaced and 0.6 µm across

on average in scanning electron micrographs, form single layer on entire body, except for oral dome, recognizable in vivo only with interference contrast optics and, after protargol impregnation, only in over-stained specimens. Scale baseplate ring-shaped with an average of 14 minute perforations, gives rise to three to four, usually four convex arcs about as high as baseplate radius, forming minute dome with one, occasionally two tiny perforations on top (Fig. 31x–z; 314q–u; Table 27).

Cilia in vivo only about 6 µm long, rather widely spaced, cylindrical with conical distal end. Kinetodesmal fibres conspicuous after silver carbonate impregnation and directed obliquely anteriorly (Fig. 314d). Ciliary rows meridionally and equidistantly arranged, three of them differentiated to dorsal brush rows anteriorly (Fig. 31a, r–w; 314a, k–n, r, v–y; Table 27). Brush row 1 about half as long as rows 2 and 3, composed of closely spaced dikinetids having about 4 µm long, rod-shaped bristles directed obliquely anteriorly. Brush row 2 similar to row 1, but with posterior cilium of dikinetids shortened to 2–3 µm long stumps in rear third of row. Brush row 3 slightly longer than row 2, composed of rather closely spaced monokinetids having about 1 µm long, slightly tongue-shaped ciliary stumps projecting at right angles from body proper. All brush rows continue posteriorly as ordinary somatic kineties.

Oral bulge minute, cylindroidal, in vivo 3–4 µm across and 2–3 µm high, distinctly set off from body proper, brilliant because containing anterior end of extrusomes. Bulge surface flat to convex, smooth, that is, without central depression and/or opening (Fig. 314y). Circumoral kinety at base of oral bulge, dikinetidal, only one basal body of dikinetids bears an about 6 µm long cilium (Fig. 31a, b, r–u; 314b, e, k–o, r, v–y). Pharyngeal basket recognizable neither in vivo nor in protargol preparations.

Occurrence and ecology: BÜRGER (1906) discovered *E. chilensis* in an irrigation ditch; it flourished when the sample became putrid. We found *E. chilensis* at site (26), that is, in the litter-sand mixture from a dune of the Namib Desert. This sample contained much organic debris, and a rich and diverse ciliate community developed a few days after rewetting. Certainly, rewetting produced some kind of polysaprobic milieu, which this species seems to prefer, although it occurs also in only slightly polluted, mesosaprobic environments (see below). *Epitholiolus chilensis* has never been recorded from terrestrial habitats, but is common in stagnant and running waters world-wide. The following compilation is not complete but representative: Chile (BÜRGER 1906); potable water from Mexico (MADRAZO-GARIBAY & LÓPEZ-OCHOTERENA 1982); common in clean and polluted sections of the South River, Virginia, USA (CAIRNS & DICKSON 1972); common in eutrophic ponds and reservoirs and mesosaprobic and polysaprobic rivers of Czechoslovakia (MATIS 1977, MATIS & TIRJAKOVÁ 1994, MATIS et al. 1996, ŠRÁMEK-HUŠEK 1946, TIRJAKOVÁ 1993), Moldavia (VICOL & CIORIC 1994), and Russia (OLEKSIV 1985); polluted stagnant and running waters in China (MA ZHENXUE 1994, SHEN et al. 1995, YANG HAIMING 1989).

Comparison with original description: *Lacrymaria chilensis* has not been restudied since the original description. Only ŠRÁMEK-HUŠEK (1946) provided a few schematic figures from a population of a heavily polluted (polysaprobic) river in Czechoslovakia. The identification was likely correct, although the specimens were considerably smaller (35–60 µm) than those from the Chilean type population (80–100 µm). Our specimens from a sand dune in the Namib Desert matched the original data perfectly, except for the elongated and condensed cilia in the oral region (Fig. 31a, e–i; 314b). However, BÜRGER (1906) was possibly influenced in this respect by the genus *Lacrymaria*, to which he

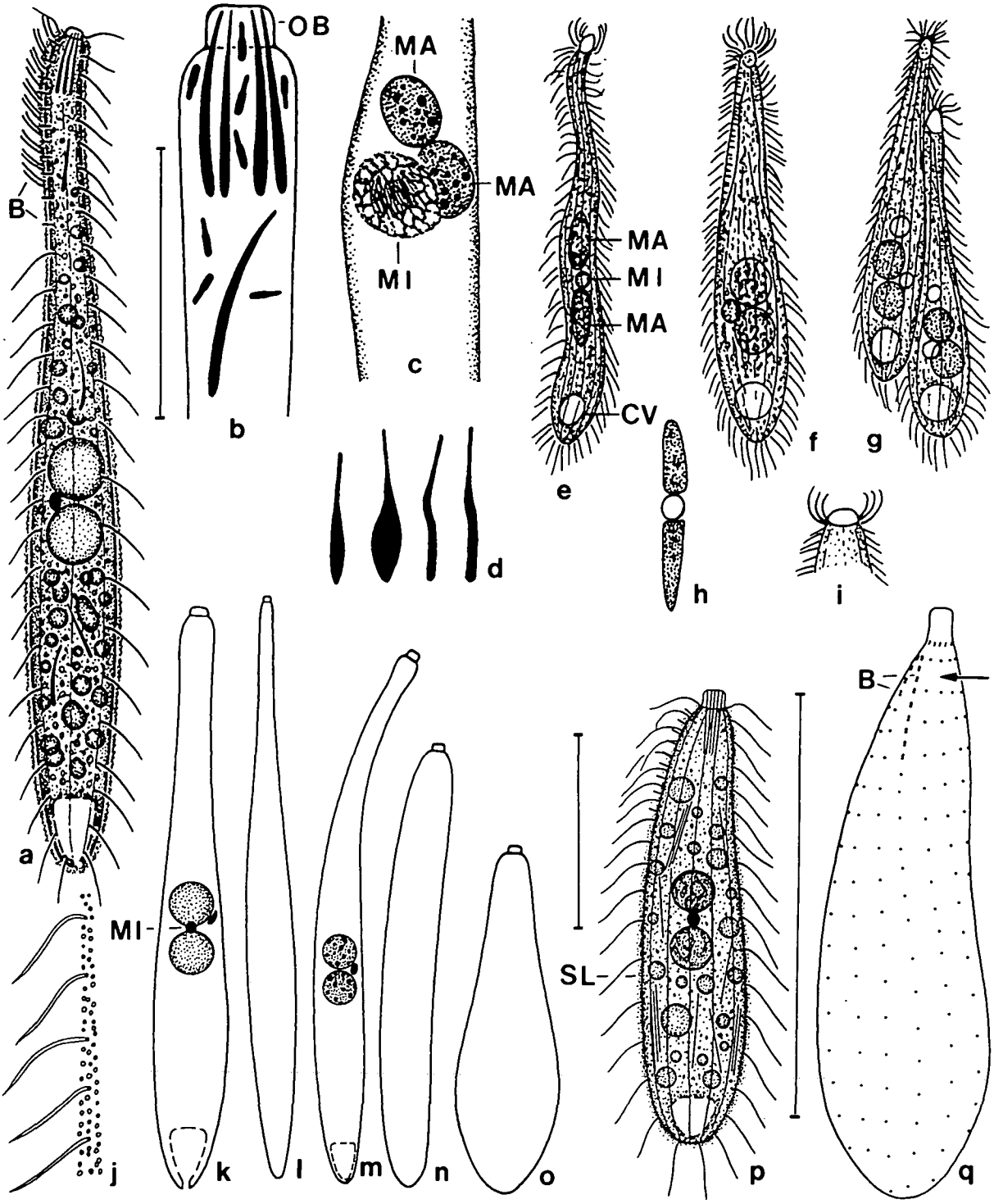

Fig. 31a–q. *Epitholiolus chilensis* (a–o; a–d, j–o, originals from Namibian population; e–i, type from Chile, redrawn from BÜRGER 1906) and *E. attenuatus* (from FOISSNER 1984) from life (a–c, e–p) and after protargol impregnation (d, q). **a:** Right lateral view of a representative specimen. **b:** Anterior portion with extrusomes. **c:** Specimen with swollen micronucleus. **d:** Cytoplasmic (developing) extrusomes. **e–i:** BÜRGER's specimens are highly similar to the Namibian neotype, size 80–100 × 8–10 µm; figure (g) shows conjugation. **j:** Cortical granulation. **k, l:** Shape variability. **m–o:** Extended, slightly contracted, and fully contracted specimen, drawn to scale. **p, q:** *Epitholiolus attenuatus* differs from *E. chilensis* in body shape, number of ciliary rows, and a bare area (arrow) left of the brush. B – dorsal brush, CV – contractile vacuole, MA – macronuclear nodules, MI – micronucleus, OB – oral bulge, SL – scale layer. Scale bars 30 µm.

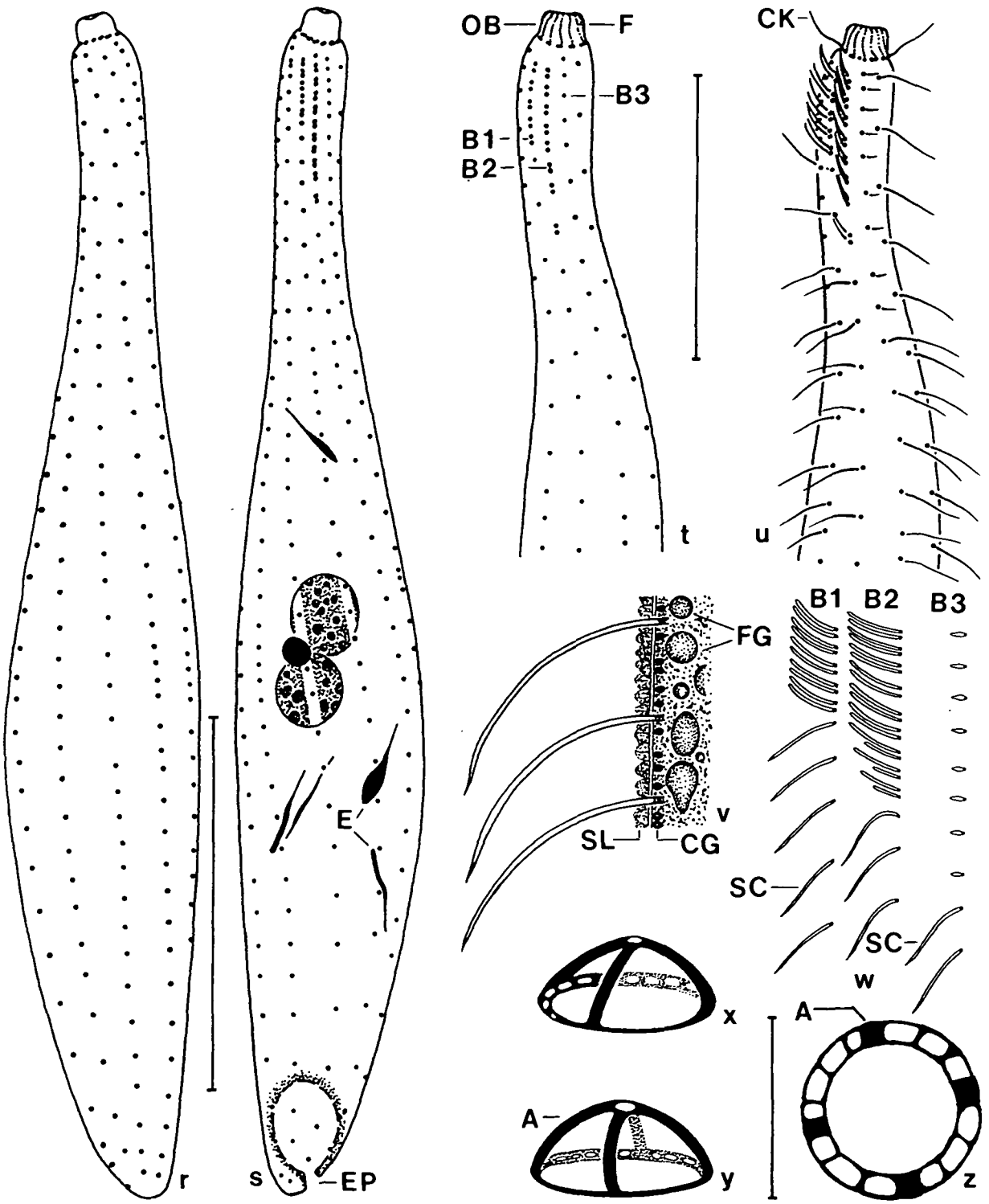

Fig. 31r–z. *Epitholiolus chilensis* from life (v, w), after protargol impregnation (r–u), and in the SEM (x–z). **r, s:** Ciliary pattern of ventral and dorsal side of holotype specimen. **t, u, w:** Ciliature of dorsal anterior portion. Brush row 3 consists of short, monokinetidal bristles. **v:** Optical section of cortex. The epicortical scale layer makes the body surface uneven. **x–z:** Epicortical scales, baseplate view (z) and oblique lateral view of scales with three, respectively, four arcs. A – arcs, B1-3 – dorsal brush rows, CG – cortical granules, CK – circumoral kinety, E – extrusomes, EP – excretory pore, F – fibres, FG – fat globules, OB – oral bulge, SC – ordinary somatic cilium. Scale bars 30 μm (r, s), 20 μm (t, u), 0.6 μm (x–z).

assigned his species, which possesses such a condensation. Furthermore, BÜRGER (1906) obviously did not observe such details carefully, otherwise he would have noted the rather conspicuous dorsal brush (possibly he saw brush row 3; Fig. 31f). Thus, identification is beyond reasonable doubt and neotypification justified.

Epitholiolus chilensis and *E. attenuatum*, as combined above, are easily distinguished from other trachelophyllids by the abutting macronuclear nodules (vs. widely separated). Be careful not to confuse *Epitholiolus* spp. with → *Apoenchelys bamforthi*, which has a similar size, shape, and nuclear pattern.

Table 27. Morphometric data on *Epitholiolus chilensis*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	83.6	83.00	13.50	2.9	16.1	64.00	115.00	21
Body, width [b]	11.5	11.00	2.00	0.5	17.8	7.00	16.00	21
Oral bulge, height	2.2	2.00	–	–	–	2.00	4.00	21
Oral bulge, maximum diameter	3.1	3.00	–	–	–	3.00	4.00	21
Anterior body end to nuclear apparatus, distance	39.3	40.00	9.40	2.1	24.0	28.00	73.00	21
Brush row 1, length [c]	6.6	6.00	1.50	0.3	23.4	4.00	10.00	21
Brush row 1, number of dikinetids	4.6	5.00	0.60	0.1	12.8	4.00	6.00	21
Brush row 2, length [c]	13.2	13.00	2.20	0.5	16.9	10.00	20.00	21
Brush row 2, number of dikinetids	8.9	9.00	0.90	0.2	9.6	8.00	11.00	21
Anterior macronuclear nodule, length [d]	6.3	6.00	1.00	0.2	16.3	5.00	9.00	21
Anterior macronuclear nodule, width [d]	5.2	5.00	0.50	0.1	9.9	4.00	6.00	21
Macronuclear nodules, number	1.8	2.00	–	–	–	1.00	2.00	30
Micronucleus, length	2.8	3.00	–	–	–	2.00	3.00	21
Micronucleus, width	2.1	2.00	–	–	–	2.00	3.00	21
Micronuclei, number	1.3	1.00	–	–	–	1.00	2.00	30
Somatic ciliary rows, number	9.3	9.00	–	–	–	9.00	10.00	21
Kinetids in a ventral kinety, number	27.1	26.00	6.20	1.4	22.8	18.00	41.00	21
Dikinetidal brush rows, number [e]	2.0	2.00	0.00	0.0	0.0	2.00	2.00	21
Epicortical scales, diameter [f]	0.59	0.59	0.07	–	12.0	0.49	0.82	56
Epicortical scales, number of arcs [f]	3.7	4.00	–	–	–	3.00	4.00	98
Epicortical scales, number of perforations in basering [f]	12.4	14.00	1.90	0.6	16.0	9.00	14.00	9
Epicortical scales, size (nm) of perforations in basering [f]	50.6	43.00	18.20	2.7	36.0	28.00	105.00	44

[a] Data based, if not otherwise stated, on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Without mucilaginous (scale) layer.

[c] Distance from circumoral kinety to last dikinetid.

[d] From specimens with two macronuclear nodules.

[e] Row 3 is monokinetidal (see description).

[f] From SEM micrographs.

Bilamellophrya nov. gen.

Diagnosis: Trachelophyllidae KENT, 1881 with type I and type II epicortical scales. Type I scales attached to pellicle, composed of a finely perforated, dish-shaped, ellipsoidal baseplate from which a widely and polygonally faceted, dome-shaped superstructure emerges. Type II scales upon type I scales, biconical, composed of a finely perforated, dish-shaped, broadly turbinate, circular baseplate from which fine, concave arcs emerge to form a conical superstructure.

Type species: *Bilamellophrya australiensis* nov. spec.

Etymology: Composite of the Latin words *bi* (two) and *lamella* (thin plate) and the Greek noun *ophrya* (eyebrow ~ cilia ~ ciliate s. l.), meaning "a ciliate having two types of platelets". Feminine gender.

Comparison with related genera: *Bilamellophrya* is unique in having two kinds of epicortical scales, of which type II is unparalleled. Thus, at least generic separation seems appropriate. Possibly, further studies will reveal that such taxa belong to a distinct family.

Three new species will be described from Gondwanan soils. However, FOISSNER et al. (1994) published a few scanning electron micrographs of a "*Lepidotrachelophyllum* sp." from a river in Germany. It differs from → *B. australiensis* mainly by the type II scales, whose conical superstructure is not curtain-like but polygonal. Detailed data are lacking from the German population, but the observations show that trachelophyllids with two scale types are not restricted to Gondwanan areas.

Bilamellophrya australiensis nov. spec. (Fig. 32a–v, 33a–g; 315a–s; Table 28)

Diagnosis: Size about 200 × 30 µm in vivo, highly contractile; slenderly claviform. 2 ellipsoidal, widely distant macronuclear nodules with a micronucleus each. Two types of rod-shaped extrusomes: type I slightly curved, 15–25 µm long; type II only 2 µm long. On average 24 ciliary rows. Type I scales on average 1.6 × 1 µm and with 8 polygons in superstructure; type II scales about 2 µm across and high, conical superstructure composed of an average of 10 meridional arcs and 2 transverse rings.

Type location: Soil from Murray River floodplain near the town of Albury at the landside of Ryans road, Australia, 37°S 147°E.

Etymology: Named after the country discovered.

Description (including data from a second Australian population, see discussion): Size of extended specimens 150–250 × 25–40 µm in vivo, length:width ratio about 6–8:1, on average 4–7:1 in protargol preparations (Table 28). Slenderly clavate to fusiform with neck slightly widened in oral region and gradually merging into broadened trunk; slightly to distinctly flattened dorsoventrally. Anterior end button-shaped and refractive due to the extrusomes

contained, posterior end narrowly rounded to slightly tapered (Fig. 32a, e). Cells very flexible and contractile by up to 50% of body length, especially in neck region, fully contracted specimens fusiform (Fig. 32b; 315a); contracts and extends slowly, preserved specimens thus of similar size and shape as live ones. Nuclear apparatus in middle third of cell. Macronuclear nodules broadly ellipsoidal, stand out as bright blisters from granulated cytoplasm, usually distinctly apart and never connected by a fine strand, very rarely abutting as in → *Epitholiolus chilensis*, occasionally small specimens with only one nodule; nucleoli scattered, globular, minute (0.2–2 µm). Micronuclei usually attached to macronuclear nodules, conspicuously large and fusiform (Fig. 32a, u, 33b; 315b; Table 28). Contractile vacuole in posterior end, with single, about 3 µm long, posterolateral excretory pore. Two size-types of basically rod-shaped extrusomes (Fig. 32a, c, i, l, m, 33c; 315b), the large type originates in conspicuous blisters and is acicular and protargol-affine during development (Fig. 32j, k). Type I extrusomes conspicuous because 15–20 × 0.5 µm (20–25 µm in second population), rod-shaped and slightly curved, form highly refractive bundles in oral bulge and cytoplasm, do not impregnate with protargol, except for proximal, toxin-containing portion; become acicular, very hyaline, and up to 60 µm long when exploded. Type II extrusomes inconspicuous because only about 2 µm long, mainly in oral bulge, do not impregnate with protargol. Cytoplasm colourless and rather hyaline, contains fat globules 5–10 µm across and many ring-shaped granules (similar to those found in certain *Plagiocampa* and *Dexiotricha* species) about 1 µm across. Likely feeds on small ciliates. Glides rapidly on microscope slide and serpentinely between debris, often almost immobile for some time, slowly contracting and extending.

Cortex thin and flexible, contains scattered, colourless granules about 0.3 µm across (Fig. 32h); covered with an up to 5 µm thick, mucilaginous layer of epicortical scales producing serrate body margin both in vivo and protargol preparations (Fig. 32a, c, g, u, 33b; 315a, b, e, f). Mucilaginous layer composed of two kinds of scales lying one upon the other (Fig. 32a, g, 33d–g; 315g–s; Table 28). Type I scales in one to two layers on body surface, except for oral bulge, tightly spaced, 1.6 × 1 µm on average and thus hardly recognizable in the light microscope, domed superstructure with 8 polygons on average. Type II scales complicated and beautiful, upon and more loosely arranged than type I scales, about 2 µm across and 2 µm high and thus well-recognizable in the light microscope, baseplate broadly obconical and often somewhat undulated, gives rise to an average of 10 concave arcs forming conspicuous cone producing serrate body margin described above; arcs rather unevenly spaced and connected by two transverse rings.

Cilia 15–20 µm (!) long in vivo, rather widely spaced, only that portion of each cilium which extends beyond the mucilaginous layer vibrates. Postciliary microtubule ribbons distinct, form conspicuous fibre between kineties. Ciliary rows meridionally and equidistantly arranged, three of them differentiated to dorsal brush rows anteriorly (Fig. 32a, c, f, u, Fig. 33b; 315a, c, p, q; Table 28). Brush row 1 about one third shorter than row 2, composed of fairly widely spaced dikinetids bearing 2–3 µm long, distally slightly inflated bristles, posterior bristle shortened and rod-shaped. Brush row 2 like row 1. Brush row 3 extends to near posterior body end, composed of monokinetids having about 4 µm long, rod-shaped bristles projecting at right angles from body proper; kinetids closely spaced anteriorly, where the row diverges slightly and then curves right, producing rather conspicuous widening between rows 2 and 3. All brush rows continue posteriorly as ordinary somatic kineties.

Oral bulge in vivo rather conspicuous because about 6 × 6 µm in size, distinctly set off from

body proper, and highly refractive due to the extrusomes contained; conspicuously anvil-shaped soon becoming cylindroidal under slight cover glass pressure. Bulge surface flat to slightly convex, without central depression and/or opening, in protargol preparations usually studded with minute granules. Circumoral kinety at base of oral bulge, composed of rather unevenly spaced dikinetids each bearing a single cilium; gives rise to delicate fibres extending anteriorly and to fine nematodesmata forming slightly conical oral basket (Fig. 32a, c, d, 33b, c; 315a, c, d, k).

Occurrence and ecology: To date found at type location and in a soil sample from a small river floodplain between the village of Erldunda and Ayers Rock, Central Australia. The sample from the type location, kindly provided by Mag. Hubert BLATTERER, was a mixture of leaf litter (mainly from red gum trees and dried *Myriophyllum*) and light brown, loamy soil, pH 5.2. It contained a very rich (about 80 species) mixture of limnetic and euedaphic ciliate species. The soil from the second site was loamy and sandy, had pH 7.2, and was covered with a dry algal crust. Possibly, occurs also in Austria (see below).

Comparison with related species: We found two populations of this species in floodplain soils from Australia. They were very similar, except for the number of ciliary rows, which differed considerably (Table 28). We did not separate the populations at species or subspecies level because data about the variability of kinety number were sparse in *Trachelophyllum* and the epicortical scales appeared similar, although a detailed comparison was impossible because the scanning electron micrographs from the second population were obtained with a different method (315o–s).

KAHL (1930a), the last reviser of *Trachelophyllum*, recognized seven species. Since then, nine species have been described: *T. flavicans* GAJEWSKAJA, 1933; *T. lineare* LEPSI, 1960; *T. triangulatum* TUCOLESCO, 1962; *T. biacuminatum* TUCOLESCO, 1962; *T. sphagnetorum* GROLIERE, 1977; *T. hyalinum* FOISSNER, 1983b; *T. attenuatum* FOISSNER, 1983b; *Lepidotrachelophyllum fornicis* NICHOLLS & LYNN, 1984, and *Spetazoon australiense* FOISSNER, 1994c. Furthermore, DUMAS (1930, 1937) described seven new species, most of which, however, are pleurostomatids. None of these species matched the Australian populations to an extent that would make identification beyond reasonable doubts; thus, we classified them as a new species. In the following paragraphs, we shall compare only those species that might be confused with *B. australiensis*.

As concerns shape, *B. australiensis* resembles *T. brachypharynx*, which LEVANDER (1894) discovered at the Finnish Gulf coast near Helsinki (Fig. 32o). However, *T. brachypharynx* is considerably larger than *B. australiensis* (350–400 µm vs. 150–250 µm), has shorter extrusomes (10–15 µm vs. 15–25 µm), and possibly lacks a distinct mucilaginous layer because LEVANDER (1894) did not mention one. Furthermore, *T. brachypharynx* possibly has three macronuclear nodules and two contractile vacuoles. Unfortunately, LEVANDER's description is meagre and no redescription is available for a more detailed comparison with *B. australiensis*. We emphasize, however, that the considerable size difference strongly argues against conspecificity. Further, care must be taken not to confuse *B. australiensis* with *Spetazoon australiense* FOISSNER, 1994d, which occurs in the same region, but has spherical epicortical scales (Fig. 26).

Unfortunately, none of the marine *Trachelophyllum* species has been investigated with modern methods. It is even unknown whether they have an epicortical slime (scale) layer.

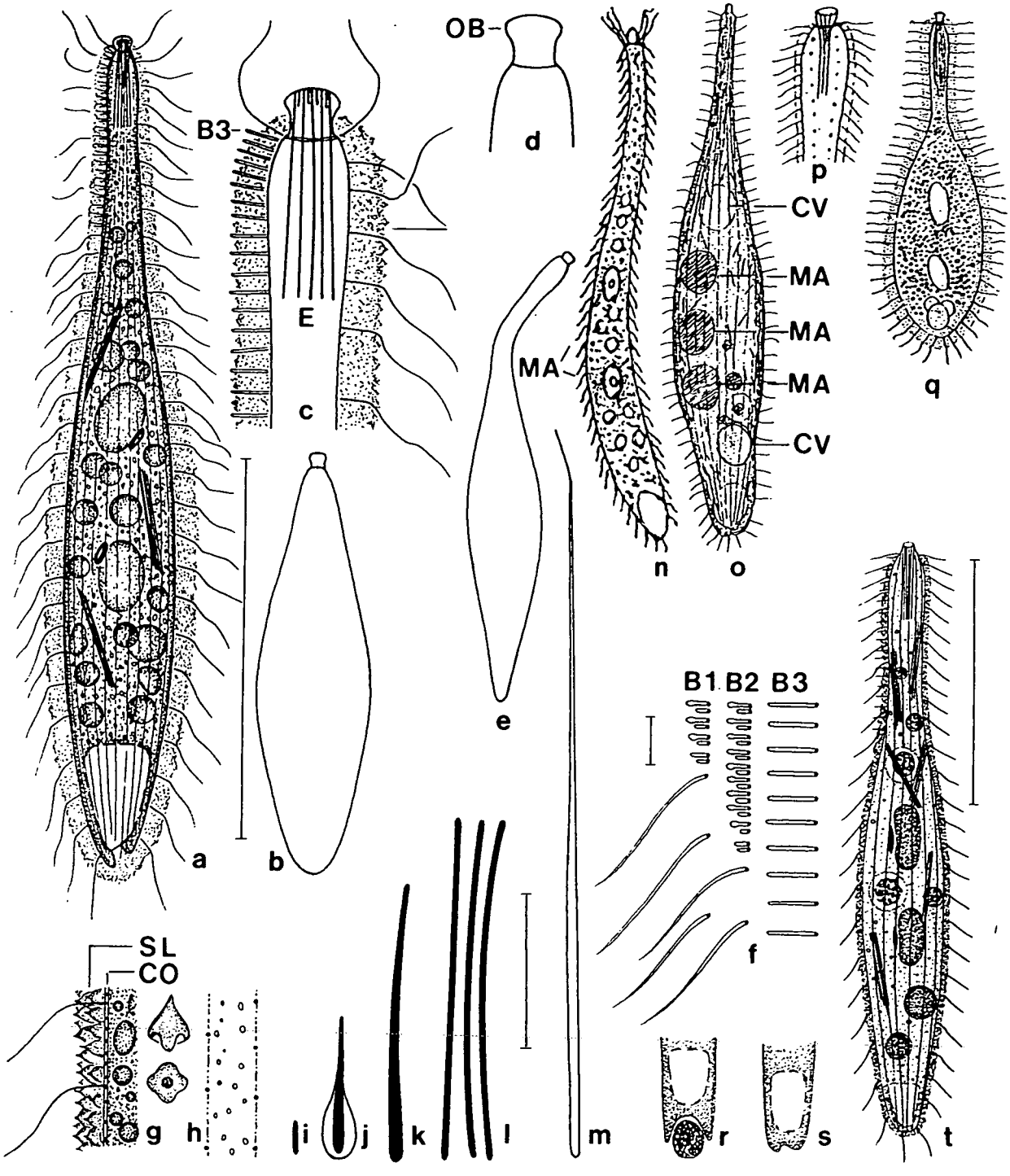

Fig. 32a–t. *Bilamellophrya australiensis* (a–m) and related species (n–t) from life. **a, b:** Extended and fully contracted specimen, drawn to scale. **c, d:** Anterior portion showing oral bulge with two types of extrusomes. **e:** Shape variant. **f:** Proximal brush region. **g:** The mucilaginous layer is composed of about 2 µm-sized scales shown in lateral and posterior polar view. **h:** Surface view showing cortical granulation. **i–m:** Resting (i, l), developing (j, k), and exploded extrusomes (m), drawn to scale. **n:** *Trachelophyllum filum*, size ? (from DUMAS 1930). **o:** *T. brachypharynx*, 350–400 µm (from LEVANDER 1894). **p, q:** *T. vestitum*, 250 µm (from KAHL 1930a and STOKES 1884). **r–t:** *T. vestitum*, 240 µm (from FOISSNER 1983b); figures (r, s) show defecation. B1-3 – dorsal brush rows, CO – cortex, CV – contractile vacuole, E – extrusomes, MA – macronuclear nodules, OB – oral bulge, SL – mucilaginous layer. Scale bars 4 µm (f), 10 µm (i–m), and 100 µm (a, t).

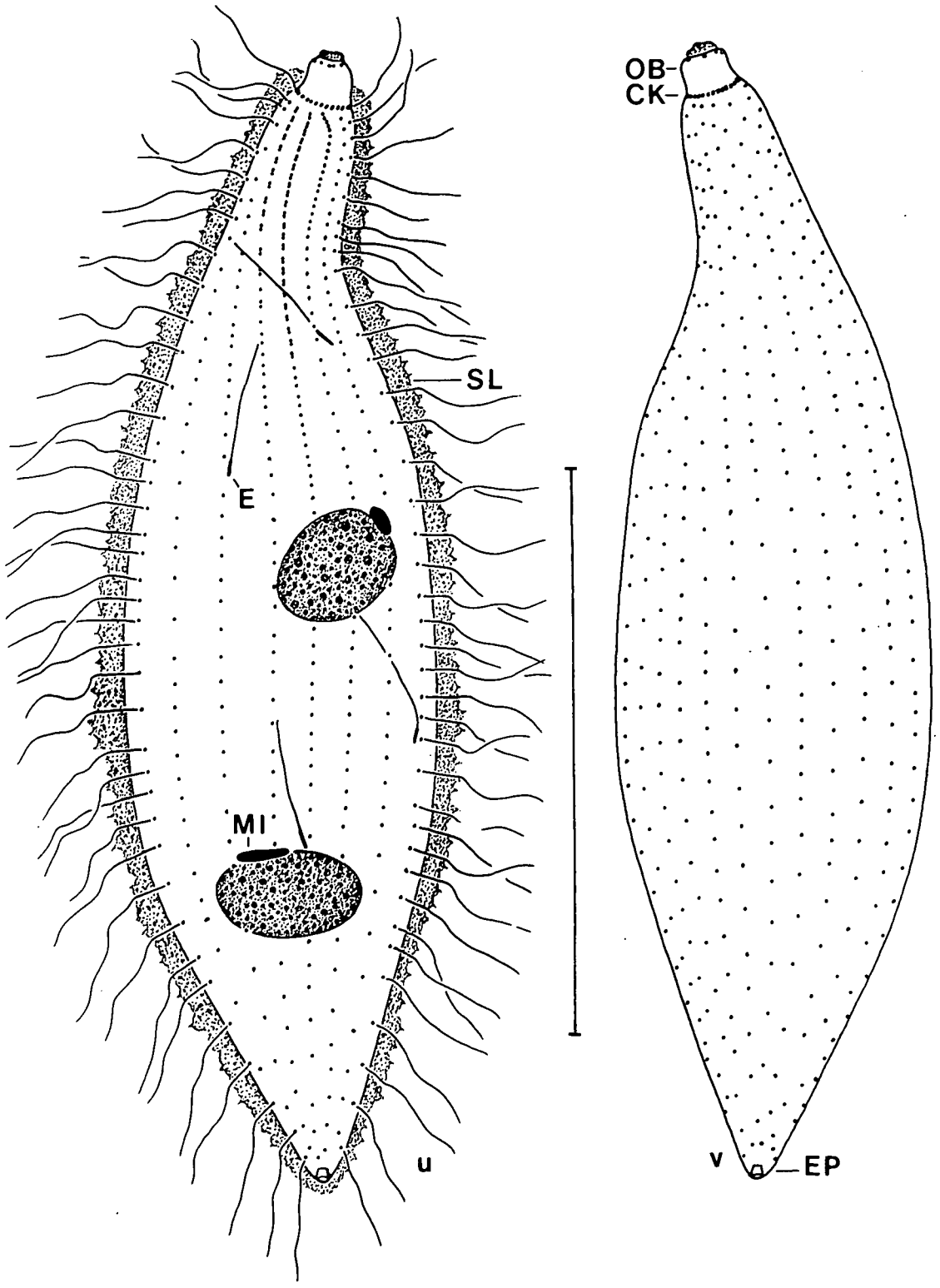

Fig. 32u, v. *Bilamellophrya australiensis*, ciliary pattern of dorsal and ventral side and nuclear apparatus of holotype specimen after protargol impregnation. Note granule accumulation on top of oral bulge and mucilaginous (scale) layer. Further details, see next plate. CK – circumoral kinety, E – developing extrusome, EP – excretory pore of contractile vacuole, MI – micronucleus, OB – oral bulge, SL – mucilaginous (scale) layer. Scale bar 80 μm.

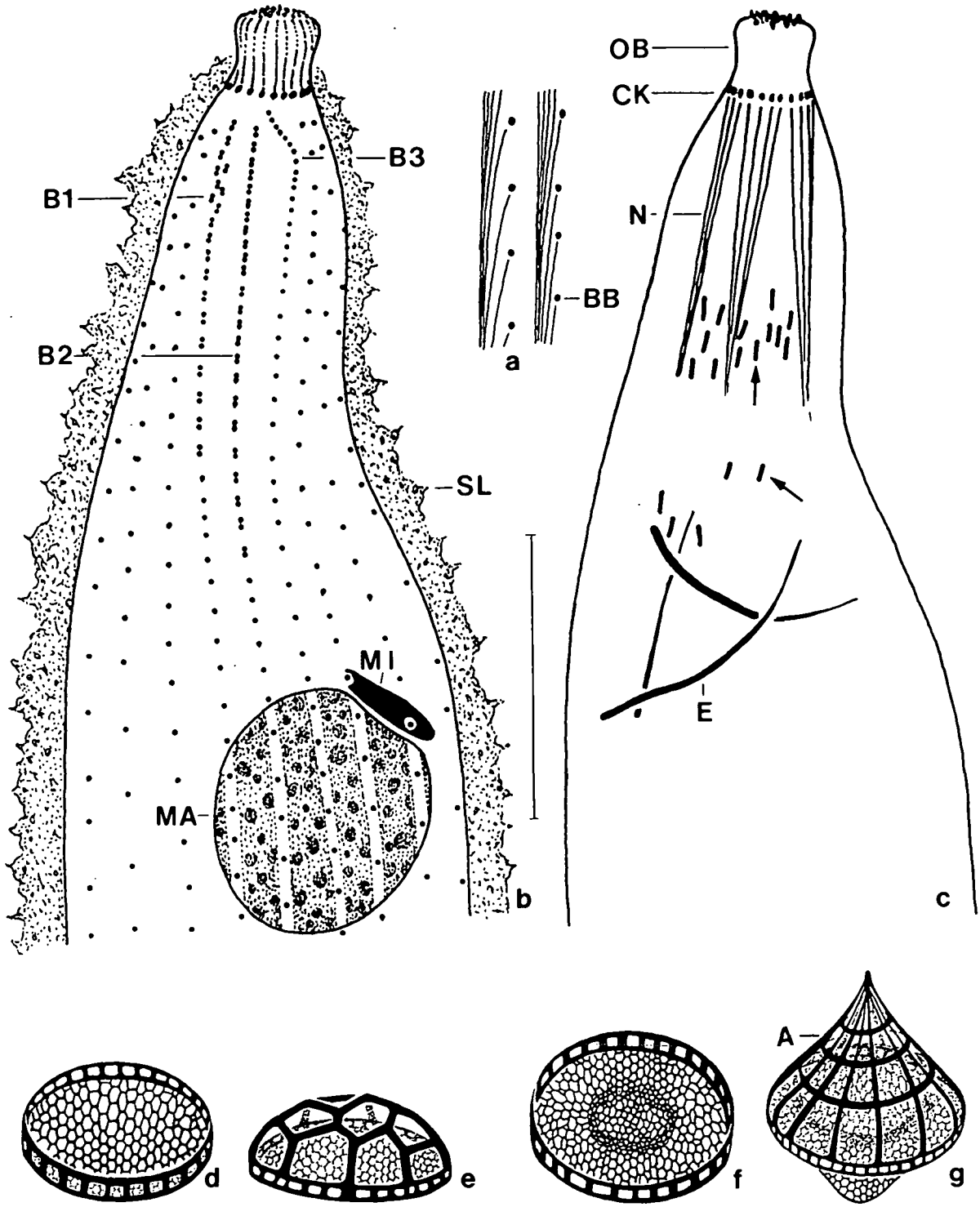

Fig. 33a–g. *Bilamellophrya australiensis* after protargol impregnation (a–c) and in the SEM (d–g). **a:** Surface view showing postciliary fibres. **b, c:** Ciliary pattern of anterior dorsal side and cytoplasmic details. Arrows mark posterior, toxin-containing portion of long extrusomes (Fig. 32 l). The mucilaginous layer is serrated by conical type II scales (Fig. 32g). **d–g:** Baseplates and oblique lateral views of type I (d, e; about 1.6 × 1 × 1 µm) and type II (f, g; about 2 × 2 × 2 µm) scales. A – arcs, B1-3 – dorsal brush rows, BB – basal body, CK – circumoral kinety, E – extrusomes, MA – macronucleus, MI – micronucleus, N – nematodesmata, OB – oral bulge, SL – scale layer. Scale bar 20 µm.

Trachelophyllum vestitum STOKES, 1884 is similar to *B. australiensis* in many respects (size, shape of oral bulge, extrusomes, nuclear apparatus, distinct mucilaginous layer), but has a different shape (Fig. 32p, q). However, FOISSNER (1983b) assumed that STOKES (1884) illustrated a contracted specimen and identified a slender species from an alpine pool with STOKES' creature, mainly because of the distinct slime layer and the conspicuous, rod-shaped extrusomes (Fig. 32r–t). We do not hold this view any longer because STOKES (1884), a very careful observer, definitely stated: "the length from four to five times the breath", which is distinctly different from both FOISSNER's alpine population and *B. australiensis* (6–8:1). Furthermore, and possibly of greater importance, partially (315a) and fully (Fig. 32b) contracted specimens of *B. australiensis* do not resemble STOKES' *T. vestitum* (Fig. 32q). Likely, FOISSNER's population belongs to *B. australiensis*.

Data for *Trachelophyllum filum* DUMAS, 1930 are too sparse to be reliably compared with *B. australiensis*, especially because the measurements given cannot be transformed to modern standards. However, the cylindroidal shape indicates that it is different from *B. australiensis* (Fig. 32n).

Table 28. Morphometric data on two Australian populations of *Bilamellophrya australiensis* (upper line: type population from soil of Murray River floodplain; lower line: from floodplain soil of a river between Erldunda and Ayers Rock).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	157.7	160.0	13.1	2.9	8.3	130.0	190.0	21
	161.7	165.0	20.5	5.3	12.7	125.0	200.0	15
Body, width [b]	38.9	38.0	7.8	1.7	20.0	23.0	56.0	21
	24.1	24.0	2.5	0.7	10.6	20.0	29.0	15
Oral bulge, height	5.4	5.0	0.9	0.2	16.0	4.0	7.0	21
	4.4	4.0	–	–	–	4.0	5.0	15
Oral bulge, diameter	6.3	6.0	1.1	0.2	17.5	4.0	9.0	21
	5.3	5.0	0.6	0.2	11.6	4.0	6.0	15
Anterior body end to nuclear apparatus, distance	54.0	54.0	9.7	2.1	18.0	36.0	79.0	21
	51.9	50.0	11.7	3.0	22.6	25.0	78.0	15
Circumoral kinety to last dikinetid of brush row 1, distance	25.7	26.0	6.6	1.5	25.8	6.0	34.0	21
	20.4	19.0	4.1	1.1	20.1	15.0	30.0	15
Brush row 1, number of dikinetids	16.0	17.0	3.8	0.8	23.7	5.0	21.0	21
	14.1	14.0	2.4	0.6	17.3	8.0	18.0	15
Circumoral kinety to last dikinetid of brush row 2, distance	33.4	36.0	6.3	1.4	18.7	20.0	40.0	21
	32.9	33.0	5.2	1.3	15.8	25.0	44.0	15
Brush row 2, number of dikinetids	21.7	22.0	3.6	0.8	16.5	13.0	26.0	21
	22.5	23.0	4.0	1.0	17.6	16.0	30.0	15
Anterior macronuclear nodule, length	18.7	18.0	2.3	0.5	12.3	16.0	25.0	21
	17.2	17.0	1.6	0.4	9.1	14.0	20.0	15
Anterior macronuclear nodule, width	13.0	13.0	1.2	0.3	9.4	10.0	15.0	21
	9.2	9.0	1.4	0.4	15.5	7.0	12.0	15
Macronuclear nodules, distance in between	23.5	26.0	12.8	2.8	54.2	0.0	46.0	21
	20.3	20.0	8.5	2.2	41.7	5.0	34.0	15

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15
Micronuclei, length	7.5	7.0	1.3	0.3	17.1	5.0	10.0	21
	5.1	5.0	0.6	0.2	11.6	4.0	6.0	15
Micronuclei, width	2.3	2.0	–	–	–	2.0	3.0	21
	2.4	2.0	–	–	–	2.0	3.0	15
Micronuclei, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15
Somatic ciliary rows, number	24.2	25.0	1.6	0.4	6.6	22.0	27.0	21
	16.8	16.0	1.1	0.3	6.8	16.0	20.0	15
Kinetids in a ventral kinety, number	32.2	32.0	4.2	0.9	13.0	25.0	40.0	21
	40.1	40.0	5.9	1.5	14.8	30.0	48.0	15
Dikinetidal brush rows, number [c]	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15
Mucilaginous (scale) layer, maximum thickness	3.3	3.0	0.9	0.2	25.7	2.0	5.0	21
	2.8	3.0	–	–	–	2.0	4.0	15
Type I scales, length [d]	1.6	1.6	0.2	0.02	11.7	1.3	2.0	56
Type I scales, width [d]	1.0	1.0	0.2	0.02	15.8	0.7	1.4	56
Type I scales, number of polygons in superstructure [d]	7.8	8.0	1.3	0.20	16.3	5.0	11.0	54
Type II scales, diameter [d]	1.9	1.9	0.2	0.04	12.3	1.6	2.9	35
Type II scales, height [d]	1.8	1.8	0.2	0.04	13.0	1.4	2.2	27
Type II scales, number of arcs forming cone [d]	10.2	10.0	1.2	0.20	11.7	7.0	13.0	23
Type II scales, number of transverse rings on cone [d]	2.1	2.0	0.4	0.10	20.4	1.0	3.0	22

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Without mucilaginous (scale) layer.

[c] Row 3 is monokinetidal (see description).

[d] From SEM micrographs of specimens from type location.

Bilamellophrya etoschensis nov. spec. (Fig. 34a–q; 316a–m; Table 29)

Diagnosis: Size about 140 × 15 µm in vivo, highly contractile; slenderly claviform. 2 ellipsoidal, apart macronuclear nodules with a micronucleus each. Extrusomes rod-shaped, about 4 µm long. On average 11 ciliary rows. Type I scales on average 1.1 × 0.7 µm and with 6 polygons in superstructure; type II scales about 1.3 × 1 × 0.9 µm, conical superstructure composed of an average of 7 concave, meridional arcs.

Type location: Soil from margin (*Sporobolus* grass girdle) of Etosha Pan, Namibia, 19°10'S 15°55'E (site 60 in figures 2, 3 and chapter 2.1.2).

Etymology: Named after the area discovered.

Description: Size of extended specimens 90–150 × 10–20 µm in vivo, length:width ratio in vivo about 9:1, after protargol impregnation 3.5–13:1, on average 7:1 (Table 29). Slenderly clavate to fusiform with neck often slightly widened in oral region and gradually merging into broadened trunk, slightly to distinctly flattened dorsoventrally. Anterior end conical and hyaline, posterior narrowly rounded (Fig. 34a, b, h; 316a, b). Cells very flexible, amoeboidal and contractile by up to 50% of body length under cover glass pressure, strongly contracted specimens slenderly to broadly claviform (Fig. 34f, i); contracts and extends slowly, preserved specimens thus of similar size and shape as live ones. Nuclear apparatus in middle third of cell. Macronuclear nodules globular to distinctly (3:1) ellipsoidal, on average broadly ellipsoidal; usually with rather irregular outline, fairly close together and connected by a fine strand; nucleoli scattered, globular, minute. Micronuclei near or attached to macronuclear nodules, conspicuously large, that is, 6 × 2 µm on average, globular to slenderly (4:1) ellipsoidal (Fig. 34a, g, h, i, q; 316a; Table 29). Contractile vacuole in posterior end, with single, about 2.5 µm long pore near pole centre. Only one type of minute and thus inconspicuous extrusomes in oral bulge, viz., rod-shaped, about 4 × 0.4 µm-sized toxicysts, which do not impregnate with protargol (Fig. 34a, b, d; 316c). Cytoplasm colourless and rather hyaline, contains fat globules 1–5 µm across and some irregular, compact inclusions, likely remnants of preyed ciliates. Swims rather rapidly and glides serpentinely on microscope slide and among debris (Fig. 316a, b).

Cortex thin and flexible, covered by an about 2 µm thick, mucilaginous layer of epicortical scales producing serrate body margin; serration more distinct in protargol-impregnated than live specimens. Mucilaginous layer composed of two kinds of scales lying one upon the other; individual scales minute and adhering to each other and thus hardly recognizable in the light microscope (Fig. 34a, b, e, j, m–o; 316d–m). Type I scales on body surface, except for oral bulge, tightly spaced, on average 1.1 × 0.7 µm and with 6 polygons in domed superstructure. Type II scales also very tightly spaced, 1.3 × 1 × 0.9 µm on average in the scanning electron microscope, baseplate broadly obconical, gives rise to an average of seven strongly concave arcs forming conspicuous cone; produce serrate body margin in vivo and protargol preparations, as described above, and conspicuously dotted surface in the scanning electron microscope at low magnification (Fig. 316d–f).

Cilia about 10 µm long in vivo, rather widely and irregularly spaced, arranged in meridional, equidistant rows, three of them differentiated to dorsal brush rows anteriorly (Fig. 34a–c, g, p; 316c, e). Brush rows 1 and 2 on average of same length and structure, composed of fairly widely spaced dikinetids bearing acicular, V-like spread bristles about 3 µm (anterior bristle of dikinetids) to 5 µm (posterior bristle) long; bristles immobile and obliquely attached to body surface, thus entirely covered by epicortical scale layer and invisible in the scanning electron microscope. Brush row 3 extends to mid-body, composed of monokinetids having about 3 µm long, acicular, immobile bristles projecting at right angles from body proper and piercing scale layer; thus recognizable in scanning electron micrographs (Fig. 316e). All brush rows continue posteriorly as ordinary somatic ciliary rows.

Oral bulge inconspicuous both in vivo and protargol preparations because hyaline and only about 3 × 3 µm in size, conical (very rarely cylindroidal) and indistinctly set off from body proper, contains extrusomes as described above. Circumoral kinety at base of oral bulge, composed of about 10 dikinetids each bearing a single cilium and a fine nematodesma forming a conical pharyngeal basket (Fig. 34a, b, f–i, p, q; 316a–c).

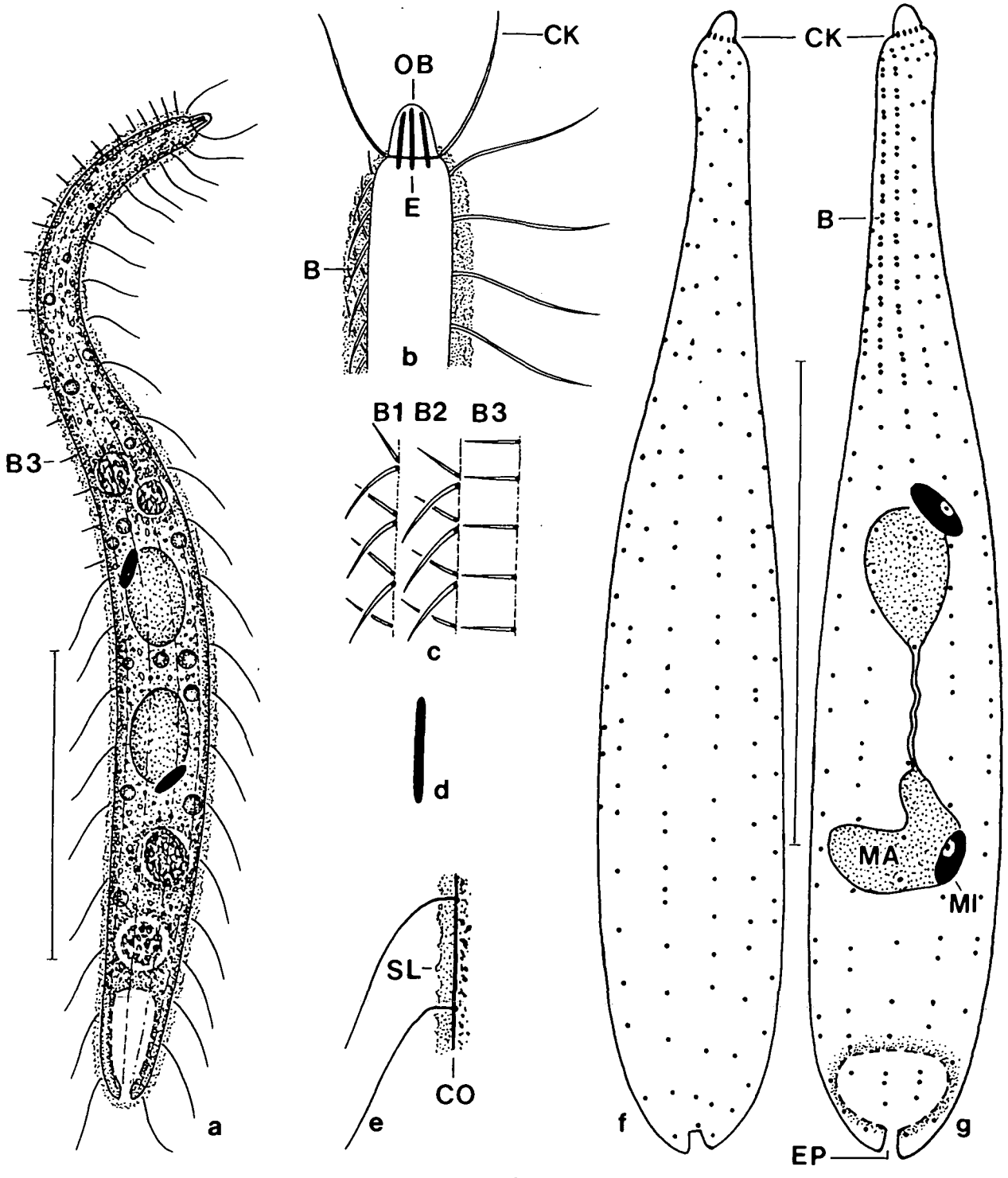

Fig. 34a–g. *Bilamellophrya etoschensis* from life (a–d) and after protargol impregnation (e–g). **a:** Right lateral view of a representative specimen. **b:** Details of anterior body portion. The bristles of brush rows 1 and 2 are obliquely attached to the cell's surface and do not pierce the epicortical scale layer. **c:** Middle region of dorsal brush. **d:** Extrusomes are rod-shaped and only 4 µm long. **e:** Optical section showing epicortical slime layer. **f, g:** Ciliary pattern of ventral and dorsal side of holotype specimen. B – dorsal brush, B1-3 – dorsal brush rows, CK – circumoral kinety, CO – cortex, E – extrusomes, EP – excretory pore, MA – macronuclear nodules, Mi – micronucleus, OB – oral bulge, SL – scale layer. Scale bars 40 µm.

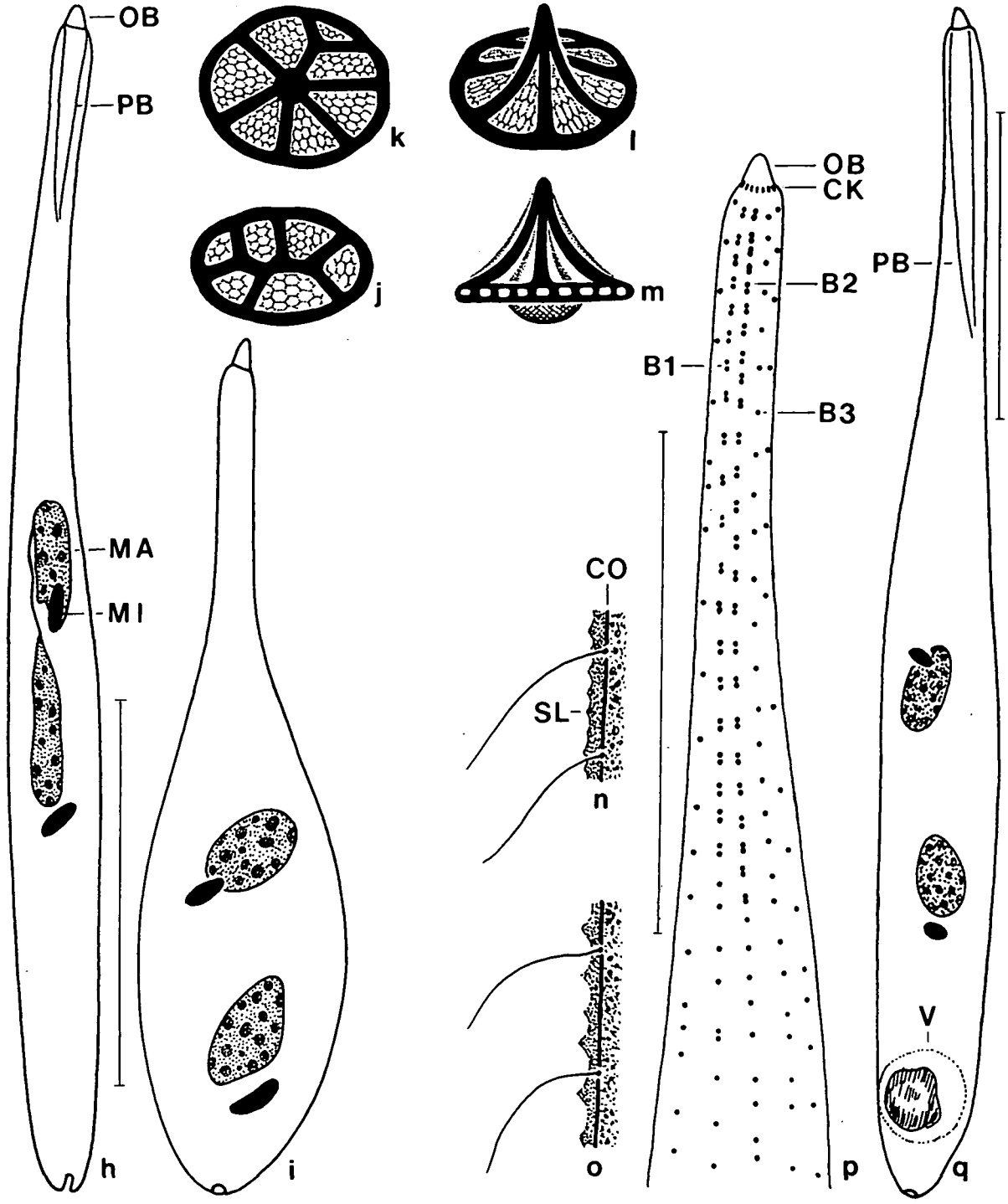

Fig. 34h–q. *Bilamellophrya etoschensis* from type location (h–m) and the Galàpagos Islands (n–q) after protargol impregnation (h, i, n–q) and in the SEM (j–m). **h, i:** Extreme shape and size variants, drawn to scale. **j:** Vertical projection of a type I scale. **k–m:** Vertical projection, oblique distal view, and side view of type II scales. The honey-combed pattern of the baseplate was hardly recognizable, likely due to suboptimal preparation. **n, o:** Optical sections showing serrate epicortical layer (cp. figures 316g–i). **p:** Ciliary pattern of dorsal anterior third. **q:** Shape and nuclear apparatus of a representative specimen. B1-3 – dorsal brush rows, CK – circumoral kinety, CO – cortex, MA – macronuclear nodules, MI – micronuclei, OB – oral bulge, PB – pharyngeal basket, SL – slime (scale) layer, V – food vacuole. Scale bars 40 µm.

Table 29. Morphometric data on *Bilamellophrya etoschensis* (upper line, Namibian type population), *B. etoschensis* (middle line, from Galàpagos Islands), and *B. hawaiiensis* (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	92.1	95.0	19.7	5.5	21.4	60.0	128.0	13
	148.2	154.0	16.6	5.0	11.2	122.0	168.0	11
	121.9	118.0	12.8	3.3	10.5	105.0	145.0	15
Body, width [b]	15.0	14.0	3.6	1.0	23.9	10.0	21.0	13
	15.8	16.0	2.1	0.6	13.5	14.0	21.0	11
	22.3	23.0	2.6	0.7	11.8	18.0	26.0	15
Oral bulge, height	2.5	3.0	–	–	–	2.0	3.0	13
	2.9	3.0	–	–	–	2.0	4.0	11
	2.9	3.0	–	–	–	2.0	4.0	15
Oral bulge, diameter	2.7	3.0	–	–	–	2.0	3.0	13
	3.2	3.0	–	–	–	3.0	4.0	11
	2.7	3.0	–	–	–	2.0	3.0	15
Anterior body end to nuclear apparatus, distance	42.2	42.0	9.8	2.7	23.2	23.0	60.0	13
	73.7	78.0	13.1	3.9	17.7	50.0	96.0	11
	44.9	45.0	8.8	2.3	19.5	31.0	65.0	15
Circumoral kinety to last dikinetid of brush row 1, distance	30.1	30.0	7.8	2.2	25.8	18.0	45.0	13
	52.4	52.0	2.5	1.1	4.8	50.0	55.0	5
	26.5	27.0	6.5	1.7	24.6	10.0	38.0	15
Brush row 1, number of dikinetids	13.9	13.0	2.3	0.6	16.5	11.0	18.0	13
	19.4	20.0	1.3	0.6	6.9	18.0	21.0	5
	14.5	14.0	3.1	0.8	21.1	6.0	18.0	15
Circumoral kinety to last dikinetid of brush row 2, distance	29.8	30.0	6.7	1.9	22.5	20.0	45.0	13
	54.2	55.0	5.2	2.3	9.5	46.0	59.0	5
	30.1	32.0	5.8	1.5	18.9	20.0	44.0	15
Brush row 2, number of dikinetids	14.4	14.0	2.8	0.8	22.5	12.0	20.0	13
	22.8	23.0	2.8	1.2	12.2	20.0	26.0	5
	19.2	20.0	3.8	1.0	19.8	10.0	25.0	15
Anterior macronuclear nodule, length	11.1	11.0	2.1	0.6	18.6	7.0	15.0	13
	14.8	14.0	2.2	0.7	15.0	12.0	20.0	11
	16.5	17.0	2.1	0.6	12.8	13.0	20.0	14
Anterior macronuclear nodule, width	6.4	7.0	1.1	0.3	17.6	4.0	8.0	13
	6.1	6.0	0.5	0.2	8.9	5.0	7.0	11
	8.2	8.0	1.2	0.3	14.5	7.0	10.0	14
Macronuclear nodules, distance in-between	6.0	6.0	3.8	1.1	63.5	0.0	12.0	13
	14.2	16.0	4.1	1.2	28.5	6.0	18.0	11
	13.3	14.0	7.4	2.0	55.5	0.0	28.0	14
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	13
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	14
Micronuclei, length	5.9	6.0	1.3	0.4	22.0	4.0	9.0	13
	4.6	5.0	–	–	–	4.0	5.0	11
	4.6	4.0	0.9	0.3	19.8	4.0	6.0	8
Micronuclei, width	2.5	2.0	0.7	0.2	26.0	2.0	4.0	13
	2.4	2.0	0.6	0.2	26.9	2.0	4.0	11

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	2.1	2.0	–	–	–	2.0	3.0	8
Micronuclei, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	13
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	10
Somatic ciliary rows, number	10.9	11.0	0.5	0.1	4.5	10.0	12.0	13
	11.4	11.0	–	–	–	11.0	12.0	10
	12.9	13.0	0.6	0.2	4.6	12.0	14.0	15
Kinetids in a ventral kinety, number	24.4	25.0	4.3	1.2	17.5	18.0	30.0	13
				not determined				
	34.1	35.0	5.0	1.3	14.6	25.0	40.0	14
Dikinetidal brush rows [c]	2.0	2.0	0.0	0.0	0.0	2.0	2.0	13
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	14
Type I scales, length [d]	1.1	1.1	0.1	0.04	12.1	0.9	1.3	13
				no data				
	1.3	1.3	0.2	0.04	13.9	1.1	1.9	20
Type I scales, width [d]	0.7	0.7	0.1	0.03	14.3	0.5	0.8	13
				no data				
	0.6	0.6	0.1	0.02	12.8	0.5	0.8	20
Type I scales, number of polygons in superstructure [d]	5.8	6.0	1.0	0.3	17.0	4.0	8.0	13
				no data				
	7.4	8.0	1.6	0.4	21.3	5.0	11.0	20
Type II scales, length [d]	1.3	1.3	0.2	0.03	12.7	0.9	1.7	33
				no data				
	1.4	1.3	0.1	0.02	9.2	1.2	1.6	36
Type II scales, width [d]	1.0	1.0	0.1	0.02	9.7	0.8	1.2	33
				no data				
	1.2	1.2	0.1	0.02	8.7	1.0	1.4	36
Type II scales, height [d]	0.9	0.9	0.1	0.03	14.0	0.7	1.2	24
				no data				
	1.2	1.2	0.2	0.03	12.6	1.0	1.6	36
Type II scales, number of polygons (arcs) forming cone [d]	6.9	7.0	1.2	0.2	17.1	5.0	10.0	33
				no data				
	15.6	16.0	2.8	0.5	17.9	10.0	21.0	36

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Without mucilaginous layer.

[c] Row 3 is monokinetidal (see description).

[d] From SEM micrographs.

Occurrence and ecology: To date found at type location, that is, a slightly saline, reddish to greyish soil in the *Sporobolus-Sueda* girdle surrounding the Pan, and on the Galàpagos Islands, where it occurred in a sample containing darkbrown soil and much litter, pH 7.4. Due to its narrow, flexible body, the species is well adapted to explore fine soil pores.

Comparison with related species: As mentioned above, *B. etoschensis* was also found in a soil sample from the Galàpagos Islands (Fig. 34n–q; Table 29). This population, which was not studied in the scanning electron microscope, was highly similar to the Namibian species, especially in having 4 µm long, rod-shaped extrusomes and about 11 ciliary rows. The specimens were, however, considerably larger (length in vivo up to 200 µm), the mucilaginous layer was more distinctly serrate in protargol preparations, and the brush cilia were shorter (< 3 µm) and hardly V-like spread. These differences are small compared to the conformities, and thus the populations are likely conspecific.

Bilamellophrya etoschensis is, in vivo, easily separated from its congeners by the minute extrusomes and, in the scanning electron microscope, by fine structural details of the type II scales. The general appearance of *B. etoschensis* is very similar to members of the → *T. apiculatum* group. The extrusomes, in contrast, are almost unique by their small size. Such small extrusomes occur only in one other species, namely → *Trachelophyllum africanum*. This species is similar to *B. etoschensis* also in many other features, but not in the epicortical scales.

Bilamellophrya hawaiiensis **nov. spec.** (Fig. 35a–l; 317a–h; Table 29)

Diagnosis: Size about 150 × 25 µm in vivo, slightly contractile; slenderly fusiform. 2 ellipsoidal, distant macronuclear nodules with a micronucleus each. Two types of extrusomes: type I acicular and 12 µm long; type II rod-shaped, inconspicuous because only 2 µm long. On average 13 ciliary rows. Type I scales on average 1.3 × 0.6 µm and with 8 polygons in superstructure; type II scales about 1.3 × 1.2 × 1.2 µm, conical superstructure composed of an average of 16 polygons.

Type location: Arable field soil between the village of Honomu and the Akaka Falls, Big Island, Hawaii, 19°50'N 155°10'W.

Etymology: Named after the country discovered.

Description: Size of extended specimens 120–170 × 20–30 µm in vivo, usually about 150 × 25 µm, length:width ratio in vivo about 6:1, after protargol impregnation 4–7:1, on average 5.5:1 (Table 29). Slenderly fusiform with neck slightly widened in oral region and gradually merging into broadened trunk, flattened about 2:1 dorsoventrally. Anterior end button-shaped and refractive due to the extrusomes contained, posterior end narrowly rounded to bluntly tapered (Fig. 35a, j). Cells very flexible and contractile by up to 30% of body length; contracts and extends very slowly, preserved specimens thus of similar size and shape as live ones. Nuclear apparatus in middle third of cell. Macronuclear nodules broadly (1.5:1) to slenderly (2.5:1) ellipsoidal, length:width ratio on average 2:1, stand out as bright blisters from granulated cytoplasm, usually distinctly apart and connected by a fine strand, rarely abutting as in → *Epitholiolus chilensis*; nucleoli scattered, about 2 µm across. Micronuclei usually attached to macronuclear nodules, ellipsoidal (Fig. 35a, j). Contractile vacuole in posterior end, with conspicuous, about 3 µm long excretory pore occupying pole centre (Fig. 35a, j; 317f). Two types of extrusomes in oral bulge and cytoplasm (Fig. 35a, b): type I

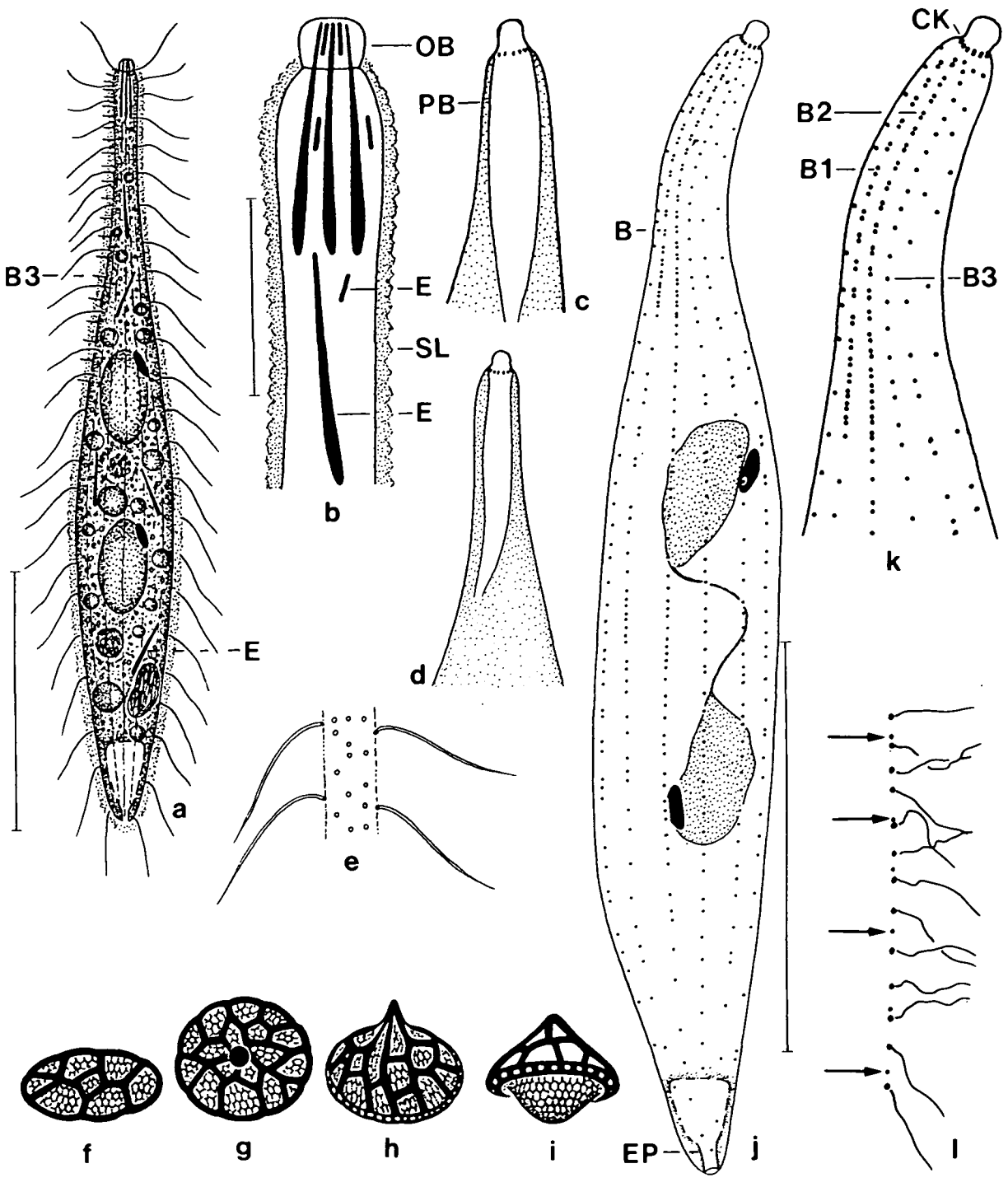

Fig. 35a–l. *Bilamellophrya hawaiiensis* from life (a, b, e), after protargol impregnation (c, d, j–l), and in the scanning electron microscope (f–i). **a:** Dorsolateral view of a representative specimen. **b–d:** Details of anterior body region. **e:** Surface view showing cortical granulation. **f:** Vertical projection of a type I scale. **g–i:** Vertical projection, oblique distal view, and oblique proximal view of type II scales. **j–l:** Ciliary pattern of dorsal side of holotype specimen. About one third of the basal bodies are unciliated (arrows). B – dorsal brush, B1-3 – brush rows, CK – circumoral kinety, E – extrusomes, EP – excretory pore, OB – oral bulge, PB – pharyngeal basket, SL – scale layer. Scale bars 10 µm (b) and 50 µm (a, j).

conspicuous because about 12 × 1 µm and acicular with broadest site slightly subterminal, does not form bundles in cytoplasm and does not impregnate with protargol; type II rod-shaped and inconspicuous because only about 2 µm long, mainly attached to surface of oral bulge, does not impregnate with protargol. Cytoplasm colourless and rather hyaline, contains some food vacuoles with heterotrophic flagellates and medium-sized ciliates (*Vorticella astyliformis*) and, depending on nutrition, few to many fat globules 1–8 µm across. Glides rather rapidly on microscope slide and among debris.

Cortex thin and flexible, contains scattered, colourless granules (0.4 × 0.2 µm) and a faintly impregnated fibre system very similar to that described in → *T. apiculatum*; covered with an about 2 µm thick, mucilaginous layer of epicortical scales producing tuberculate or indistinctly serrate body margin both in vivo and protargol preparations (Fig. 35a, b, e). Mucilaginous layer very hyaline and thus hardly recognizable in the light microscope, composed of two kinds of scales lying one upon the other (Fig. 35f–i; 317a–h). Type I scales in single layer on body surface, except for oral bulge, tightly spaced, elliptical, 1.3 × 0.6 µm on average in the scanning electron microscope, domed superstructure with 8 polygons on average. Type II scales upon and more loosely arranged than type I scales, about 1.3 µm across and 1.2 µm high; baseplate obconical, gives rise to a conical, slightly concave superstructure composed of an average of 16 scattered polygons.

Cilia 12 µm long in vivo and rather widely spaced because ciliated kinetids irregularly alternate with slightly smaller, bare granules (Fig. 35j, l)[4]. Ciliary rows meridionally and equidistantly arranged, three of them differentiated to dorsal brush rows anteriorly (Fig. 35a, j, k). Details of dorsal brush as in → *B. etoschensis*; row 3 only slightly longer than row 2.

Oral bulge inconspicuous because only about 3 µm across, button-shaped, distinctly set off from body proper and bright due to the extrusomes contained. Bulge surface smooth and without argyrophilic granules. Circumoral kinety at base of oral bulge, composed of about 12 dikinetids, each bearing a single cilium; gives rise to delicate fibres extending into the oral bulge and to fine nematodesmata forming a conical, slightly bulbous pharyngeal basket (Fig. 35c, d).

Occurrence and ecology: To date found only at type location. The sample was taken from the rhizosphere (0–10 cm) of a just ploughed fallow with remains of sugar-cane. The red-brown soil had pH 6.4 and was mixed with litter and fine roots collected at various sites of the field.

Comparison with related species: At first glance, *B. hawaiiensis* highly resembles → *B. australiensis* due to the body shape and the conspicuous extrusomes. However, both differ in the fine structure of the type II scales (superstructure polygonally faceted vs. composed of equidistantly spaced arcs), in the shape of the extrusomes (acicular vs. rod-shaped[5]) and oral bulge (button vs. anvil-shaped), and in the number of ciliary rows

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[4] Although sometimes not mentioned, unciliated granules (basal bodies?) occur in all trachelophyllids described in this monograph.

[5] A difficult feature in this species because developing and exploding extrusomes of → *B. australiensis* are acicular like the mature, resting toxicysts of *B. hawaiiensis*. Interestingly, cytoplasmic extrusome bundles occur only in → *B. australiensis*; possibly, only rod-shaped extrusomes form bundles. This shows that even "minor" features must be thouroughly documented because they might gain taxonomic importance when the group is better known.

(13 vs. 24). → *Bilamellophrya etoschensis* is also very similar to *B. hawaiiensis* in general appearance and most morphometrics (Table 29). However, the extrusomes are totally different (4 × 0.4 µm and rod-shaped vs. 12 × 1 µm and acicular) and the type II scales are rather dissimilar (conical superstructure composed of six rather regularly spaced arcs vs. polygonally faceted). Accordingly, → *B. australiensis*, *B. hawaiiensis*, and → *B. etoschensis* are well-defined species easily distinguishable both with the light microscope and the scanning electron microscope. *Bilamellophrya hawaiiensis*, is also different from the *Trachelophyllum* species of the older literature, basically by the same features discussed in *B. australiensis*.

Enchelyotricha jesnerae nov. spec. (Fig. 36a–n; 318a–h; Table 30)

Diagnosis: Size about 120 × 25 µm in vivo. Obclavate, contractile by up to 40%. 2 broadly ellipsoidal macronuclear nodules 20 µm apart on average. Extrusomes rod-shaped, about 20 × 0.3 µm in size. Cortical granules approximately 1.5 × 1 µm, tightly spaced forming plate-like layer. On average 25 ciliary rows and 9 dikinetids in long dorsal brush row.

Type location: Mud and soil from road puddles in the Bambatsi Guest Farm, Namibia, 20°10'S 15°25'E (site 49 in figure 2 and chapter 2.1.2).

Dedication: Wilhelm FOISSNER dedicates this new species to Mag. Dr. Brigitte JESNER-KRASSNIGG for her friendship over many years.

Description: Size 80–140 × 20–35 µm in vivo, usually near 120 × 25 µm, considerably stouter in protargol preparations, where most specimens are contracted, often showing a strongly wrinkled cortex, very much like trachelocercids (Fig. 36 l; Table 30). Extended specimens claviform to cylindroidal, slightly flattened; contracts and extends rather slowly, contracted cells roughly fusiform to broadly fusiform or dumb-bell-shaped (Fig. 36a, d–f, j; 318e). Macronuclear nodules in central body region, on average 20 µm apart, never connected by a bridge or thread; elongate ellipsoidal to almost globular, on average broadly ellipsoidal; nucleoli small, scattered, globular. On average four globular micronuclei near or attached to macronuclear nodules (Fig. 36a, j; Table 30). Contractile vacuole in posterior body end with single, distinct excretory pore in pole centre. Extrusomes conspicuous, although very slender, because forming bundles in oral bulge and cytoplasm, impregnate strongly with silver carbonate, while protargol stains lightly only some cytoplasmic developmental stages; individual extrusomes slightly curved and 18–25 × 0.3–0.5 µm in size (Fig. 36a–c; 318d, g, h). Cortex conspicuous because studded with compact granules about 1.5 × 0.8 µm in size, similar to → *Pseudoholophrya terricola*; granules form plate-like layer and usually impregnate more or less strongly with protargol hiding the ciliary pattern. Cytoplasm colourless, often contains many bright globules and indistinct food vacuoles, indicating that prey is digested quickly; feeds on various ciliates, even on the very fast → *Phialina minima*. Glides slowly on microscope slide and organic debris.

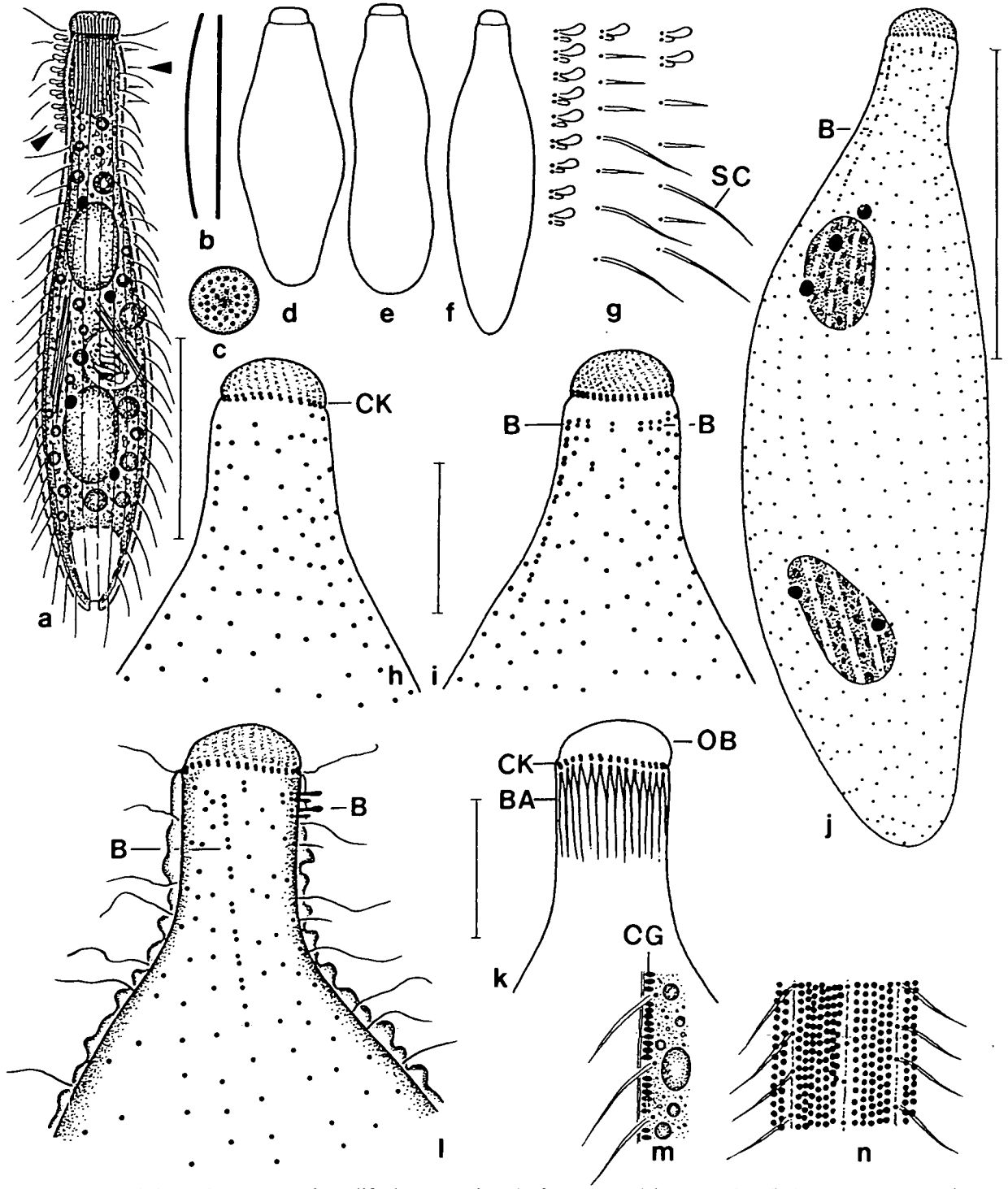

Fig. 36a–n. *Enchelyotricha jesnerae* from life (a–g, m, n) and after protargol impregnation (h–l). **a:** A representative, extended specimen. Arrowheads mark dorsal brush bristles. **b:** Extrusomes, length 20 µm. **c:** Frontal view of oral bulge studded with extrusomes. **d–f:** Fully and partially contracted specimens. **g:** Main portion of dorsal brush. **h, i:** Ciliary pattern of ventral and dorsal side in anterior body region. **j:** Ciliary pattern of dorsal side. **k, l:** Same specimen showing ciliary pattern of dorsal side and oral basket. Note the wrinkled cortex. **m, n:** Optical section and surface view showing the dense cortical granulation. B – dorsal brush, BA – oral basket, CG – cortical granules, CK – circumoral kinety, OB – oral bulge, SC – ordinary somatic cilium. Scale bars 40 µm (a, j) and 10 µm (h, i, k, l).

Cilia about 10 µm long in vivo, rather loosely spaced, especially in oral region, arranged in an average of 25 meridional, equidistant rows distinctly separated from circumoral kinety and differentiated to a complex dorsal brush anteriorly, except of about five ventral rows (Fig. 36a, g–j, l; 318a–c, e, f). Right brush margin marked by a row of about nine inflated, up to 3 µm long, paired bristles; most other rows commence with one or two bristle pairs, followed by some about 5 µm long, monokinetidal bristles mixed with ordinary cilia; some rows commence with such monokinetidal bristles or with ordinary cilja, especially on ventral side.

Oral bulge occupies anterior body end, conspicuous because about 10 × 5 µm in size, bright due to the extrusome bundle contained, and distinctly set off from body proper by a furrow containing the circumoral kinety; disc-shaped to slightly convex in vivo and scanning electron micrographs, while almost hemispherical in protargol-impregnated specimens; contains rather thick, lightly impregnated fibres originating from circumoral dikinetids and extending spirally to bulge centre. Circumoral kinety composed of comparatively widely spaced dikinetids, associated with bulge fibres described above and fine, bifurcated nematodesmata producing an indistinct oral basket (Fig. 36a, h–k; 318a–c, e, f).

Table 30. Morphometric data on *Enchelyotricha jesnerae*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	90.5	93.0	14.4	3.5	16.0	62.0	112.0	17
Body, width	32.4	34.0	7.2	1.4	22.2	22.0	45.0	17
Oral bulge, width	8.5	8.0	1.2	0.3	13.9	6.0	11.0	17
Oral bulge, height	3.9	4.0	0.7	0.2	17.0	3.0	5.0	17
Circumoral kinety to end of long brush row, distance	16.2	16.0	3.3	0.8	20.4	12.0	25.0	17
Dikinetids in long dorsal brush row, number	9.0	9.0	1.5	0.7	17.1	6.0	12.0	17
Anterior body end to first macronuclear nodule, distance	28.8	28.0	6.9	1.7	23.9	15.0	45.0	17
Macronuclear nodules, distance in between	18.1	15.0	10.2	2.5	56.7	1.0	35.0	17
Macronuclear nodules, length	15.4	15.0	4.1	1.0	26.6	10.0	28.0	17
Macronuclear nodules, width	10.4	10.0	2.0	0.5	19.5	7.0	14.0	17
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	17
Micronuclei, length	2.3	2.2	–	–	–	2.0	3.0	17
Micronuclei, width	2.1	2.0	–	–	–	2.0	2.5	17
Micronuclei, number	4.5	4.0	1.2	0.3	27.5	2.0	6.0	17
Somatic kineties, number	25.2	25.0	2.0	0.5	7.9	20.0	28.0	17
Ciliated kinetids in 10 µm of a kinety in mid-body, number	3.4	3.0	0.6	0.2	18.1	3.0	5.0	17

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Occurrence and ecology: To date found only at type location, where it was moderately abundant in the non-flooded Petri dish culture.

Family classification and comparison with related species: The Namibian population matches the definition of *Enchelyotricha* FOISSNER, 1987b, that is, has a

special dorsal brush, as described above. In contrast, family classification is uncertain. FOISSNER (1987b) assigned *Enchelyotricha* to the → Trachelophyllidae because of contractility and general similarities. However, our new definition of the → Trachelophyllidae excludes both *E. binucleata*, type of the genus, and *E. jesnerae* because they lack epicortical scales. Likewise, our new definition of the → Enchelyodontidae excludes *Enchelyotricha* because of the different dorsal brush. Possibly, *Enchelyotricha* is related to the Lacrymariina (see → *Phialina* spp.), with which it has three important features in common, viz., contractility, many brush rows, and an oral basket composed of bifurcated nematodesmata (Fig. 36k; GRAIN 1984, FOISSNER & FOISSNER 1988).

Enchelyotricha jesnerae differs from the type species and sole congener, *E. binucleata* FOISSNER, 1987b, by the macronuclear nodules (widely separated vs. connected by a distinct bridge), the cortical granules (very narrowly spaced forming a plate-like layer vs. loose, inconspicuous rows), and the number of ciliary rows (25 vs. 17). *Enchelyotricha jesnerae* is similar to several → *Trachelophyllum* and *Enchelyodon* species, some of which possibly belong to *Enchelyotricha*, for instance, *Enchelyodon contractilis* VUXANOVICI, 1963 (stouter and spirally contracting) and *E. retortus* VUXANOVICI, 1963 (stouter and only 50–60 µm long). However, data are too incomplete for a definite classification.

Family Fuscheriidae nov. fam.

Diagnosis: Acropisthiina FOISSNER & FOISSNER, 1988 with enchelyodontid general organization, that is, meridionally arranged somatic kineties, of which two, rarely three are anteriorly differentiated to dorsal brush rows. Oral bulge apical, circular, flat or domed and with central opening. Oral dikinetids clearly separated from somatic ciliary rows, producing a distinct circumoral kinety. Nematodesmal bundles originate from typical haptorid oral dikinetids **and** from ciliated oralized somatic monokinetids.

Type genus: *Fuscheria* BERGER, FOISSNER & ADAM, 1983.

Further genera assigned: *Actinorhabdos* FOISSNER, 1984; *Diplites* FOISSNER, 1998b; *Dioplitophrya* nov. gen.

Family Acropisthiidae FOISSNER & FOISSNER, 1988

Improved diagnosis: Gymnostome haptorids CORLISS, 1974 with spathidiid general organization, that is, anteriorly curved somatic kineties, of which three, rarely two or four are anteriorly differentiated to dorsal brush rows. Oral bulge apical, obliquely truncate, ovate and with dorsally shifted (acentric) opening in frontal view. Oral dikinetids indistinctly separated from somatic ciliary rows, do not produce a distinct circumoral kinety. Nematodesmal bundles originate from typical haptorid oral dikinetids **and** from ciliated oralized somatic monokinetids.

Type genus: *Acropisthium* PERTY, 1852.

Further genera assigned: *Chaenea* QUENNERSTEDT, 1867; *Sikorops* FOISSNER, 1999b; *Clavoplites* nov. gen.

Classification: Originally, all genera mentioned above were united in the families Trachelophyllidae (FOISSNER 1984) or Acropisthiidae (FOISSNER 1998b, 1999b). However, in Namibia and soils globally, we discovered quite a lot of inconspicuous haptorids whose detailed investigation showed that all have oralized somatic monokinetids plus haptorid oral dikinetids, indicating that they belong to the haptorid suborder Acropisthiina, as defined by FOISSNER & FOISSNER (1988). These species and some others described previously not only have a conspicuous extrusome diversity, but also a different arrangement of the ciliary rows and shape and structure of the oral bulge. We consider these differences as important at family level because they likely have a different evolutionary history. The Fuscheriidae probably originated from an enchelyodontid ancestor (for instance → *Enchelyodon*), while the Acropisthiidae likely have a spathidiid progenitor (for instance → *Spathidium*). Most of the species united in the Acropisthiidae have a spathidiid general appearance and were classified as "*Spathidium* sp." in our notebook. Furthermore, they have an acentric bulge opening, an important feature found also in some typical spathidiids, viz., *Spathidium seppelti seppelti* PETZ & FOISSNER, 1997 and *Arcuospathidium multinucleatum* FOISSNER, 1999b, which have, in addition to the usual long bulge (oral) slit, a minute, obconical opening near the dorsal edge of the bulge.

Accordingly, the special type of oral basket likely evolved independently in two haptorid lines. Certainly, this hypothesis needs further investigation, but the differences in the general organization of the two groups are sufficient for a familiar separation, independently of their evolutionary history. *Chaenea* QUENNERSTEDT, 1867 is now also assigned to one of these families because LIPSCOMB & RIORDAN (1990) showed that it has haptorid oral dikinetids and oralized somatic monokinetids.

Generic classification is based on extrusome shape and arrangement in both families. Certainly, this is not a "strong" feature, but probably the best we have in these feature-poor ciliates. The following key contains all described genera from both families.

Key to the genera of the Acropisthiidae and Fuscheriidae

(Identification of most genera and species needs live observation, to reveal the shape and arrangement of the extrusomes, and protargol impregnation, to reveal the number of dorsal brush rows).

1 Body rod-shaped. Many small macronuclear nodules. Oral ciliature more or less distinctly lacrymariid in vivo. Extrusomes rod-shaped or acicular. Four dorsal brush rows in unique, subapical position ..... *Chaenea* QUENNERSTEDT, 1867 (several species)

– Body cylindroidal, spathidiform, or rape-shaped. Single or few macronuclei 2

2 Body rape-shaped. With distinct subapical ciliary wreath. Extrusomes rod-shaped. Three

dorsal brush rows ..... *Acropisthium* PETRY, 1852 (single species)

– Body cylindroidal, spatulate, or barrel-shaped 3

3 Punctate (ellipsoidal or comma-shaped) extrusomes in oral bulge **plus** rows of rod-shaped extrusomes in somatic cortex. Two dorsal brush rows ..... *Diplites* FOISSNER, 1998b (two species)

– Extrusomes in oral bulge and scattered in cytoplasm 4

4 Clavate **and** pin-shaped extrusomes in oral bulge. Three dorsal brush rows..... *Dioplitophrya otti* nov. gen., nov. spec. (single species)

– Oral bulge contains only one type of extrusomes 5

5 Extrusomes oblanceolate or fusiform. Two to three dorsal brush rows ..... *Sikorops* FOISSNER, 1999b (four species)

– Extrusomes different 6

6 Oral bulge disc-shaped. Ciliary rows not curved anteriorly. Two dorsal brush rows..... 7

– Oral bulge spathidiform (ovate and/or obliquely truncate). Ciliary rows more or less distinctly curved anteriorly. Three to four dorsal brush rows..... 8

7 Extrusomes pin-shaped..... *Fuscheria* FOISSNER, 1983b (four species)

– Extrusomes awl-shaped..... *Actinorhabdos trichocystiferus* FOISSNER, 1984 (single species)

8 Extrusomes claviform, drumstick-shaped, or pseudofusiform..... *Clavoplites* nov. gen. (three species)

Fuscheria terricola BERGER, FOISSNER & ADAM, 1983 (Fig. 37a–j; 333j–m; Table 31)

1983 *Fuscheria terricola* BERGER, FOISSNER & ADAM, J. Protozool., 30: 529 (morphology and ontogenesis).
1984 *Fuscheria terricola* BERGER, FOISSNER & ADAM, 1983 — FOISSNER, Stapfia, 12: 49 (oral details).
1988 *Fuscheria terricola* BERGER et al., 1983 — FOISSNER & FOISSNER, Arch. Protistenk., 135: 213 (TEM fine structure).

Supplementary observations: *Fuscheria terricola* is common in soils globally. Genus recognition is easy due to the uniquely nail-shaped extrusomes (Fig. 37e–h), while species identification is sometimes problematic. The populations from Benin (Africa) and Namibian site (49) differ from many others by the extrusomes, which are not 6–10 µm but only 3–4 µm long. However, there are transitions, suggesting conspecificity (Fig. 37e–h; 333j; Table 31). This is emphasized by the morphometrics, which match the Austrian type population.

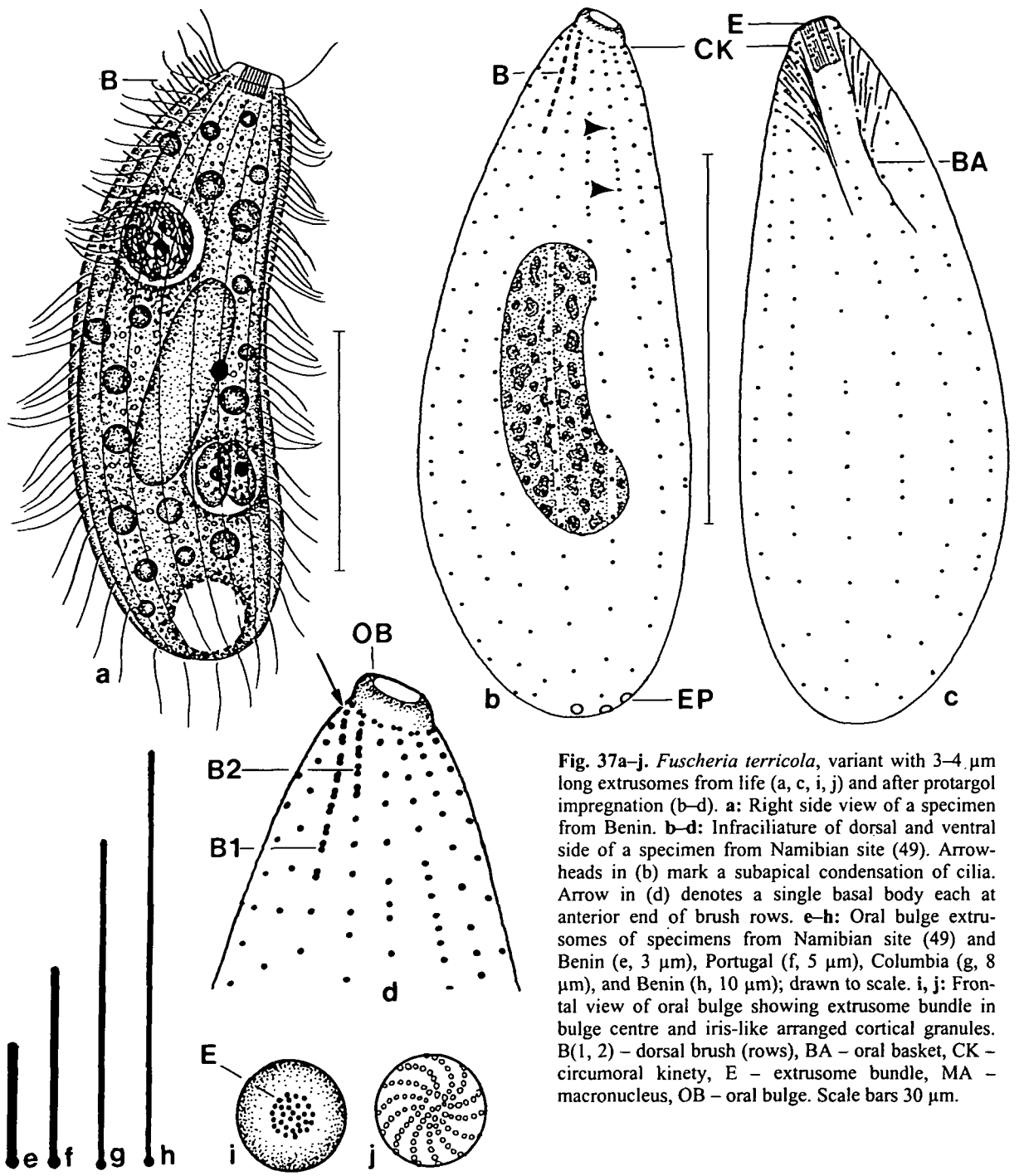

Fig. 37a–j. *Fuscheria terricola*, variant with 3–4 µm long extrusomes from life (a, c, i, j) and after protargol impregnation (b–d). **a:** Right side view of a specimen from Benin. **b–d:** Infraciliature of dorsal and ventral side of a specimen from Namibian site (49). Arrowheads in (b) mark a subapical condensation of cilia. Arrow in (d) denotes a single basal body each at anterior end of brush rows. **e–h:** Oral bulge extrusomes of specimens from Namibian site (49) and Benin (e, 3 µm), Portugal (f, 5 µm), Columbia (g, 8 µm), and Benin (h, 10 µm); drawn to scale. **i, j:** Frontal view of oral bulge showing extrusome bundle in bulge centre and iris-like arranged cortical granules. B(1, 2) – dorsal brush (rows), BA – oral basket, CK – circumoral kinety, E – extrusome bundle, MA – macronucleus, OB – oral bulge. Scale bars 30 µm.

Further observations: (i) Body shape is highly variable, as also mentioned in the original description, the Benin specimens are conspicuously sausage-shaped (Fig. 37a); (ii) Macronucleus shape is highly variable between and within populations, viz., ellipsoidal to elongate ellipsoidal (5:1), reniform, C-shaped, or even somewhat tortuous; (iii) Several excretory pores in posterior pole are (Fig. 37b); (iv) The extrusomes form a conspicuous bundle in the centre of the oral bulge in more than 30 populations checked (Fig. 37c, i); (v) The posterior globule of the extrusomes impregnate more or less distinctly with protargol, and thus the length of the

organelles can be measured in the preparations (Fig. 333j); (vi) The cortical granule rows extend onto the oral bulge, where they form an iris-like pattern (Fig. 37j); (vii) There is a single, ordinary cilium at the anterior end of each dorsal brush row (Fig. 37d); (viii) There is a subapical ciliary condensation in the second kinety left of brush row 2 (Fig. 37b). This condensation occurs in all populations studied (> 30), but its distinctiveness varies; (ix) Dorsal brush row 2 has a monokinetidal bristle tail; (x) There are four to eight oralized somatic monokinetids at the anterior end of the ciliary rows (Fig. 37c; 333k, l).

Table 31. Morphometric data on *Fuscheria terricola* from Namibian site (49).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	68.5	68.0	8.8	1.9	12.8	50.0	88.0	21
Body, width	21.6	23.0	3.2	0.7	14.8	15.0	26.0	21
Body length:width, ratio	3.2	3.1	0.5	0.1	14.3	2.6	4.5	21
Oral bulge, width	5.2	5.0	0.5	0.1	10.3	4.0	6.0	21
Oral bulge, height	1.6	1.5	–	–	–	1.0	2.0	21
Anterior body end to macronucleus, distance	27.9	30.0	6.4	1.4	22.8	14.0	39.0	21
Macronucleus, length	24.5	24.0	5.6	1.2	23.0	16.0	36.0	21
Macronucleus, width	7.6	8.0	0.9	0.2	12.1	6.0	10.0	21
Micronucleus, length	3.1	3.0	–	–	–	2.5	4.0	7
Micronucleus, width	1.9	2.0	–	–	–	1.0	4.0	7
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	7
Circumoral kinety to last dikinetid of brush row 1	9.2	9.0	1.8	0.4	19.3	6.0	14.0	21
Circumoral kinety to last dikinetid of brush row 2	4.1	4.0	0.7	0.2	17.1	3.0	5.0	21
Somatic kineties, number	14.6	14.0	1.1	0.2	7.7	13.0	16.0	21
Ciliated kinetids in a ventral kinety, number	25.4	24.0	7.8	1.7	30.7	12.0	45.0	21
Dorsal brush rows, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Dikinetids in brush row 1, number	8.1	8.0	1.6	0.3	19.2	5.0	11.0	21
Dikinetids in brush row 2, number	3.3	3.0	0.7	0.2	21.7	2.0	4.0	21
Oral bulge extrusomes, length	3.1	3.0	–	–	–	2.5	3.5	21

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Diplites arenicola nov. spec. (Fig. 38a–g; Table 32)

Diagnosis: Size about 55 × 17 µm in vivo; elongate reniform. Macronucleus ellipsoidal to C-shaped. Oral extrusomes ellipsoidal, about 1.2 × 0.6 µm, body extrusomes rod-shaped, about 2.5 × 0.2 µm. On average 9 slightly spiral somatic kineties, 4 dikinetids in brush kinety 1, and 3 dikinetids in brush kinety 2.

Type location: Dune soil (sand) in the Central Namib Escarpment north of the village of Solitaire, Namibia, 23°50'S 16°E (site 33 in figure 2 and chapter 2.1.2).

Etymology: The Latin *arenicola* (living in sand) refers to the habitat the species was discovered.

Description: Size 40–70 × 10–20 µm in vivo, usually near 55 × 17 µm, length:width ratio about 3:1 both in vivo and protargol preparations. Shape fairly constant, elongate reniform to bursiform, rarely cylindroidal, front half slightly narrowed with anterior end transverse-truncate (Fig. 38a, b, d); unflattened and acontractile. Macronucleus in middle body third, ellipsoidal to C-shaped, usually reniform, contains many small nucleoli. Micronucleus broadly ellipsoidal, about 3 × 2 µm in vivo, attached to macronucleus at various positions, rarely recognizable in protargol preparations because of many similarly sized and impregnated cytoplasmic inclusions. Contractile vacuole in posterior body end, some excretory pores in pole area. Body extrusomes in rows as long as body, rod-shaped, about 2.5 × 0.2 µm, that is, very fine and thus easily overlooked (Fig. 38a, d); do not impregnate with the protargol method used, and thus their exact location (within or between ciliary rows) could not be determined. Cortex flexible, contains some loosely arranged, bright granules (mucocysts?) 0.2 µm across, so deeply furrowed along ciliary rows that small bulges become recognizable subapically in swimming specimens; furrows extend onto oral bulge and are also distinct in the protargol preparations (Fig. 38a–c). Cytoplasm colourless, contains few to many fat globules up to 5 µm across. Likely feeds on small ciliates and flagellates. Swims conspicuously slowly by rotation about main body axis, frequently almost motionless for some seconds.

Cilia about 8 µm long in vivo, rather widely spaced, arranged in slightly spiral, equidistant rows commencing underneath circumoral kinety (Fig. 38a–c; Table 32). Postciliary microtubule ribbons occasionally impregnated, extend between ciliary rows, that is, do not form bundles right of kineties, as in *D. telmatobius* (Fig. 38f). More or less closely spaced basal bodies (dikinetids?) occur at irregular intervals in all somatic kineties, possibly produced by just divided basal bodies, as indicated by the lack of cilia in the anterior kinetosomes. Dorsal brush composed of two minute rows, right row in shallow depression recognizable both in vivo and appropriately orientated, impregnated cells. Brush row 1 composed of an average of four dikinetids bearing about 3 µm long, distally inflated bristles. Brush row 2 composed of an average of three dikinetids having about 3 µm long, cylindroidal bristles; continues with about 2 µm long, monokinetidal bristles to mid-body (Fig. 38a, b, d, g; Table 32).

Oral bulge occupies anterior body end, hardly set off from body proper and thus indistinct in vivo, cylindroidal or cylindroidal with conical cap in about 50% of specimens, on average 5 µm across and 2.5 µm high in protargol preparations (Fig. 38a–d; Table 32). Oral extrusomes ellipsoidal, minute but compact, that is, about 1.2 × 0.6 µm in size and refractive in vivo, attached to oral bulge and occasionally lightly impregnated with protargol (Fig. 38a, b, d). Circumoral kinety at base of oral bulge, produced by a horizontally orientated dikinetid at anterior end of each somatic ciliary row; right basal body of dikinetids barren, left with an about 8 µm long cilium. Oral basket very inconspicuous in live cells, composed of fine nematodesmata originating from barren circumoral basal bodies and three to four basal bodies at anterior end of all somatic kineties (oralized somatic monokinetids, see FOISSNER & FOISSNER 1988); nematodesmata extend to body midline and form small bundles rather distinctly impregnated with protargol (Fig. 38a–d).

Occurrence and ecology: To date found only at type location, that is, a sand dune in the Namib Escarpment. The second species, → *D. telmatobius*, also occurs in Namibia, but in

mud of rock-pools in a mountain river. Furthermore, *Diplites* spp. as yet have been found only in Namibia and Venezuela, where another new species occurs. These data indicate habitat and biogeographic specialization.

Comparison with related species: *Diplites arenicola* differs from → *D. telmatobius* mainly by the shape of the oral extrusomes (ellipsoidal vs. clavate) and the number of ciliary rows (9 vs. 16). Minor differences occur in body shape (elongate reniform vs. elongate bursiform), course of the ciliary rows (spiral vs. meridional), and number of dikinetids composing dorsal brush row 1 (4 vs. 7). Altogether, the differences are conspicuous and species status of the two populations thus indisputable. Live observation is necessary for a reliable identification because the extrusomes often do not impregnate.

No species was found in the literature that might be identical to *D. arenicola*. However, the general body plan and the infraciliature are virtually identical to those of *Fuscheria* spp. and

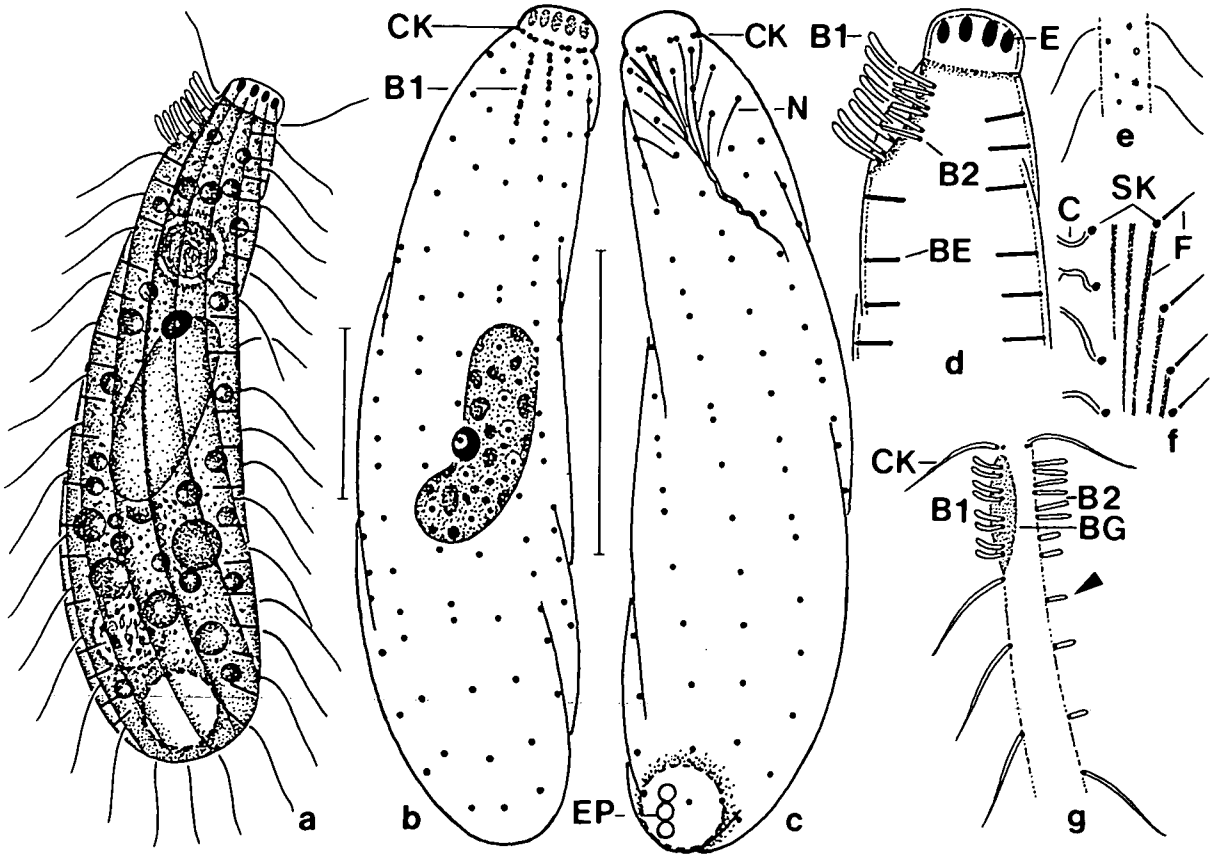

Fig. 38a–g. *Diplites arenicola* from life (a, d, e, g) and after protargol impregnation (b, c, f). **a:** Right side view of a representative specimen. Note the subapical "wings" caused by the deep cortical furrows along the ciliary rows. **b, c:** Ciliary pattern of dorsal and ventral side and nuclear apparatus of holotype specimen. **d, g:** Anterior body portion showing main features of the genus and species, viz., the brush groove (BG) containing dorsal brush row 1, the oral extrusomes (1.2 × 0.6 µm), and the body extrusomes (2.5 × 0.2 µm). Arrowhead marks the monokinetidal bristle tail of brush row 2. **e:** Surface view showing the inconspicuous cortical granulation. **f:** Cortical fibre system. B1, 2 – dorsal brush rows, BE – body extrusomes, BG – dorsal brush groove, C – somatic cilia, CK – circumoral kinety, E – oral extrusomes, EP – excretory pores, F – fibre systems, N – nematodesmata, SK – somatic kineties. Scale bars 20 µm.

Actinorhabdos trichocystiferus FOISSNER, 1984. Thus, these species are easily confused both in vivo and protargol preparations. In fact, they can be reliably distinguished only by the extrusomes, a rather sophisticated feature, which must be determined from live specimens because the extrusomes do not usually impregnate with protargol and/or change shape and size due to the preparation procedures.

Table 32. Morphometric data on *Diplites arenicola* (upper line) and *Diplites telmatobius* (lower line; from FOISSNER 1998b).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	54.4	55.0	7.6	1.7	14.0	40.0	67.0	19
	51.2	53.0	5.5	1.3	10.6	41.0	59.0	19
Body, width	16.9	17.0	1.9	0.5	11.5	15.0	22.0	19
	21.3	20.0	3.5	0.4	16.3	16.0	28.0	19
Oral bulge, width	4.6	5.0	–	–	–	4.0	5.0	19
	4.8	5.0	–	–	–	4.0	5.0	19
Oral bulge, height	2.2	2.5	–	–	–	1.0	2.5	19
	2.3	3.0	–	–	–	2.0	3.0	19
Anterior body end to macronucleus, distance	22.1	22.0	4.4	1.0	19.4	16.0	32.0	19
	22.4	23.0	4.7	1.0	21.0	15.0	35.0	19
Macronucleus, length	14.7	14.0	2.9	0.7	19.6	10.0	20.0	19
	19.3	19.0	3.2	0.7	16.7	13.0	26.0	19
Macronucleus, width	5.8	6.0	1.0	0.2	16.4	4.0	8.0	19
	7.3	7.0	1.0	0.2	13.7	6.0	10.0	19
Macronuclei, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
Circumoral kinety to last dikinetid of dorsal brush row 1, distance	4.6	5.0	0.6	0.1	12.9	4.0	6.0	19
	6.3	6.0	1.0	0.2	15.8	5.0	9.0	19
Circumoral kinety to last dikinetid of dorsal brush row 2, distance	2.7	3.0	–	–	–	2.0	3.0	19
	3.4	3.0	0.6	0.1	17.7	2.0	4.0	19
Somatic kineties, number	9.0	9.0	0.7	0.2	7.4	8.0	10.0	19
	15.9	16.0	0.5	0.1	3.3	15.0	17.0	19
Ciliated basal bodies in a ventral somatic kinety, number	17.8	17.0	3.3	0.8	18.5	14.0	25.0	19
	19.2	18.0	4.2	1.0	21.6	12.0	26.0	19
Dorsal brush kineties, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
Dikinetids in dorsal brush row 1, number	4.4	4.0	0.6	0.1	13.7	4.0	6.0	19
	6.7	7.0	1.0	0.2	15.5	5.0	9.0	19
Dikinetids in dorsal brush row 2, number	2.6	3.0	–	–	–	2.0	3.0	19
	3.3	3.0	–	–	–	2.0	4.0	10

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Diplites telmatobius FOISSNER, 1998 (Fig. 39a–g; 304 l–q; Table 33)

Additional observations: This species was discovered at Namibian site (29). Here, we report on some observations from specimens found at sites (49) and (73). The site (49) population was also morphometrically analyzed and shows values highly similar to those of the type population (Table 33).

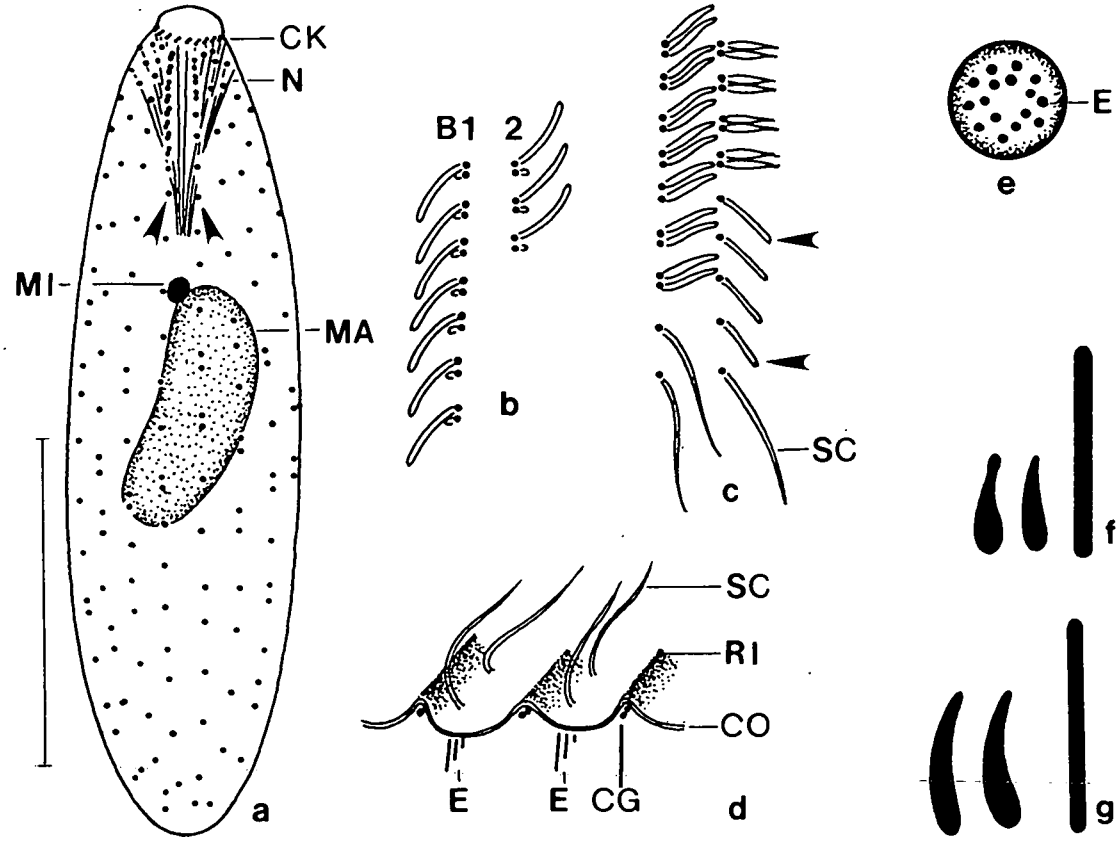

Fig. 39a–g. *Diplites telmatobius* from Namibian site 49 (a, c, d, f) and 73 (b, e, g) from life (b–g) and after protargol impregnation (a). **a:** Somatic and oral ciliary pattern and nuclear apparatus of a representative specimen. Arrowheads mark the inconspicuous dorsal brush rows. Note that the oral basket is formed by nematodesmata originating from the circumoral dikinetids and from the anterior basal bodies of the somatic kineties (oralized somatic monokinetids). **b, c:** Dorsal brush of site (73) and (49) specimens. Arrowheads mark monokinetidal bristle tail of row 2. Note that the posterior cilium of the dikinetids is reduced to a minute stump in the site (73) specimens (b). **d:** Transverse section showing main cortical organelles. The body extrusomes are located within the ciliary rows. **e:** Frontal view of oral bulge. **f, g:** Oral and somatic extrusomes of site (49) and (73) specimens. B1, 2 – dorsal brush rows, CG – cortical granules, CK – circumoral kinety, CO – cortex, E – extrusomes, MA – macronucleus, MI – micronucleus, N – nematodesmata, RI – cortical ridge, SC – ordinary somatic cilium. Scale bars 20 µm (a) and 2 µm (f, g).

The following observations were made: (i) Shape and arrangement of the oral and somatic extrusomes are similar to the type in both populations (Fig. 39f, g; 304 l–n, q); (ii) The somatic extrusomes are located within the ciliary rows (Fig. 39d); (iii) Cortex of site (49) specimens with distinct ridges containing refractive granules, which occasionally impregnate with protargol (Fig. 39d; 304o); (iv) Dorsal brush row 2 has a short, monokinetidal tail composed of about 4 µm long bristles (Fig. 39c); (v) The fine structure of the dorsal brush of site (49) specimens is similar to the type material (Fig. 39c), while rather different in site (73) specimens, in which the posterior cilium of the dikinetids is almost completely reduced and the bristles of row 1 are directed posteriorly, while those of row 2 are directed anteriorly (Fig. 39b). Such differences might indicate subspecies status, although all other features and the morphometrics agree with the type material.

Table 33. Morphometric data on *Diplites telmatobius* from Namibian sites 29 (type location; upper line) and 49 (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	51.2	53.0	5.5	1.3	10.6	41.0	59.0	19
	56.7	54.0	8.6	2.1	15.2	46.0	72.0	17
Body, width	21.3	20.0	3.5	0.8	16.3	16.0	28.0	19
	20.7	20.0	4.2	1.0	20.3	14.0	30.0	17
Oral bulge, width	4.8	5.0	–	–	–	4.0	5.0	19
	4.7	5.0	–	–	–	4.0	6.0	17
Oral bulge, height	2.3	3.0	–	–	–	2.0	3.0	19
	2.3	2.0	–	–	–	2.0	3.0	17
Anterior body end to macronucleus, distance	22.4	23.0	4.7	1.1	21.0	15.0	35.0	19
	22.7	22.0	6.1	1.5	27.0	13.0	39.0	17
Macronucleus, length	19.3	19.0	3.2	0.7	16.7	13.0	26.0	19
	15.8	16.0	4.1	1.0	25.7	11.0	29.0	17
Macronucleus, width	7.3	7.0	1.0	0.2	13.7	6.0	10.0	19
	7.5	7.0	1.7	0.4	23.1	5.0	11.0	17
Micronucleus, length	2.8	3.0	–	–	–	2.0	4.0	19
	3.3	3.0	–	–	–	2.5	5.0	17
Micronucleus, width	2.3	2.0	–	–	–	2.0	4.0	19
	2.4	2.0	–	–	–	1.0	5.0	17
Circumoral kinety to end of brush row 1, distance	6.3	6.0	1.0	0.2	15.8	5.0	9.0	19
	6.9	7.0	1.0	0.3	14.8	5.0	8.0	17
Circumoral kinety to end of brush row 2, distance	3.4	3.0	0.6	0.1	17.7	2.0	4.0	19
	3.5	3.0	0.6	0.2	18.0	3.0	5.0	17
Somatic kineties, number	15.9	16.0	0.5	0.1	3.3	15.0	17.0	19
	16.6	16.0	0.8	0.2	4.8	16.0	19.0	17
Ciliated basal bodies in a ventral somatic kinety, number	19.2	18.0	4.2	1.0	21.6	12.0	26.0	19
	17.2	17.0	2.5	0.6	14.6	14.0	22.0	17
Macronuclei, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
	1.0 [b]	1.0	0.0	0.0	0.0	1.0	1.0	17
Micronuclei, number	1.2	1.0	–	–	–	1.0	2.0	19
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	17
Dorsal brush kineties, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	17
Dikinetids in brush row 1, number	6.7	7.0	1.0	0.2	15.5	5.0	9.0	19
	7.2	7.0	1.1	0.3	15.8	4.0	9.0	17
Dikinetids in brush row 2, number	3.3	3.0	0.7	0.2	20.2	2.0	4.0	19
	3.1	3.0	0.6	0.2	19.3	2.0	4.0	17

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Dissociated into two globular nodules in one out of 30 specimens.

Dioplitophrya nov. gen.

Diagnosis: Fuscheriidae with three dorsal brush rows and clavate and pin-shaped extrusomes in the oral bulge.

Type species: *Dioplitophrya otti* nov. spec.

Etymology: Composite of the Greek words *di* (two), *hoplites* (soldier ~ extrusomes), and *ophrya* (eyebrow ~ cilia ~ ciliate), meaning "a ciliate with two types of extrusomes". Feminine gender.

Comparison with related genera: *Dioplitophrya* has an apical cytostome, straight ciliary rows, three brush rows, extrusomes within the oral opening, and nematodesmal bundles originating from oral dikinetids **and** from oralized somatic monokinetids (Fig. 40i, j, l). Accordingly, it belongs to the family Fuscheriidae, as defined above. *Dioplitophrya* is unique in having two types of extrusomes in the oral bulge.

Dioplitophrya otti nov. spec. (Fig. 40a–n; 319a–f; Table 34)

Diagnosis: Size about 100 × 35 µm in vivo; cylindroidal to elongate reniform. Macronucleus U-shaped. Pin-shaped extrusomes 8 µm long, clavate extrusomes 5 µm long. On average 26 ciliary rows.

Type location: Soil from the ghost tree forest (*Moringa ovalifolia*) in the Etosha National Park, Namibia, 19°S 15°40'E (site 56 in figures 2, 3 and chapter 2.1.2).

Dedication: We dedicate this new species to Prof. Dr. Jörg OTT, Vienna University,

famous marine biologist and friend of the ciliates (BAUER-NEBELSICK et al. 1996a, b, OTT et al. 1998).

Description: Size 70–130 × 30–40 µm, usually about 100 × 35 µm in vivo. Shape basically cylindroidal with an average length:width ratio of about 3.5:1 in vivo, while only 2.5:1 in protargol preparations, where specimens tend to become inflated (Table 34); usually slightly asymmetrical and reniform with posterior body end more broadly rounded than anterior; unflattened and acontractile (Fig. 40a, f, n). Macronúcleus in middle third of cell, usually U-shaped, rarely a simple rod or C-shaped; fragmented into four nodules in two out of 40 specimens, likely due to postconjugational reorganization processes; nucleoli globular and minute. Micronucleus not observed. Contractile vacuole in rear body end, many excretory pores in posterior pole area; cortex often wrinkled when vacuole has contracted. Two types of extrusomes in oral bulge and scattered in cytoplasm (Fig. 40a–c, e, i; 319a, b, d–f): type I extrusomes as in genus *Fuscheria* FOISSNER, 1983b, that is, pin-shaped and 7–8 µm long, form dense bundle in oral opening and impregnate lightly with protargol; type II extrusomes as in *Diplites* FOISSNER, 1998b, that is, asymmetrically clavate and about 5 µm long, not as numerous as type I, do not impregnate with protargol. Cortex highly flexible and rather distinctly furrowed by ciliary rows in vivo, contains minute (~ 0.2 µm), colourless granules having the same arrangement as the postciliary microtubule ribbons, that is, form long, slightly oblique rows (Fig. 40m; 319c). Cytoplasm colourless, packed with 1–20 µm-sized globular and irregular fat inclusions in all specimens seen; some about 5 µm-sized vacuoles with granular content and cytoplasmic crystals from prey scattered between fat globules. Likely feeds on ciliates. Swims slowly by rotation about main body axis, showing great flexibility when squeezing itself through soil aggregates and under cover-glass pressure.

Cilia about 10 µm long in vivo, rather closely spaced (1.8 µm) producing nice metachronal waves; arranged in an average of 26 longitudinal, equidistant rows commencing underneath circumoral kinety and extending to posterior pole area forming indistinct, minute sutures. Closely spaced basal bodies (dikinetids?) occur at irregular intervals in most kineties and specimens, likely produced by just divided basal bodies, as indicated by the lack of cilia in the anterior kinetosomes and the increasing number of pairs in early dividers. Postciliary microtubule ribbons conspicuous in protargol preparations, occupy space between kineties (Fig. 40a, f–h; Table 34). Dorsal brush inconspicuous because occupying merely 12% of body length and having only 4 µm long bristles, usually composed of three rows, rarely of four (in one out of 30 specimens); all rows of similar structure, that is, at anterior end of three ordinary somatic kineties and composed of closely spaced dikinetids bearing rod-shaped, about 4 µm long bristles; row 3 only about half as long as rows 1 and 2, but with short monokinetidal bristle tail; rows slightly obliquely orientated in about one third of specimens (Fig. 40a, f, h, k).

Oral apparatus occupies most of anterior pole area, oral bulge ring-shaped and inconspicuous, that is, about 10 µm wide and only 2 µm high in vivo; mouth centre slightly depressed, contains extrusomes as described above. Circumoral kinety at base of oral bulge, composed of rather widely spaced dikinetids with only the left (posterior) basal body ciliated. Oral basket inconspicuous in vivo, composed of fine nematodesmata originating from barren circumoral basal bodies and about eight ciliated basal bodies in anterior region of all somatic kineties (oralized somatic monokinetids, see FOISSNER & FOISSNER 1988); nematodesmata extend to midline of cell, forming small bundles rather distinctly impregnated with protargol and assuming a funnel-shaped pattern (Fig. 40a, g, j, l).

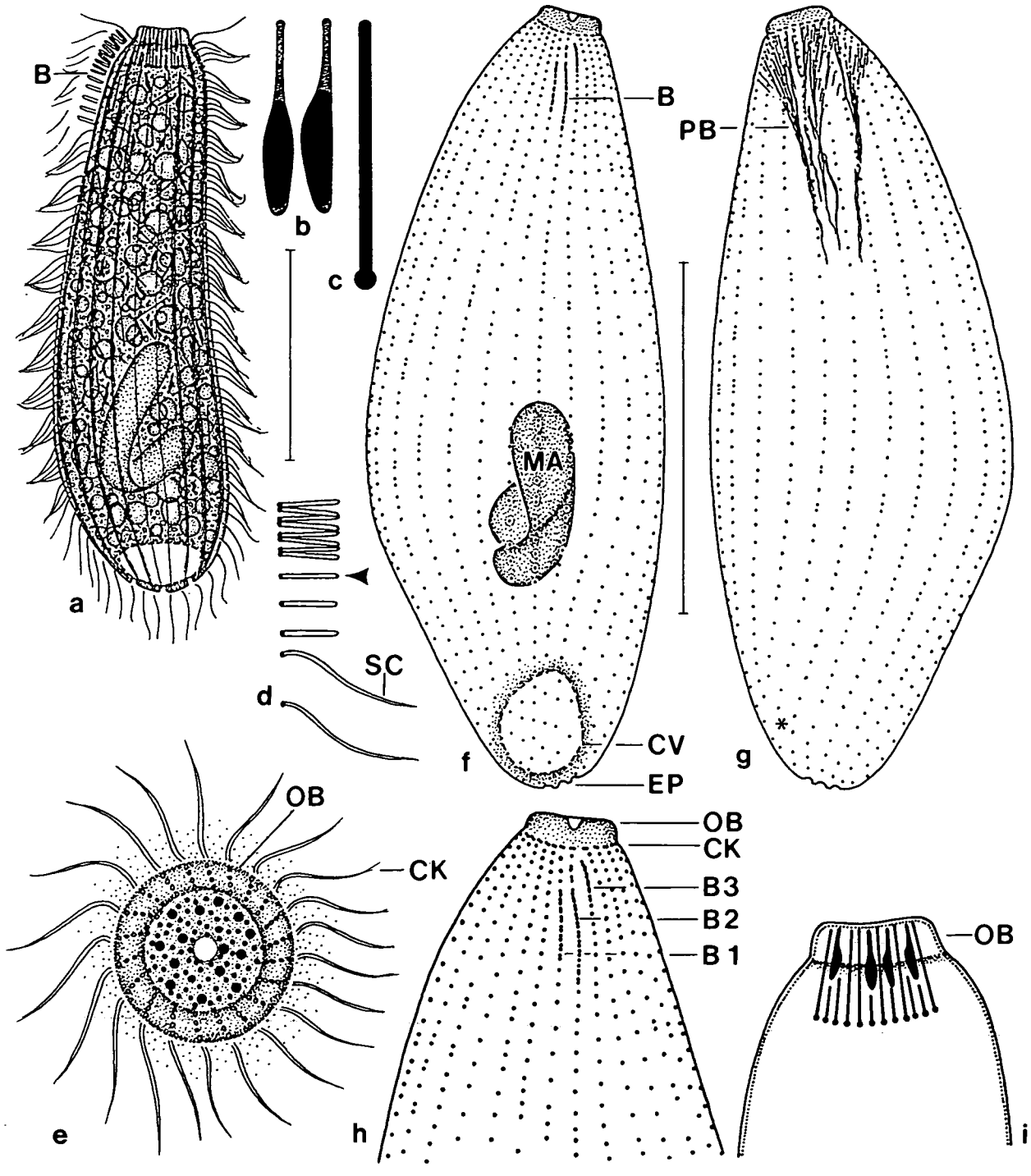

Fig. 40a–i. *Dioplitophrya otti* from life (a–e, i) and after protargol impregnation (f–h). **a:** Right lateral view of a representative specimen packed with fat globules. **b, c, i:** *Dioplitophrya* has two types of extrusomes in the mouth and cytoplasm: clavate, about 5 µm long, and pin-shaped, about 8 µm long toxicysts. **d:** Dorsal brush row 3 has a short monokinetidal bristle tail (arrowhead). **e:** Frontal view showing the mouth filled with thin, pin-shaped, and thick, clavate extrusomes. **f–h:** Ciliary pattern of dorsal and ventral side. Asterisk marks minute, subterminal suture. B – dorsal brush, B1, 2, 3 – dorsal brush rows, CK – circumoral kinety, CV – contractile vacuole, EP – excretory pore of the contractile vacuole, MA – macronucleus, OB – oral bulge, PB – pharyngeal basket, SC – ordinary somatic cilium. Scale bars 40 µm.

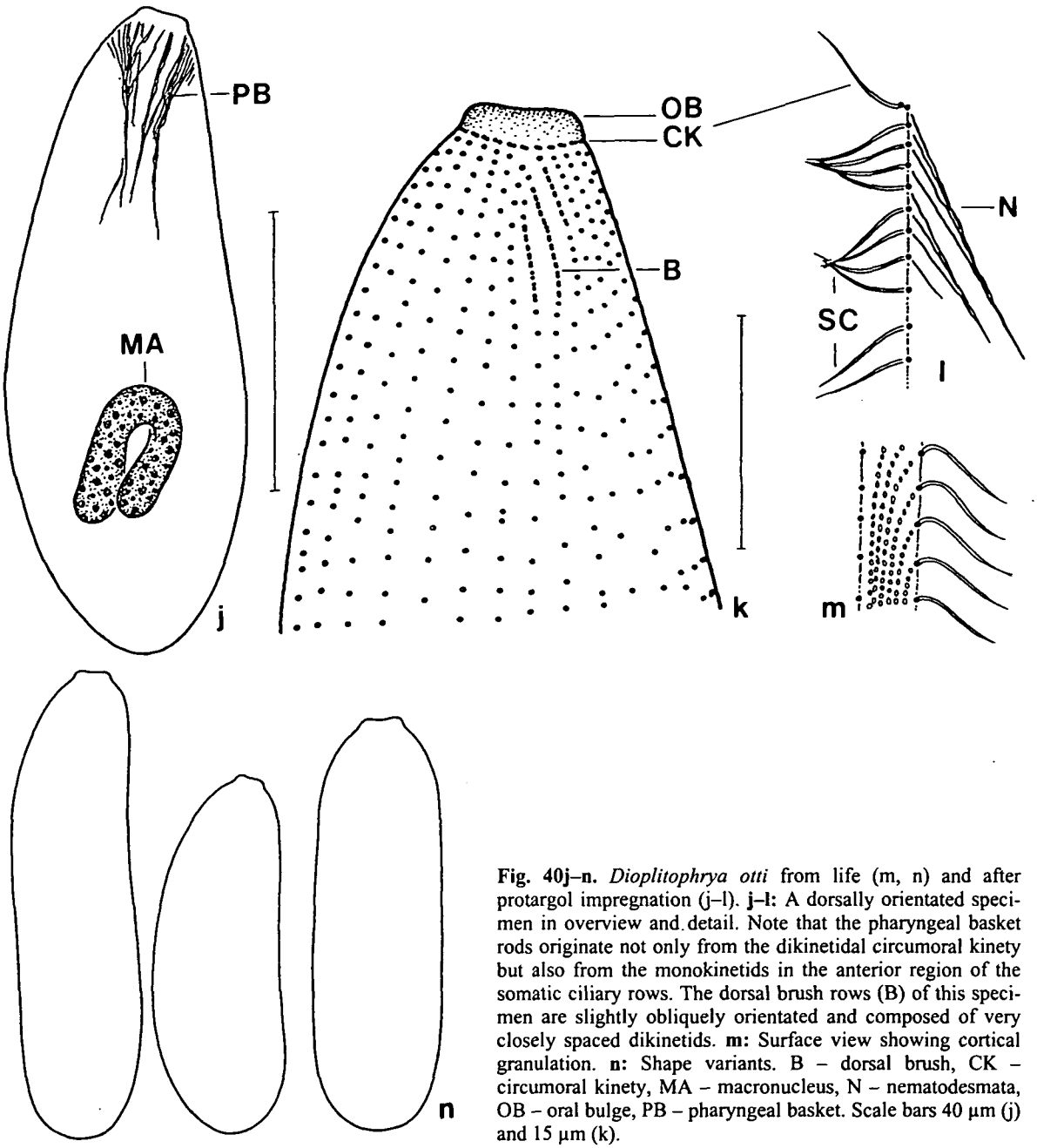

Fig. 40j–n. *Dioplitophrya otti* from life (m, n) and after protargol impregnation (j–l). **j–l:** A dorsally orientated specimen in overview and detail. Note that the pharyngeal basket rods originate not only from the dikinetidal circumoral kinety but also from the monokinetids in the anterior region of the somatic ciliary rows. The dorsal brush rows (B) of this specimen are slightly obliquely orientated and composed of very closely spaced dikinetids. **m:** Surface view showing cortical granulation. **n:** Shape variants. B – dorsal brush, CK – circumoral kinety, MA – macronucleus, N – nematodesmata, OB – oral bulge, PB – pharyngeal basket. Scale bars 40 μm (j) and 15 μm (k).

Occurrence and ecology: To date found only at type location, a local biodiversity centre with many new species (Table 5). When we re-visited the site in year 2001, we did not find this species again.

Comparison with related species: Basically, *D. otti* is easily identified by the two types of extrusomes filling the mouth, a unique feature not found in any other member of the

family or in other similar ciliates. However, recognizing the extrusomes requires live observation with a high power objective (oil immersion)! Otherwise, *D. otti* is easily confused with *Fuscheria* spp., which have a similar size and general appearance and are common in soils globally. There are several species in the old literature resembling *D. otti* (KAHL 1930–35); however, apparently none has two types of oral extrusomes, although these were often not studied in detail. On the other hand, we cannot assign our species to any of these taxa because the extrusomes are a main feature and can thus hardly be added to an original description.

Table 34. Morphometric data on *Dioplitophrya otti*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	92.8	92.0	12.6	2.7	13.5	65.0	117.0	21
Body, width	38.0	37.0	4.8	1.1	12.7	31.0	46.0	21
Oral bulge, width	7.7	8.0	1.0	0.2	13.1	6.0	10.0	21
Oral bulge, height	1.6	–	–	–	–	1.0	2.0	21
Anterior body end to macronucleus, distance	42.8	42.0	11.4	2.5	26.5	17.0	66.0	21
Macronucleus, length [b]	45.6	45.0	–	–	–	30.0	60.0	21
Macronucleus, width	7.1	7.0	0.8	0.2	11.2	6.0	9.0	21
Circumoral kinety to end of brush row 1, distance	9.5	10.0	1.7	0.4	18.1	7.0	12.0	21
Circumoral kinety to end of brush row 2, distance	10.8	11.0	1.3	0.3	12.0	8.0	13.0	21
Circumoral kinety to end of brush row 3, distance [c]	5.7	6.0	1.0	0.2	16.9	4.0	7.0	21
Oral basket, length of longest nematodesmal bundle	30.5	30.0	6.3	1.4	20.6	20.0	40.0	21
Ciliary rows, number	26.1	26.0	2.1	0.4	7.9	24.0	30.0	21
Ciliated kinetids in a lateral kinety, number	52.5	52.0	10.3	2.3	19.7	36.0	80.0	21
Oralized somatic monokinetids in a kinety, number	7.8	8.0	2.1	0.5	26.5	4.0	10.0	21

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Rough estimation because usually U-shaped.

[c] Dikinetidal portion measured only.

Sikorops namibiensis nov. spec. (Fig. 41a–o, 42a–o; 320a–r; Table 35)

Diagnosis: Size about 115 × 33 µm in vivo. Spatulate with obliquely truncate, about 9 µm wide oral bulge. Macronucleus elongate reniform. Extrusomes obovate, about 2 × 1 µm. On average 14 ciliary rows and 11 dikinetids in brush row one, 14 in row two, and 6 in row three.

Type location: Bark of a *Colophospermum mopane* tree at the Bambatsi Guest Farm, Namibia, 20°10'S 15°25'E (site 51 in figure 2 and chapter 2.1.2).

Etymology: Named after the country discovered.

Description: Size and shape highly variable because small, slender theronts and large, broad trophonts occur; variability coefficients thus high (Table 35). Size 80–160 × 20–50 µm in vivo, usually about 115 × 33 µm, length:width ratio 1.8–5.5:1, on average 3.5:1 in protargol preparations. Spatulate, bottle-shaped or elongate ellipsoidal, occasionally slightly curved, anterior end usually ≤ 10 µm wide and obliquely truncate, posterior narrowly to moderately broadly rounded (Fig. 41a, c, h, j; 320a, b); theronts slightly flattened. Nuclear apparatus in middle body third (Fig. 41a, h, j; 320a, b, i). Macronucleus elongate reniform, rod-shaped, U-shaped or ellipsoidal, length:width ratio 2–7:1, on average 3.5:1, that is, about 30 × 8 µm; nucleoli minute or large and lobate. Micronucleus about 4 × 3 µm, usually near mid-portion of macronucleus, often impregnates only faintly with protargol and shows a fibrous composition. Contractile vacuole in rear end, several excretory pores in posterior pole area. Extrusomes mainly in oral bulge, obovate, rarely broadly fusiform, about 2 × 1 µm in vivo, compact and thus highly refractive; fusiform and up to 4 µm long in protargol preparations, possibly due to beginning explosion; clavate, hyaline and up to 5 µm long when extruded (Fig. 41a, d–f, h; 320c, d). Cortex very flexible, contains about five rows of colourless, highly refractive granules approximately 0.8 µm across between each two ciliary rows (Fig. 41g; 320 l). Cells colourless, theronts hyaline, trophonts packed with small and large fat inclusions and thus dark at low magnification. Feeds on small ciliates, such as *Colpoda steinii*, which are ingested whole because still identifiable in the food vacuoles. Swims rather rapidly by rotation about main body axis.

Cilia about 8 µm long, rather irregularly spaced with some kinetids obviously unciliated within individual rows, slightly more closely spaced in oral region. Ciliary rows extend meridionally and equidistantly, anterior portion slightly curved. Dorsal brush in anterior region of three dorsolateral kineties, inconspicuous and of ordinary structure, that is, consists of closely spaced dikinetids with up to 3 µm long bristles; usually some monokinetids or very closely spaced dikinetids at anterior end of individual brush rows. Brush rows 1 and 2 of almost same length, composed of 11–14 dikinetids on average; row 3 distinctly shortened, consists of an average of only six dikinetids, associated with a monokinetidal tail of short bristles extending to near body end (Fig. 41a, h, i, k, n, o; 320j–l, q, r; Table 35).

Oral bulge rather conspicuous, domed to spathidiform, that is, obliquely truncate occupying anterior body end, obovate to broadly obovate in frontal view with extrusomes appearing as bright dots. Circumoral kinety at base of oral bulge, indistinct with details as difficult to recognize as in congeners; not of ordinary structure, that is, consists of one, rarely two oblong granules (very likely dikinetids with one ciliated basal body) at anterior end of somatic ciliary rows and a minute, unciliated granule between each two somatic kineties, respectively, dikinetids; each granule associated with a rather distinct fibre obliquely extending anteriad to the acentric bulge centre, where the individual fibres converge and plunge into the cytopharynx. Oral basket also very inconspicuous, not recognizable in live specimens and only rarely impregnated with protargol, composed of fine nematodesmata originating from circumoral kinetids **and** about six basal bodies at anterior end of somatic kineties (Fig. 41a–c, h–o; 320e–h, m–p).

Observations on other populations (Fig. 42a–o; 320j–r): Three other populations were studied both in vivo and protargol preparations. This showed that body size (~ 60–160 × 10–50 µm) and shape and extrusome size (length 2–4 µm) are highly variable, while the

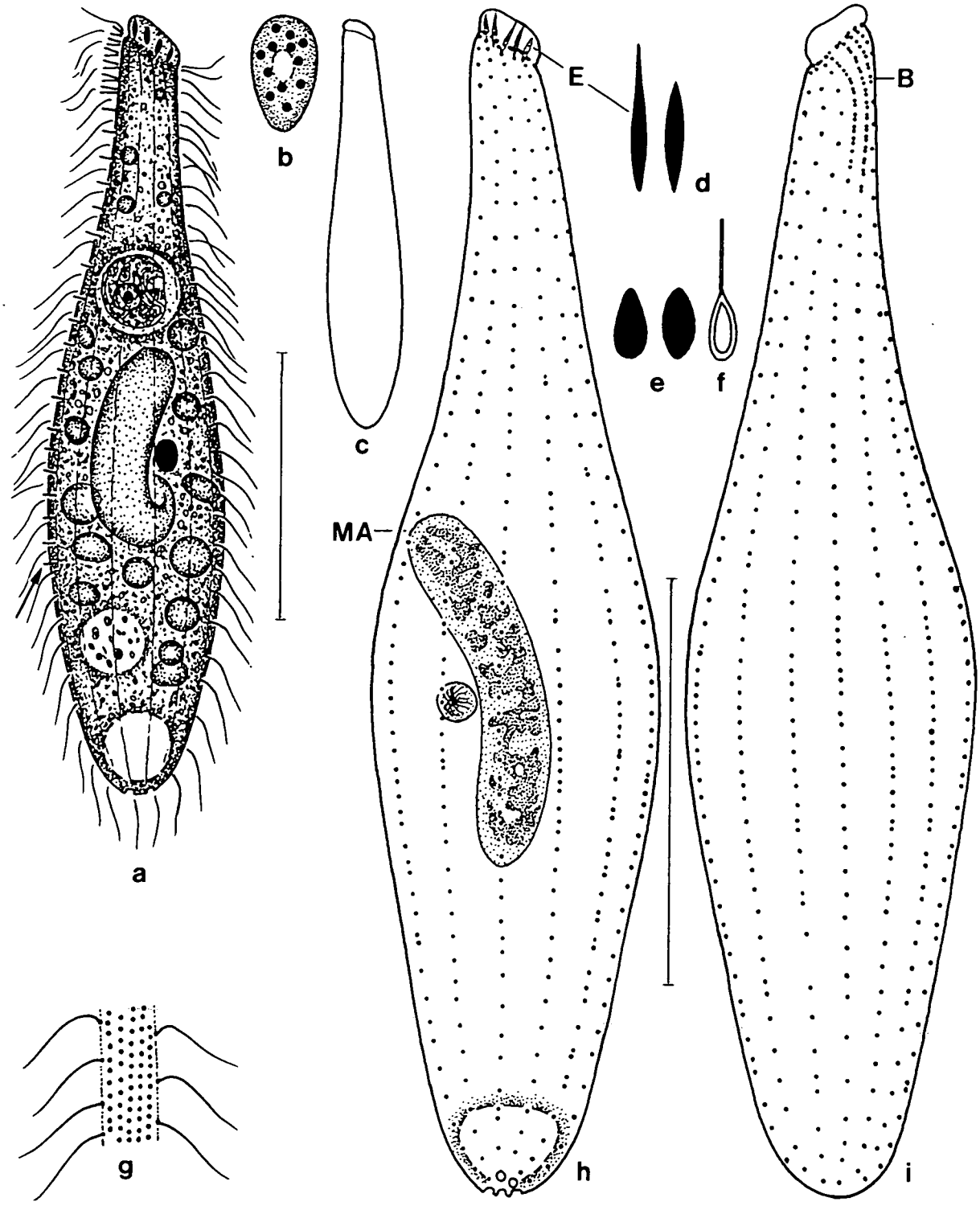

Fig. 41a–i. *Sikorops namibiensis* from life (a–c, e–g) and after protargol impregnation (d, h, i). **a:** Right side view of a representative specimen showing monokinetidal bristle tail of brush row 3 extending above mid-body (arrow). **b:** Frontal view of oral bulge. **c:** Slender theront. **d:** Extrusomes after protargol impregnation. **e, f:** Resting (e) and exploded (f) extrusomes in vivo. **g:** Surface view showing cortical granule rows. **h, i:** Ciliary pattern of right and left side of holotype specimen. For details, see next plate. B – dorsal brush, E – extrusomes, MA – macronucleus. Scale bars 40 µm.

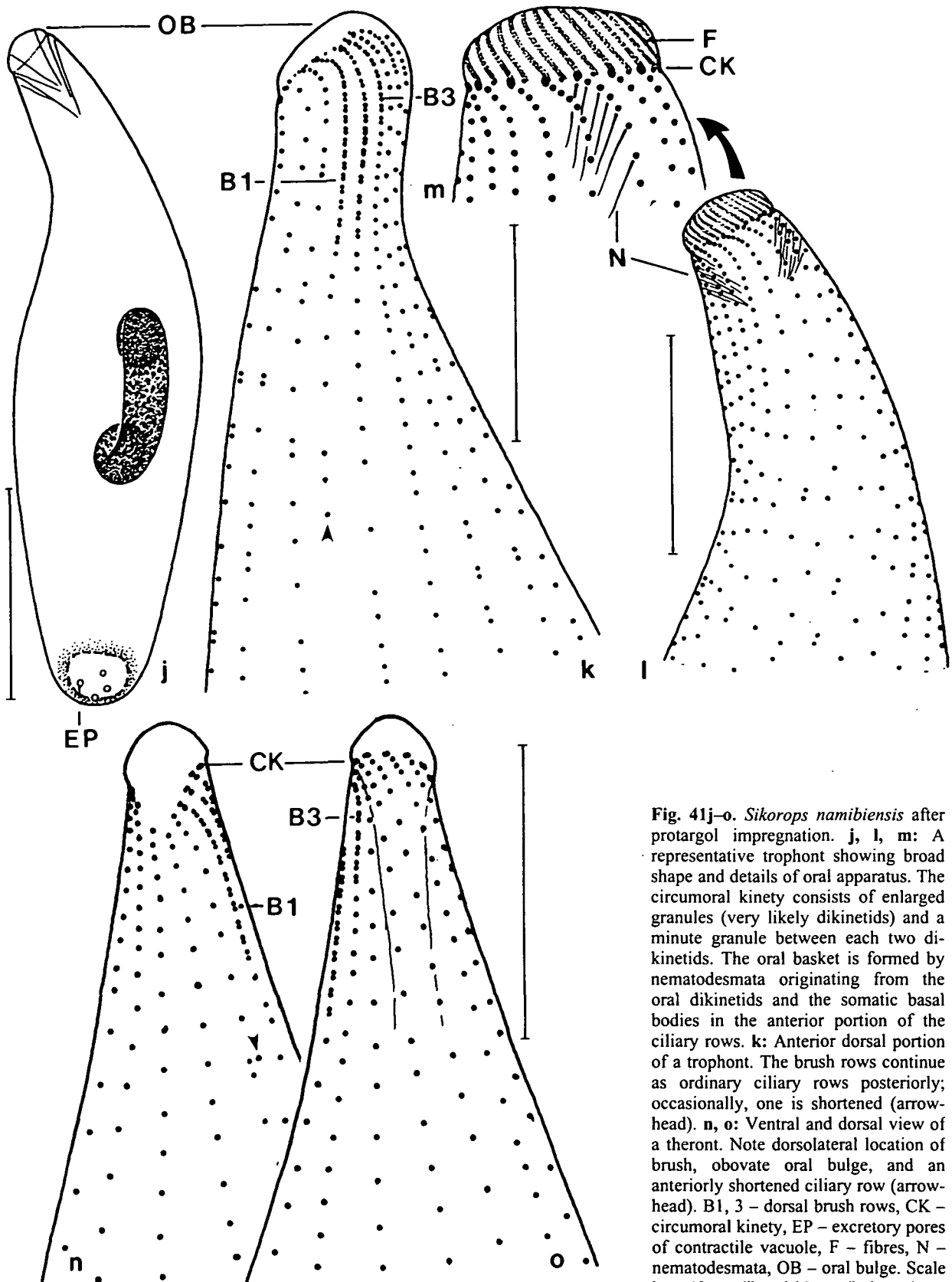

Fig. 41j–o. *Sikorops namibiensis* after protargol impregnation. **j, l, m:** A representative trophont showing broad shape and details of oral apparatus. The circumoral kinety consists of enlarged granules (very likely dikinetids) and a minute granule between each two dikinetids. The oral basket is formed by nematodesmata originating from the oral dikinetids and the somatic basal bodies in the anterior portion of the ciliary rows. **k:** Anterior dorsal portion of a trophont. The brush rows continue as ordinary ciliary rows posteriorly; occasionally, one is shortened (arrowhead). **n, o:** Ventral and dorsal view of a theront. Note dorsolateral location of brush, obovate oral bulge, and an anteriorly shortened ciliary row (arrowhead). B1, 3 – dorsal brush rows, CK – circumoral kinety, EP – excretory pores of contractile vacuole, F – fibres, N – nematodesmata, OB – oral bulge. Scale bars 40 μm (j) and 20 μm (k, l, n, o).

nuclear pattern and extrusome shape are stable and thus the most important features of the species. The very characteristic, obovate to oblanceolate extrusomes, which highly resemble those of → *Arcuospathidium namibiense tristicha*, are difficult to recognize in all populations due to their small size. In contrast, the oral bulge is rather conspicuous, in spite of being rather small, likely because it contains the refractive and thus bright extrusomes.

The Australian specimens are very slender and have only 8–10 ciliary rows; thus, they might be a distinct subspecies (Fig. 42d–f, j). The Venezuelan specimens, which could be cultivated (see below), were studied in the scanning electron microscope (Fig. 320j–r). This confirmed the lack of an ordinary circumoral kinety and revealed highly conspicuous bulge fibres, similar to those found in *Enchelys gasterosteus* and *Balantidion pellucidum* (FOISSNER et al. 1995, 1999). Further details, see figure explanations.

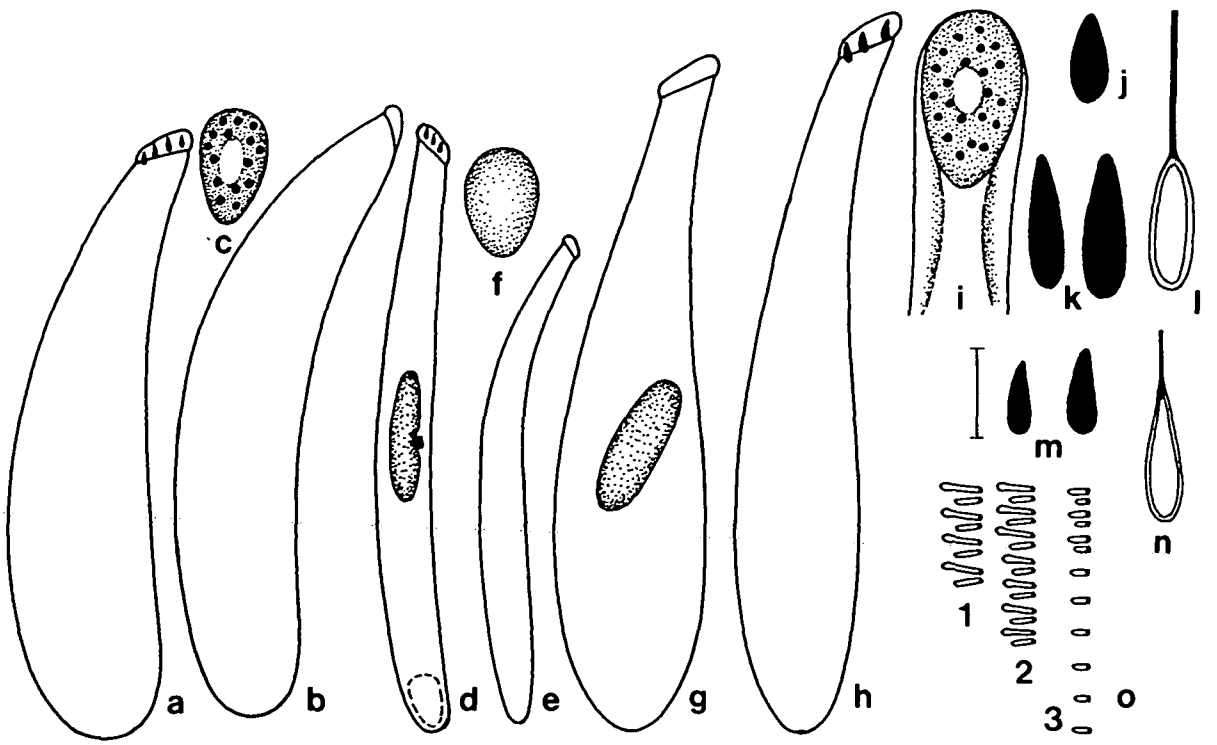

Fig. 42a–o. *Sikorops namibiensis* from life. Extrusomes (j–n) drawn to scale (2 µm). **a–c, m–o:** Shape variants (~ 120 × 30 µm), frontal view of oral bulge, resting extrusomes (~ 1.5–2 × 0.8 µm), an exploded toxicyst (~ 3 × 1 µm), and posterior portion of the three-rowed dorsal brush of Venezuelan population. **d–f, j:** Shape variants (110–130 × 10–15 µm), frontal view of oral bulge, and a resting extrusome (~ 2 µm) of Australian population. **g–i, k, l:** Shape variants (60–110 × 15–30 µm), frontal view of oral bulge, resting extrusomes (~ 3–5 × 0.8–1 µm), and an exploded toxicyst (~ 6 µm) of Namibian site (56) population.

Table 35. Morphometric data on *Sikorops namibiensis* (upper line) and *S. minor* (lower line) from type localities.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	104.1	101.0	21.3	4.6	20.5	76.0	142.0	21
	50.9	51.0	4.6	1.0	9.0	43.0	61.0	21
Body, width at base of oral bulge	7.3	7.0	2.0	0.4	27.8	4.0	11.0	21
	3.4	3.5	–	–	–	3.0	4.0	21
Body, width	29.1	27.0	10.5	2.3	36.0	17.0	52.0	21
	12.8	12.0	1.8	0.4	13.9	10.0	17.0	21
Anterior body end to macronucleus, distance	46.8	48.0	11.9	2.6	25.5	18.0	73.0	21
	25.5	25.0	3.0	0.7	11.7	20.0	31.0	21
Macronucleus, length [b]	29.8	29.0	–	–	–	16.0	50.0	21
	12.1	12.0	1.4	0.3	11.6	10.0	14.0	21
Macronucleus, width	8.2	8.0	1.7	0.4	21.0	6.0	12.0	21
	5.7	6.0	0.6	0.1	10.2	5.0	7.0	21
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Micronucleus, length	4.2	4.0	0.9	0.2	22.3	3.0	6.0	18
	3.0	3.0	–	–	–	2.5	3.5	21
Micronucleus, width	3.4	3.0	1.0	0.3	30.2	2.0	5.0	18
	2.4	2.5	–	–	–	2.0	3.0	21
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	18
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Somatic kineties, number in mid-body	14.4	14.0	3.5	0.8	24.5	10.0	22.0	21
	7.1	7.0	–	–	–	7.0	8.0	21
Kinetids in a right lateral kinety, number	40.2	40.0	12.7	2.8	31.6	21.0	65.0	21
	20.7	21.0	2.8	0.6	13.5	15.0	25.0	21
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Circumoral kinety to end of dikinetidal portion of brush row 1, distance	13.8	13.0	3.1	0.7	22.2	9.0	21.0	21
	5.1	5.0	0.8	0.2	15.1	4.0	7.0	21
Circumoral kinety to end of dikinetidal portion of brush row 2, distance	16.3	17.0	3.5	0.8	21.6	10.0	27.0	21
	11.5	12.0	1.6	0.4	13.9	9.0	15.0	21
Circumoral kinety to end of dikinetidal portion of brush row 3, distance	6.8	6.0	1.8	0.4	27.2	4.0	12.0	21
	5.5	5.0	1.0	0.2	18.7	4.0	9.0	12
Dikinetids in brush row 1, number	11.2	11.0	2.8	0.6	24.7	8.0	20.0	21
	3.8	4.0	0.8	0.2	20.4	3.0	6.0	21
Dikinetids in brush row 2, number	14.4	13.0	3.1	0.7	21.8	11.0	25.0	21
	10.0	10.0	1.3	0.3	12.7	8.0	13.0	21
Dikinetids in brush row 3, number	6.4	6.0	2.3	0.5	36.6	4.0	15.0	21
	4.7	5.0	0.9	0.2	19.6	3.0	7.0	21

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] If curved, length of spread macronucleus was estimated; values thus approximations.

Occurrence and ecology: To date found at type location (bark of a *Colophospermum* tree), at Namibian site 56 ("ordinary soil"), in Australia (sandy, saline soil from around roots of halophytes at shore of Lake Amadeus near Alice Springs), and in Venezuela (mud from ephemeral, granitic rock pools, so-called Lajas, near Puerto Ayacucho). The Venezuelan specimens could be cultivated with diluted soil percolate and part of the natural protist community. *Sikorops namibiensis* grew well for some weeks and preferred a large *Polytoma* as food. These data show that *S. namibiensis* is an euryoecious ciliate and likely a cosmopolitan, although Laurasian records are still lacking.

Comparison with related species: The Namibian population perfectly matches the genus diagnosis of *Sikorops* FOISSNER, 1999b. This genus now already consists of four distinct species differing mainly by the macronucleus: two ellipsoidal nodules with a single micronucleus in between in *S. woronowiczae* FOISSNER, 1999b; long and filiform in *S. espeletiae* FOISSNER, 2000b; reniform in *S. namibiensis*; and ellipsoidal in → *S. minor*. Furthermore, *S. namibiensis* has brush row 3 strongly shortened, while the other species have row 1 shortened. Size, shape, extrusomes, and number of ciliary rows are rather similar in most species. Likewise, the peculiar oral ciliature is very similar in all species and thus a further genus or family character. In vivo, *S. namibiensis* is easily confused with *Spathidium claviforme* (redescribed in FOISSNER 1987b) and *Protospathidium terricola* FOISSNER, 1998a, which have a similar size, shape and nuclear apparatus. Fortunately, both have simple, rod-shaped extrusomes distinctly different from the obovate to oblanceolate toxicysts of *Sikorops* spp.

Sikorops minor nov. spec. (Fig. 43a–l; Table 35)

Diagnosis: Size about 65 × 15 µm in vivo. Bottle-shaped to elongate ovoidal with obliquely truncate, about 5 µm wide oral bulge. Macronucleus ellipsoidal. Extrusomes fusiform, about 1.5 × 1 µm. On average 7 ciliary rows and 5 dikinetids in brush row one, 10 in row two, and 5 in row three.

Type location: Highly saline, alkaline soil near the village of Himmafushi, North-Male Atoll, Maldives, 03°N 74°E.

Etymology: The Latin adjective *minor* (small) indicates that it is the smallest described species of the genus.

Description: Size 50–80 × 10–20 µm in vivo, usually about 65 × 15 µm; shrunken to 51 × 13 µm in protargol preparations showing a length:width ratio of 3–5.5:1, on average 4:1 (Table 35). Lateral view indistinctly spatulate, obclavate, bottle-shaped or almost cylindroidal, dorsal and ventral view obclavate to elongate ovoidal with posterior end moderately broadly rounded and anterior flattened up to 2:1 and bluntly pointed (Fig. 43a–d, g, i, k). Macronucleus slightly below mid-body, broadly to elongate ellipsoidal, rarely distinctly reniform; nucleoli small and globular. Micronucleus attached to macronucleus at variable position, discoidal because flattened about 2:1, broad view outline circular to broadly elliptical. Contractile vacuole in posterior body end, some excretory pores in pole area. Extrusomes only in oral bulge, fusiform, minute, that is, about 1.5 × 1 µm and thus difficult to

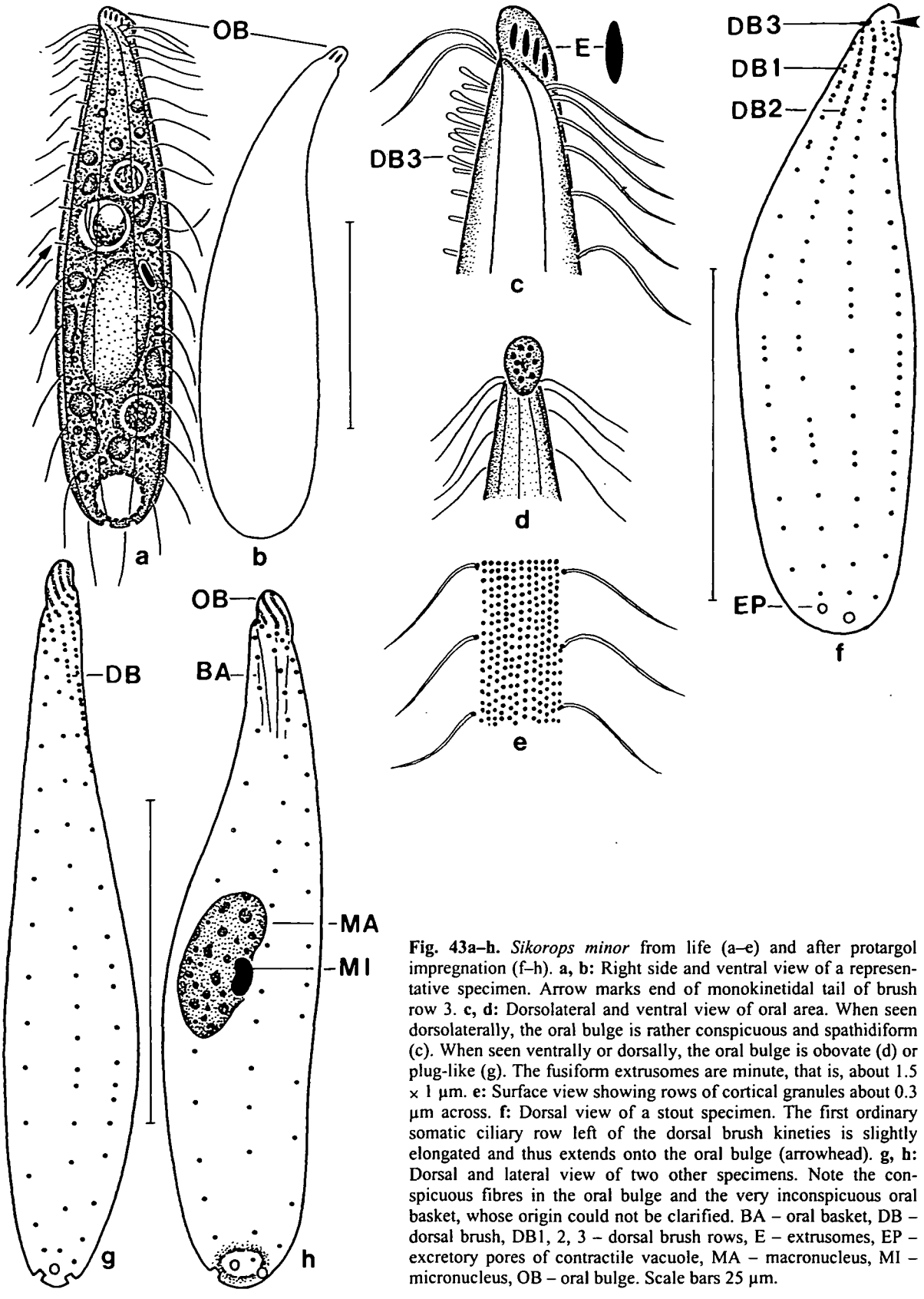

Fig. 43a–h. *Sikorops minor* from life (a–e) and after protargol impregnation (f–h). **a, b:** Right side and ventral view of a representative specimen. Arrow marks end of monokinetidal tail of brush row 3. **c, d:** Dorsolateral and ventral view of oral area. When seen dorsolaterally, the oral bulge is rather conspicuous and spathidiform (c). When seen ventrally or dorsally, the oral bulge is obovate (d) or plug-like (g). The fusiform extrusomes are minute, that is, about 1.5 × 1 µm. **e:** Surface view showing rows of cortical granules about 0.3 µm across. **f:** Dorsal view of a stout specimen. The first ordinary somatic ciliary row left of the dorsal brush kineties is slightly elongated and thus extends onto the oral bulge (arrowhead). **g, h:** Dorsal and lateral view of two other specimens. Note the conspicuous fibres in the oral bulge and the very inconspicuous oral basket, whose origin could not be clarified. BA – oral basket, DB – dorsal brush, DB1, 2, 3 – dorsal brush rows, E – extrusomes, EP – excretory pores of contractile vacuole, MA – macronucleus, MI – micronucleus, OB – oral bulge. Scale bars 25 µm.

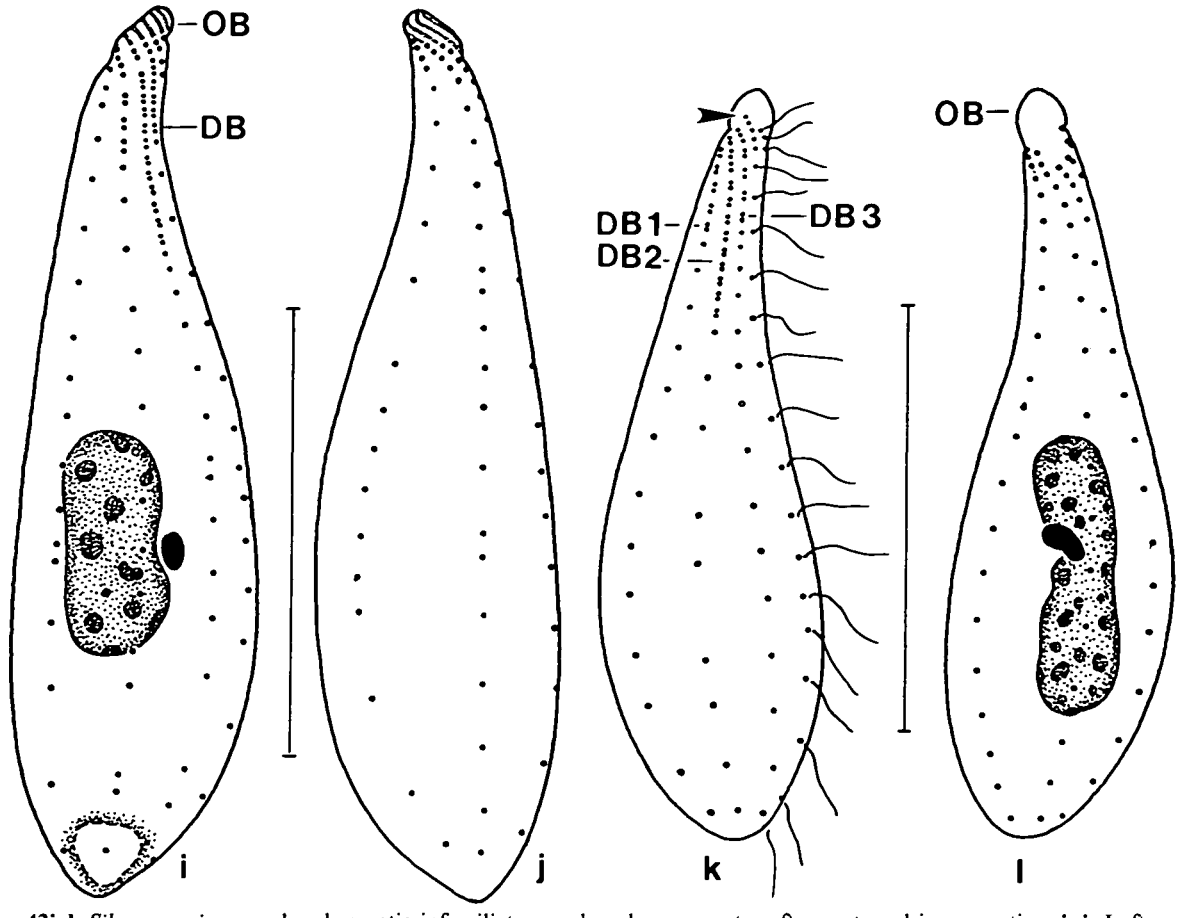

Fig. 43i–l. *Sikorops minor*, oral and somatic infraciliature and nuclear apparatus after protargol impregnation. **i, j:** Left and right side view of holotype specimen. Note the low number (7) of ciliary rows and the distinct fibres in the oral bulge. **k, l:** Dorsal and ventral view of a small, obclavate specimen. The first ordinary somatic ciliary row (arrowhead) left of the dorsal brush kineties is slightly elongated and thus extends onto the oral bulge, which is conspicuously plug-shaped in this species, if it is viewed ventrally or dorsally. Brush row 2 is distinctly longer than rows 1 and 3. There is no distinct circumoral kinety recognizable, and the first basal body of each row is ciliated. DB – dorsal brush, DB1, 2, 3 – dorsal brush rows, OB – oral bulge. Scale bars 25 µm.

recognize, do not impregnate with the protargol method used. Cortex very flexible, contains about 12 rows of colourless, refractive granules approximately 0.3 µm across between each two ciliary rows. Cytoplasm colourless, in middle third often packed with food vacuoles as well as globular and irregular fat inclusions up to 6 µm across. Feeds on heterotrophic flagellates and likely also small ciliates, both rapidly digested because prey organisms could be not identified in the food vacuoles of protargol impregnated cells. Swims slowly by rotation about main body axis.

Cilia about 8 µm long in vivo, in some specimens rather irregularly spaced due to interspersed, unciliated kinetids, closely spaced in oral region. Ciliary rows widely spaced, extend meridionally and equidistantly, anterior portion curved, first row left of dorsal brush invariably slightly elongated anteriorly and thus extending onto dorsal surface of oral bulge. Dorsal brush in anterior region of three dorsolateral kineties, inconspicuous and of ordinary structure, that is, consists of closely spaced dikinetids with up to 3 µm long bristles; two to

three monokinetids or very closely spaced dikinetids at anterior end of individual brush rows. Brush rows 1 and 3 of almost same length each consisting of an average of four to five dikinetids, row 3 associated with a monokinetidal bristle tail extending to mid-body; row 2 about twice as long as rows 1 and 3, consists of ten dikinetids on average. All brush rows continue as ordinary somatic kineties posteriorly (Fig. 43a, f–l; Table 35).

Oral bulge inconspicuous because minute, that is, about 5 × 4 µm in vivo; basically spathidiform and slanted from dorsal to ventral when cell is viewed laterally, while flattened and thus projecting plug-like when viewed ventrally or dorsally. No distinct circumoral kinety, that is, ciliary rows simply end at base of oral bulge and the anteriormost basal body of each row is ciliated and associated with a conspicuous fibre spirally curving to bulge centre. Oral basket rods recognizable only in over-impregnated specimens, rod origin remained unclear (Fig. 43a, d, f–l; Table 35).

Occurrence and ecology: The highly saline and alkaline (pH 8.6) sample from the type location, kindly provided by Dr. Wolfgang PETZ, contained much litter and some sandy soil collected under shrubs about 2 m inshore. In Namibia, *S. minor* occurs only at site (56), that is, in non-saline soil. Found also in Cedar Creak, Utah, USA. This shows that *S. minor* very likely is a euryhaline cosmopolitan.

Generic assignment and comparison with related species: Although oral dikinetids and oralized somatic kinetids could be not identified unequivocally, the general organization, the fusiform extrusomes, and the considerable similarity with → *Sikorops namibiensis* suggest that such populations belong to *Sikorops*. Actually, *S. minor* largely matches → *S. namibiensis*, but all main features are half the size (Table 35). Thus, and because *S. minor* is considerably stouter than → *S. namibiensis* (2–3:1 vs. 3–4:1), they can hardly be confused. However, we cannot exclude that the Maldivean species lacks oral dikinetids; if so, it would belong to the Enchelyina FOISSNER & FOISSNER, 1988.

Generally, *S. minor* is an inconspicuous species with few distinct features. Thus, it is difficult to identify and to compare with older, often very incomplete descriptions of seemingly similar species. There are three *Spathidium* species in the literature which have some resemblance to *S. minor*: *Spathidium cucumis* BAUMEISTER in KAHL, 1931 (likely double number of ciliary rows and longer, rod-shaped extrusomes; found in liquid manure); *S. claviforme* KAHL, 1930b (with distinct, dikinetidal circumoral kinety and 12 ciliary rows; see redescription by FOISSNER 1987b); and *S. microstomum* VUXANOVICI, 1962c (only 35–60 µm long and distinctly narrowed posteriorly providing the species with an entirely different shape).

Furthermore, some *Lagynophrya* species look similar, but the sole species so far investigated in detail has a distinct, dikinetidal circumoral kinety (FOISSNER et al. 1999).

Clavoplites nov. gen.

Diagnosis: Acropisthiidae with claviform, drumstick-shaped, or pseudofusiform extrusomes.

Type species: *Clavoplites edaphicus* nov. spec.

Etymology: Composite of the Latin noun *clava* (club) and the Greek noun *hoplites* (soldier), referring to the basically club-shaped extrusomes. Masculine gender.

Comparison with related genera: *Acropisthium* has rod-shaped extrusomes, and in *Sikorops* they are fusiform or oblanceolate. The claviform/drumstick-shaped extrusomes of *Clavoplites edaphicus* and *C. australiensis* are really conspicuous, making the species easy to identify in vivo. A reinvestigation of the type material of *Enchelydium terrenum* FOISSNER, 1984 showed that it very likely has the same features as *Clavoplites* spp. Thus, it is transferred to this genus: *Clavoplites terrenum* (FOISSNER, 1984) nov. comb.[6] The extrusomes of *C. terrenum* might be classified as "fusiform" and the species thus referred to *Sikorops*. However, the fusiform extrusomes of *C. terrenum* look different from those of *Sikorops* and likely evolved convergently by shifting the broad portion of clavate or drumstick-shaped extrusomes to the mid of the organelle, leaving a rod-shaped process anteriorly and posteriorly. Thus, we suggest that the extrusomes of *C. terrenum* are "pseudofusiform".

Clavoplites edaphicus nov. spec. (Fig. 44a–k, n, o; 321a–h; Table 36)

Diagnosis: Size about 100 × 35 µm in vivo. Spatulate with obliquely truncate, about 8 µm wide oral bulge. Macronucleus rod-shaped to semicircular, 30 × 8 µm on average. Extrusomes conspicuously clavate, 3–4 × 1.3–1.7 µm in size. On average 17 ciliary rows, 3 anteriorly differentiated to inconspicuous dorsal brush.

Type location: Red, sandy soil under shrubs between the village of Erldunda and the Ayers Rock, Australia, 26°S 132°30'E.

Etymology: *Edaphicus* (from the Greek Edaphon) because living in soil.

Description: Shape highly variable because slender theronts and broad trophonts occur, although the protargol slides contain mainly early and late trophonts (Table 36). Size 80–120 × 25–60 µm, usually near 100 × 35 µm in vivo, length:width ratio 1.7–3.3:1, on average 2.7:1 in protargol preparations. Usually slenderly to broadly spatulate with anterior portion slightly contractile and curved dorsally, providing cells with a *Spathidium claviforme*-like appearance. Anterior end obliquely truncate and ≤ 10 µm wide, posterior narrowly to broadly rounded, widest in mid-body (Fig. 44a, i, j). Nuclear apparatus in middle body third (Fig. 44a, c, d, i; 321g). Macronucleus rod-shaped, elongate reniform, semicircular or ellipsoidal, on average about 30 × 10 µm both in vivo and protargol preparations; nucleoli minute to large and lobate. Micronucleus conspicuous because about 5 × 4 µm in vivo, near or in mid-portion of macronucleus, surrounded by a distinct membrane. Contractile vacuole in rear end, several excretory pores in pole area. Extrusomes arranged ring-like in oral bulge, some scattered in cytoplasm, conspicuous because broadly clavate, that is, 3–4 × 1.3–1.7 µm in size, attached with a minute dome at broad end to oral bulge, impregnate rather intensely with protargol (Fig. 44a, e, j, n, o; 321a–h; Table 36). Cortex very flexible, contains about five rows of

[6] FOISSNER (1984) did not provide the etymology of the species' name. We consider it as a noun in apposition, meaning "living in soil"!

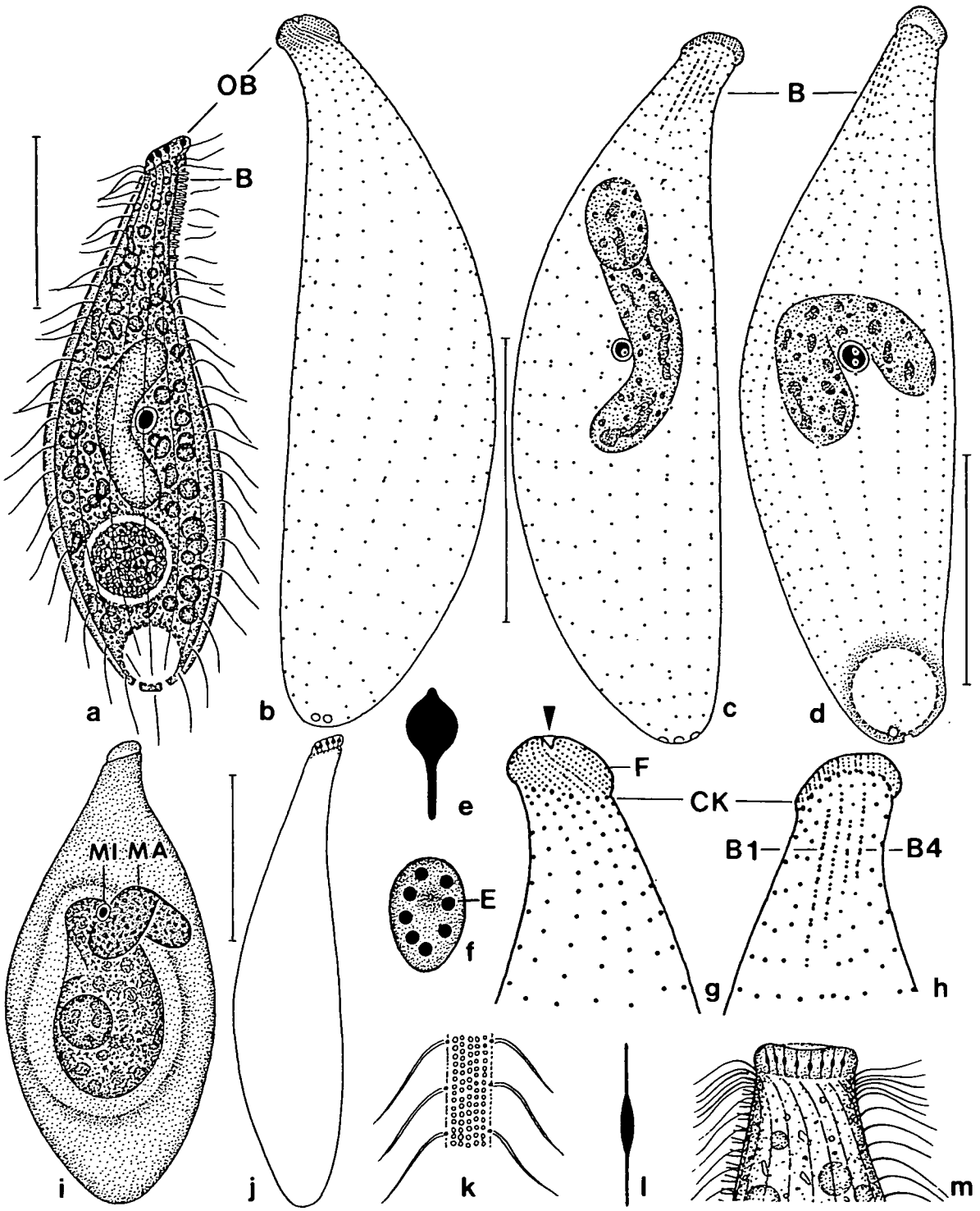

Fig. 44a–k. *Clavoplites edaphicus* from life (a, e, f, j, k) and after protargol impregnation (b–d, g–i). **a:** Left side view of a representative specimen. **b, c, g, h:** Infraciliature of ventral and dorsal side. Arrowhead marks slightly acentric bulge opening. **e:** Extrusome, length 3 µm. **f:** Frontal view of oral bulge. **i:** A specimen having just engulfed a *Colpoda maupasi*. **j:** Slender theront. **k:** Surface view showing cortical granulation. B1, 4 – dorsal brush rows, CK – circumoral kinety, E – extrusomes, F – bulge fibres, MA – macronucleus, MI – micronucleus, OB – oral bulge. Scale bars 30 µm.

Fig. 44 l, m. *Clavoplites terrenum*, extrusome (length 5 µm) and anterior body portion from life (from FOISSNER 1984).

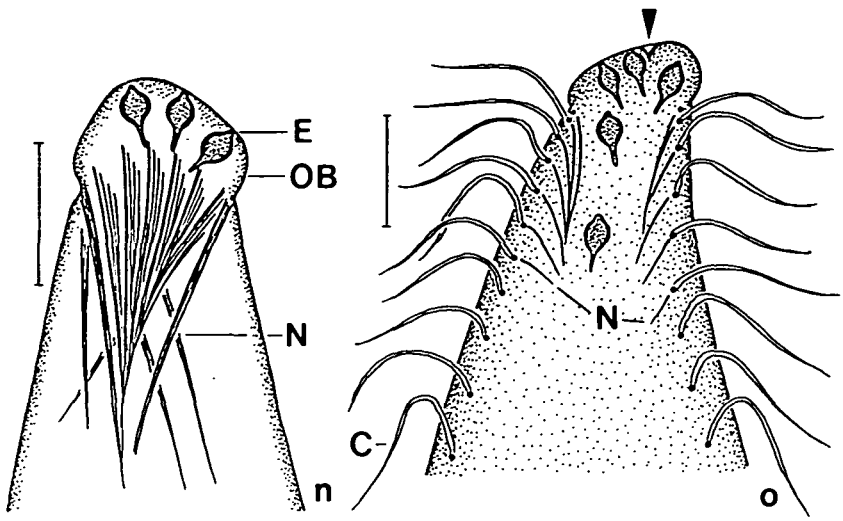

Fig. 44n, o. *Clavoplites edaphicus* after protargol impregnation. Optical section of oral region of specimens shown in figures 44c and 44d. Nematodesmata (oral basket rods) originate from the circumoral kinetids and from oralized somatic monokinetids at the anterior portion of the ciliary rows. The arrowhead marks the small, acentric bulge (oral) opening. The conspicuous extrusomes impregnate rather intensely with protargol and provide the oral region with a highly characteristic appearance. C – ordinary somatic cilium, E – extrusome, N – nematodesmata, OB – oral bulge. Scale bars 5 µm.

colourless granules approximately 0.2 µm across between each two ciliary rows. Cells colourless, but trophonts appear dark at low magnification (≤ ×100) because packed with small and medium-sized, globular to irregular fat inclusions and food vacuoles. Feeds on ciliates (*Colpoda maupasi*, *Lamtostyla australis*), which are ingested whole because still identifiable in the food vacuoles (Fig. 44i). Swims rather rapidly by rotation about main body axis.

Cilia about 10 µm long in vivo, frequently rather irregularly spaced and with some unciliated kinetids within individual rows, slightly more closely spaced in oral region. Ciliary rows extend meridionally and equidistantly, anterior portion distinctly curved dorsally on right side and ventrally on left; usually some rows shortened anteriorly or posteriorly, especially in dorsal brush region. Dorsal brush in anterior region of three, rarely four dorsolateral kineties, inconspicuous because occupying only 18% of body length on average and bristles merely up to 2 µm long; usually some widely spaced bristle pairs at posterior end of rows 1 and 2 and some ordinary somatic cilia at anterior end of all rows, but especially row 1. Brush rows 1 and 2 of almost same length and composed of 11–15 dikinetids on average; row 3 about half as long as row 2, consists of an average of 10 closely spaced dikinetids, continues to midbody with a monokinetidal tail of 1 µm long bristles (Fig. 44a–d, g, h; Table 36).

Oral bulge 7–9 µm wide and 3–5 µm high, shiny due to the highly refractive extrusomes contained; spathidiform, that is, obliquely truncate occupying anterior body end, obovate in frontal view with extrusomes appearing as conspicuous, bright dots. Bulge (oral) opening minute when not active, acentric, that is, slightly shifted to dorsal side and supported by thick fibres originating from circumoral kinety and extending spirally over oral bulge. Circumoral kinety at base of oral bulge, indistinct with details as difficult to recognize as in other genera of family; very likely as described in → *Sikorops namibiensis*. Oral basket hardly recognizable in vivo, but rather conspicuous in optimally bleached protargol preparations because the nematodesmata form distinct, somewhat irregularly arranged bundles; composed of fine nematodesmata originating from circumoral kinetids **and** about 4–6 basal bodies at anterior end of somatic kineties (Fig. 44a–c, g, h, n–p; 321f–h; Table 36). Obviously, the oral apparatus is very effective and the bulge can open widely to engulf large prey, as described above.

Occurrence and ecology: Found at type location (very sandy soil and litter under shrubs in the "red centre" of Australia; pH 5.9), at Namibian site (28), in Tunisia (gypsum semi-desert near the town of Makthar; greyish soil with much litter from shrubs; pH 8.0, moderately saline), and in Rwanda (soil, mosses, and litter from shore of Lake Kibu near the village of Kibuye). These data indicate that *C. edaphicus* is euryhaline and at least a Gondwanan cosmopolitan.

Comparison with related species: Basically, *C. edaphicus* is easily identified by the conspicuous extrusomes. Body shape and size and the nuclear apparatus are highly similar to the congeners, *Sikorops* spp., and small spathidiids, especially *Spathidium claviforme*, as redescribed by FOISSNER (1987b). Thus only extrusome shape and attachment (with the broad end!) remain as reliable features. Although they impregnate with protargol and hardly change size and shape by the preparation procedures, they must be studied in live specimens at high magnification (×1000, oil immersion) because other (or even the same!) protargol protocols might produce different results.

Table 36. Morphometric data on *Clavoplites edaphicus* (upper line) and *C. australiensis* (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	92.5	92.0	11.9	3.6	12.9	77.0	110.0	11
	110.7	108.0	13.6	3.1	12.3	95.0	135.0	19
Body, width	35.2	33.0	9.4	2.8	26.7	23.0	58.0	11
	41.0	42.0	6.0	1.4	14.5	25.0	52.0	19
Body length:width, ratio	2.7	2.7	0.6	0.2	20.1	1.7	3.3	11
	2.7	2.8	0.5	0.1	18.3	2.2	4.3	19
Anterior body end to macronucleus, distance	39.1	43.0	10.2	3.1	26.2	17.0	50.0	11
	50.3	50.0	11.2	2.6	22.3	30.0	77.0	19
Macronucleus, length (spread) [b]	31.5	26.0	–	–	–	17.0	70.0	11
	37.2	37.0	–	–	–	20.0	60.0	19
Macronucleus, width	8.0	8.0	1.6	0.5	19.4	6.0	11.0	11
	8.5	8.0	1.2	0.3	13.8	7.0	11.0	19
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	14
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	30
Micronucleus, length [c]	3.4	3.5	0.6	0.2	18.9	2.5	5.0	11
	3.6	4.0	0.8	0.2	21.9	3.0	6.0	19
Micronucleus, width [c]	3.1	3.0	0.4	0.1	12.5	2.5	4.0	11
	3.6	4.0	0.7	0.2	20.9	3.0	6.0	19
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	14
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	25
Oral bulge, maximum width	6.8	7.0	0.6	0.2	9.0	6.0	8.0	11
	9.8	10.0	1.3	0.3	13.2	7.0	12.0	19
Extrusomes, length	3.3	3.5	–	–	–	2.5	3.5	11
	5.1	5.0	–	–	–	4.0	6.0	19
Extrusomes, maximum width	1.4	1.5	–	–	–	1.2	1.6	11
	1.0	1.0	–	–	–	0.8	1.2	19
Somatic ciliary rows, number	17.5	17.0	1.3	0.4	7.4	15.0	20.0	11
	20.6	20.0	1.8	0.4	8.9	17.0	25.0	19

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Kinetids in a ventral kinety, number [d]	37.8	35.0	6.8	2.0	17.9	30.0	51.0	11
	52.0	52.0	9.4	2.2	18.0	35.0	70.0	19
Dorsal brush rows, number	3.2	3.0	–	–	–	3.0	4.0	11
	3.8	4.0	0.8	0.1	19.8	3.0	6.0	28
Anterior kinety end to end of dikinetidal portion of	16.8	14.0	8.5	2.6	50.7	10.0	41.0	11
brush row 1, distance	18.1	18.0	4.9	1.1	27.3	10.0	30.0	19
Anterior kinety end to end of dikinetidal portion of	14.0	14.0	2.7	0.8	18.9	10.0	18.0	11
brush row 2, distance	18.2	18.0	4.7	1.1	26.0	12.0	33.0	19
Anterior kinety end to end of dikinetidal portion of	10.3	7.0	10.0	3.0	97.2	5.0	40.0	11
brush row 3, distance	13.5	12.0	4.7	1.1	34.5	8.0	21.0	19
Anterior kinety end to end of dikinetidal portion of	–	–	–	–	–	–	–	–
brush row 4, distance	9.0	8.0	2.4	0.5	26.4	4.0	16.0	19
Dikinetids in brush row 1, number	10.8	11.0	3.3	1.0	30.3	5.0	15.0	11
	10.1	10.0	5.4	1.2	53.6	3.0	20.0	19
Dikinetids in brush row 2, number	14.0	15.0	1.6	0.5	11.1	11.0	16.0	11
	16.0	17.0	3.2	0.7	19.8	9.0	20.0	19
Dikinetids in brush row 3, number	10.1	10.0	3.1	1.0	31.2	5.0	18.0	11
	14.3	14.0	3.6	0.8	25.3	9.0	23.0	19
Dikinetids in brush row 4, number	–	–	–	–	–	–	–	–
	10.3	10.0	2.5	0.6	24.6	4.0	15.0	19

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), selected (as both species occur in the same sample, only such specimens were used in which the extrusomes, the main distinguishing feature, are recognizable) specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] If curved, artificially spread; values thus approximations.

[c] Including surrounding membrane.

[d] Ciliated and unciliated kinetids.

Clavoplites australiensis nov. spec. (Fig. 45a–o; 321i–s; Table 36)

Diagnosis: Size about 120 × 40 µm in vivo. Spatulate with obliquely truncate, about 10 µm wide oral bulge. Macronucleus rod-shaped to semicircular, 40 × 8 µm on average. Extrusomes conspicuously drumstick-shaped, 3–6 × 0.8–1.2 µm in size. On average 20 ciliary rows, 4 anteriorly differentiated to inconspicuous dorsal brush.

Type location: Red, sandy soil under shrubs between the village of Erldunda and the Ayers Rock, Australia, 26°S 132°30'E.

Etymology: Named after the country discovered.

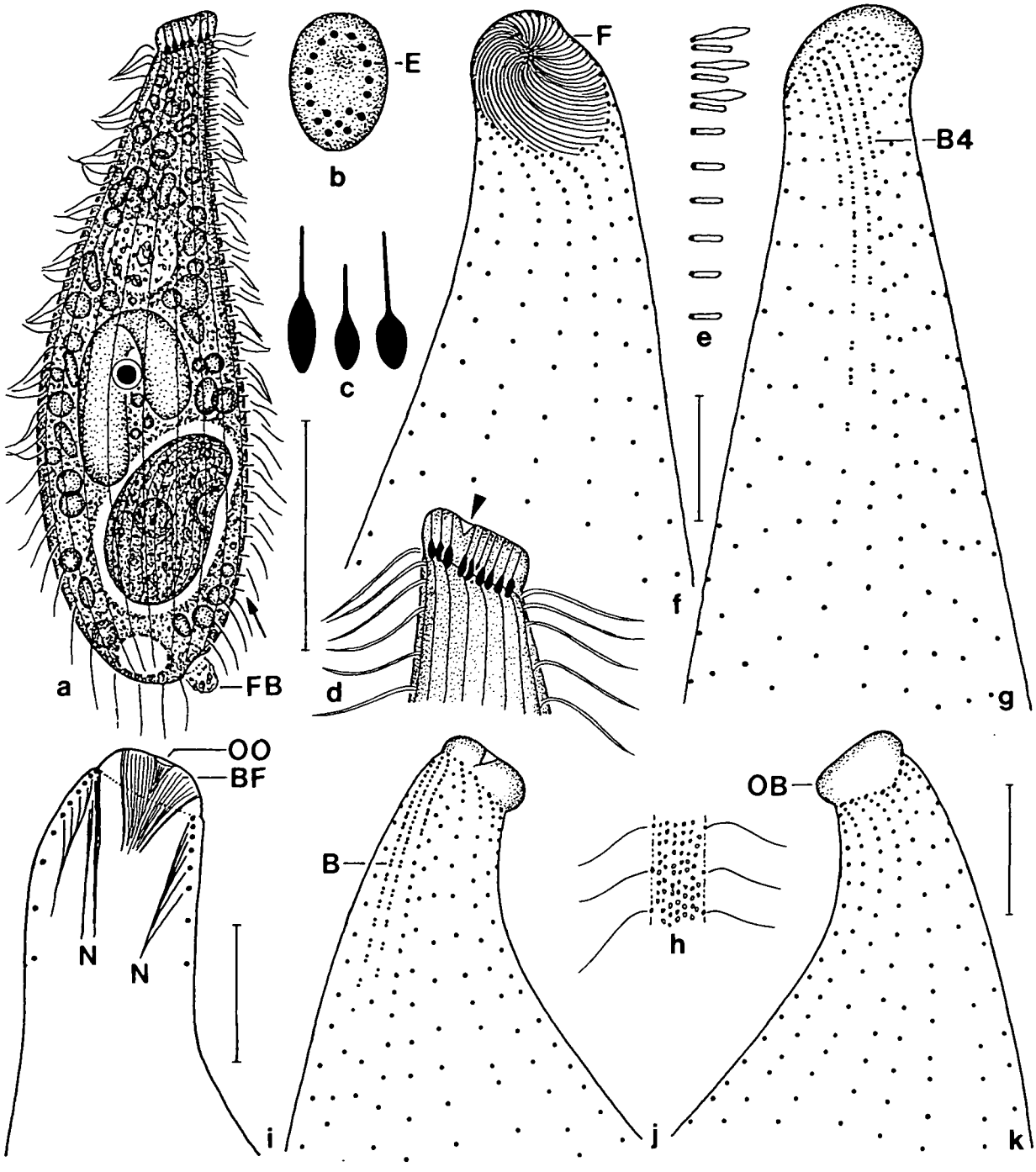

Fig. 45a–k. *Clavoplites australiensis* from life (a–e, h) and after protargol impregnation (f, g, i–k). **a, e:** Left side view of a trophont having just engulfed a *Colpoda maupasi*. Arrow marks end of monokinetidal bristle tail of brush row 3 shown at higher magnification in (e). **b:** Frontal view of oral bulge. **c:** Extrusomes, length 4–6 µm. **d:** Anterior body portion showing extrusomes and acentric oral opening (arrowhead). **f, g, j, k:** Ventral and dorsal ciliary pattern of specimens with four, respectively, three dorsal brush rows. **h:** Surface view showing cortical granulation. **i:** The oral apparatus is composed of three baskets: the central funnel (OO) is lined by fibres originating from the circumoral kinetids [see also (f)]; the middle basket is produced by fibres within the bulge; and the outer basket is formed by nematodesmata originating from the circumoral kinetids and the anterior basal bodies of the ciliary rows. B, B4 – dorsal brush (row 4), BF – bulge fibres, E – extrusomes, F – fibres, FB – faecal bale, N – nematodesmata, OO – oral opening. Scale bars 40 µm (a) and 10 µm (f, g, i–k).

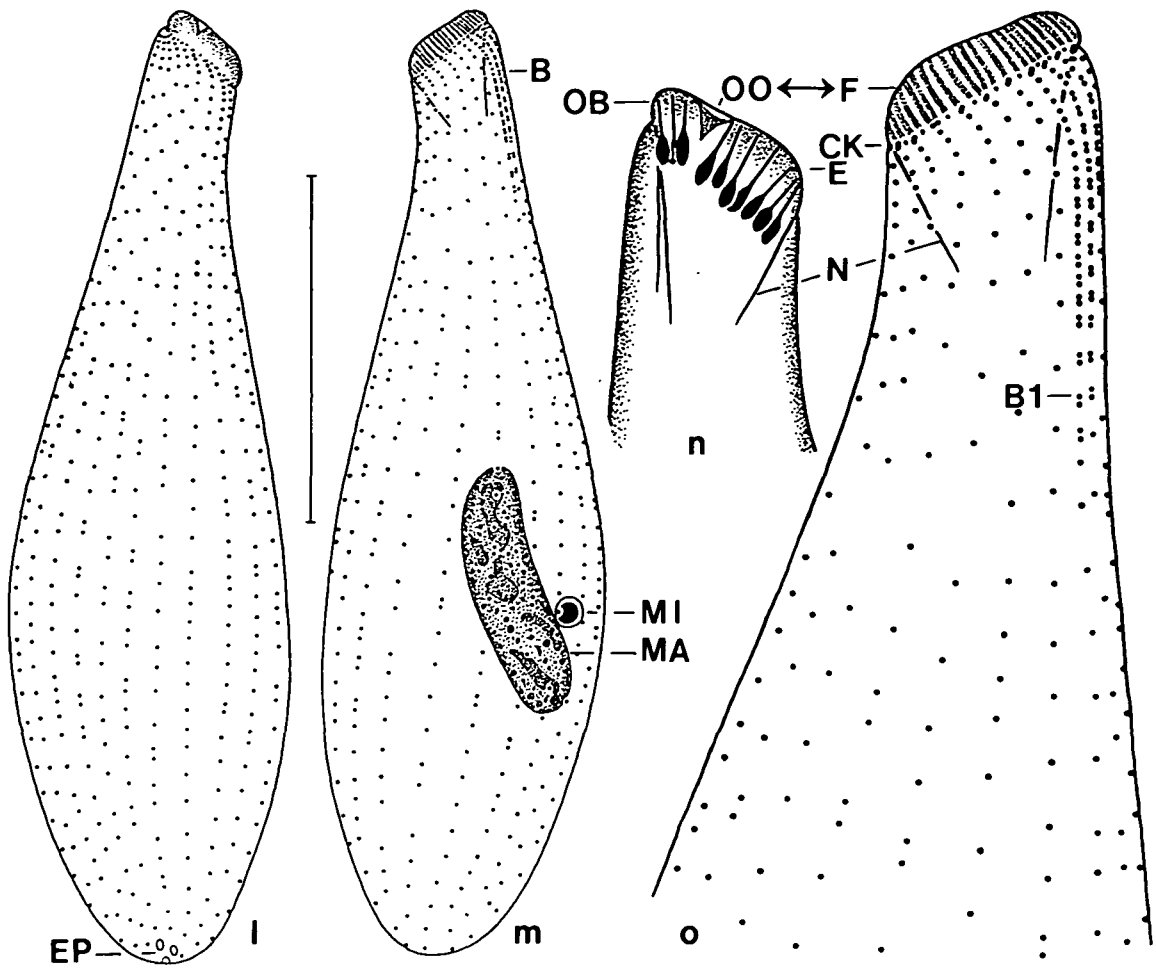

Fig. 45 l–o. *Clavoplites australiensis*, somatic and oral ciliary pattern and nuclear apparatus of holotype specimen after protargol impregnation at various magnifications and focal planes. **l, m:** Right and left side overview. **n:** Optical section of oral portion showing the acentric oral opening (OO), which is lined by fibres (F) originating from the circumoral kinety. The drumstick-shaped extrusomes are lightly impregnated. **o:** Fine structure of circumoral kinety and dorsal brush, which consists of three rows of paired bristles. The circumoral kinety likely consists of paired, occasionally lighter impregnated basal bodies of which one is ciliated at the end of the ciliary rows; between each two circumoral basal body pairs is a lighter impregnated granule. Fibres originate from these granules and the circumoral pairs and extend spirally to the acentric oral opening (see also figure 45f). B – dorsal brush, B1 – dorsal brush row 1, CK – circumoral kinety, E – extrusomes, F – fibres, MA – macronucleus, MI – micronucleus, N – nematodesmata, OB – oral bulge, OO – oral opening sensu stricto. Scale bar 40 µm.

Description and comparison with related species: The general features of this species are highly similar to those of *C. terrenum* (FOISSNER, 1984), → *C. edaphicus*, certain *Sikorops* species, and some *Spathidium* species. Thus, we refer to the description and discussion of → *C. edaphicus*, the detailed figures, and the following main features of the species.

(1) *Clavoplites australiensis* is larger than *C. terrenum* and *C. edaphicus*, but not very much, and thus the extremes overlap (Table 36).

(2) The main feature of *C. australiensis* is the drumstick-like shape of the extrusomes (Fig. 45a, c; 321i–l). In *C. edaphicus*, the extrusomes are clavate and attached with the broad end to the oral bulge (Fig. 44a, e; 321a–e, g, h), while they are pseudofusiform in *C.*

terrenum (Fig. 44 l, m). The arrangement and conspicuousness of the extrusomes of *Clavoplites* remind of certain → *Enchelydium* species which, however, have a different shape of the oral bulge and a different nuclear pattern (FOISSNER 1980d, KAHL 1930a). Furthermore, *Actinorhabdos* FOISSNER, 1984 (only two very short brush rows) and → *Dioplitophrya* from the family Fuscheriidae have similar extrusomes.

(3) *Clavoplites australiensis* has four dorsal brush rows on average, in contrast to the congeners, which have three. However, the number of brush rows is highly variable in *Clavoplites* and thus of doubtful value (Table 36).

(4) Some excellently prepared specimens show further details of the oral apparatus. *Clavoplites* has, like *Enchelys polynucleata* (FOISSNER & FOISSNER 1985), three oral fibre systems, which form a central, a mid, and an outer oral funnel (Fig. 45f, i, l–o; 321m–s): the central oral funnel, the oral opening sensu stricto, is lined by fibres originating from the circumoral kinetids; the middle oral funnel is produced by fibres within the bulge; and the outer oral funnel is formed by nematodesmata originating from the circumoral kinetids and the oralized somatic monokinetids at the anterior end of the ciliary rows.

Occurrence and ecology: To date found at type location, where it occurred together with → *C. edaphicus*, and at Namibian site (2). Obviously, this is a rare species whose geographic distribution cannot yet estimated. However, it is remarkable that the European member of the genus is a different species.

Enchelaria nov. gen.

Diagnosis: Spathidiidae (?) with small, obovate oral bulge. Ciliary rows curved at anterior end, 2 differentiated to dorsal brush. Oral basket made of nematodesmata originating exclusively from the anterior (di?) kinetid of each ciliary row (circumoral kinety).

Type species: *Enchelaria multinucleata* nov. spec.

Etymology: Composite of the Greek noun *enchelyos* (eel) and the Latin suffix *arius* (similar), referring to both, the slender shape of the type species and its similarities with the genera *Enchelys* and *Enchelyodon*. Feminine gender.

Comparison with related genera and species assignable: *Enchelaria* has a unique combination of features, viz., a two-rowed dorsal brush and an atypical circumoral kinety made of the anterior kinetid of each somatic ciliary row. This and the anteriorly curved kineties resemble the → Acropisthiidae. However, *Enchelaria* lacks oralized somatic monokinetids, although we cannot entirely exclude that the anterior kinetid is an oralized somatic monokinetid. If so, *Enchelaria* still is a distinct genus because then it would lack the haptorid oral dikinetids so typical for the → Acropisthiidae and → Fuscheriidae. On the other hand, the lack of oral dikinetids would relate *Enchelaria* to the Enchelyidae which, however, invariably have several oralized monokinetids at the anterior end of the ciliary rows.

The general appearance of *Enchelaria multinucleata* also resembles *Chaenea* (a → fuscheriid genus with oralized somatic monokinetids at the anterior end of the kineties; see FOISSNER 1984 and LIPSCOMB & RIORDAN 1990) and → *Enchelyodon* which, however, has straight

ciliary rows, a circular oral bulge, and a circumoral kinety composed of much more dikinetids than ciliary rows. Thus, we propose that *Enchelaria* is related to the Spathidiidae which not only have anteriorly curved ciliary rows, but also contain genera with a button-shaped oral bulge (several → *Protospathidium* and → *Arcuospathidium* species). However, most genera of the Spathidiidae have three dorsal brush rows and much more circumoral dikinetids than ciliary rows, including → *Semispathidium*, which highly resembles *Enchelaria* at first glance. To sum up, *Enchelaria multinucleata* represents a distinct genus, no matter the familial classification.

As yet, *Enchelaria* is monotypic, but it is likely that some of the many *Enchelys*, *Enchelyodon*, and *Spathidium* species described will be transferred to *Enchelaria* upon detailed reinvestigation. In fact, we found some specimens of a second species with rows of body extrusomes and a vermiform macronucleus at Namibian site (49).

Enchelaria multinucleata nov. spec. (Fig. 46a–h; 307a, b; Table 37)

Diagnosis: Size about 160 × 20 µm in vivo; cylindroidal. On average 127 scattered, ellipsoidal macronuclear nodules and 12 globular micronuclei. Extrusomes fusiform, about 5 × 1 µm. On average 16 ciliary rows. Brush rows with about 20 dikinetids each.

Type location: Soil from *Aloe dichotoma* forest near the Gariganus Guest Farm, Namibia, 26°30'S 18°25'E (site 5 in figure 2 and chapter 2.1.2).

Etymology: Composite of the Greek words *multi* (many) and *nucleus*, referring to a main feature of the species, viz., its many macronuclear nodules.

Description: Size 110–200 × 15–30 µm in vivo, usually about 160 × 20 µm, length: width ratio also highly variable, viz., 5–9:1, on average about 7:1 in protargol preparations. Slenderly flask-shaped or cylindroidal with subapical portion slightly widened (Fig. 46a, c; 307a; Table 37); acontractile and unflattened. Nuclear apparatus scattered, frequently slightly concentrated in middle third of cell, consists of an average of 127 macronuclear nodules and 9 globular micronuclei (Fig. 46d); individual macronuclear nodules globular to elongate ellipsoidal, contain some small nucleoli. Contractile vacuole in rear body end, some excretory pores in posterior pole area. Extrusomes in oral bulge and scattered in cytoplasm, fusiform to lanceolate, about 4–6 × 1 µm, those in cytoplasm impregnate faintly with protargol (Fig. 46a, b). Cortex very flexible, contains rows of minute, colourless granules. Cells colourless, but usually dark at low magnification (≤ ×100) because packed with lipid droplets and macronuclear nodules. Likely feeds on ciliates, as indicated by the lipid droplets. Swims rather rapidly by rotation about main body axis.

Cilia about 12 µm long, form nice metachronal waves, arranged in about 17 bipolar, equidistant rows slightly curved and more densely ciliated in oral area; some rows shortened anteriorly and loosely ciliated. Brush inconspicuous, consists of two rows occupying about 18% of body length; row 1 composed of 3–4 µm long, distally slightly inflated bristles, row 2 consists of 2–3 µm long bristles associated with the anterior basal body of the dikinetids and of 4–5 µm long, distally slightly inflated bristles associated with the posterior basal body of the dikinetids (Fig. 46a, c, e–h).

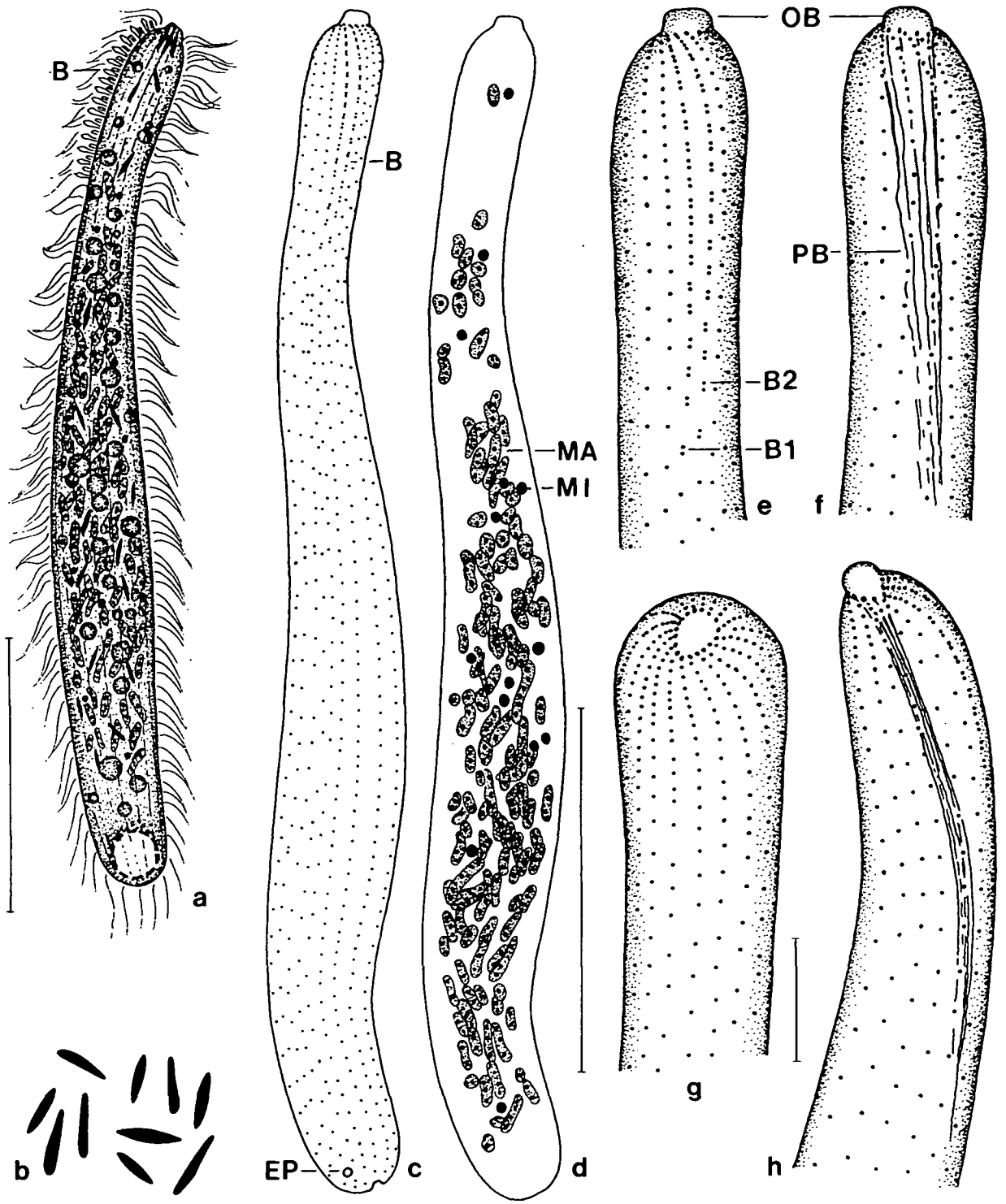

Fig. 46a–h. *Enchelaria multinucleata* from life (a, b) and after protargol impregnation (c–h). **a:** Right side view of a representative specimen packed with macronuclear nodules and lipid droplets. **b:** Extrusomes, 4–6 µm long. **c, d:** Ciliary pattern of dorsal side and nuclear apparatus of holotype specimen, which has 140 macronuclear nodules and 14 micronuclei. **e, f:** Ciliary pattern of dorsal and ventral anterior portion of specimen shown in figure 46c. **g, h:** Oblique frontal and dorsolateral view showing ovate oral bulge and slightly enlarged granule (dikinetid?) at anterior end of kineties. B – dorsal brush, B1, 2 – dorsal brush rows, EP – excretory pore of contractile vacuole, MA – macronuclear nodules, MI – micronucleus, OB – oral bulge, PB – pharyngeal basket. Scale bars 50 µm (a, c, d) and 10 µm (g, h).

Oral apparatus occupies anterior pole area (Fig. 46a, e–h; 307b). Oral bulge button-shaped and distinctly projecting from body proper in vivo and protargol preparations, ovate in frontal view with narrowed end directed to dorsal brush side. No distinct circumoral kinety: each ciliary row commences with a slightly enlarged granule, likely a dikinetid or an oralized somatic monokinetid; other oralized somatic kinetids not recognizable, not even in over-stained specimens. Oral basket laterally flattened, inconspicuous, although about 50 µm long, because composed of only few, widely spaced, fine rods originating from first kinetid of ciliary rows.

Occurrence and ecology: To date found only at type location, where it occurred two weeks after rewetting the sample. Abundance was very low, that is, about 30 cells in 16 slides. With its slender body, the species is well-adapted to the sandy habitat.

Comparison with related species: *Enchelaria* is monotypic, and *E. multinucleata* is easily identified, both in vivo and protargol slides, by the slender body, the numerous macronuclear nodules, the fusiform extrusomes, and the two dorsal brush rows. We did not find a similar species in the literature. However, several marine ciliates, such as *Chaenea vorax* and *Helicoprorodon* spp. have a similar shape and nuclear apparatus.

As mentioned above, we found a second *Enchelaria* species at site (49). It is about 200 × 30 µm in size, has a long macronucleus, rows of body extrusomes, three dorsal brush rows, and a

Table 37. Morphometric data on *Enchelaria multinucleata*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	140.1	147.0	24.4	6.5	17.5	100.0	172.0	14
Body, width	21.3	20.0	3.4	0.9	16.0	16.0	27.0	14
Body length:width, ratio	6.7	7.0	1.7	0.4	24.6	5.0	9.0	14
Macronuclear nodules, length	5.6	6.0	2.1	0.6	37.7	2.0	9.0	14
Macronuclear nodules, width	2.2	2.0	–	–	–	2.0	3.0	14
Macronuclear nodules, number	127.1	125.0	35.3	9.4	27.8	55.0	200.0	14
Micronuclei, diameter	2.0	2.0	0.0	0.0	0.0	2.0	2.0	14
Micronuclei, number	8.7	12.0	4.0	1.3	45.8	4.0	12.0	9
Somatic kineties, number in mid-body	16.7	16.0	2.6	0.7	15.6	14.0	22.0	14
Kinetids in a right lateral kinety, number	75.8	78.0	17.4	4.7	23.0	42.0	102.0	14
Dorsal brush rows, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	16
Circumoral kinety to end of brush row 1, distance	25.9	25.0	6.5	1.8	25.1	19.0	39.0	13
Circumoral kinety to end of brush row 2, distance	23.9	24.0	4.9	1.4	20.3	17.0	32.0	13
Dikinetids in brush row 1, number	20.8	21.0	3.8	1.1	18.2	15.0	28.0	12
Dikinetids in brush row 2, number	19.7	19.0	3.8	1.1	19.4	14.0	25.0	12
Oral bulge, width	4.2	4.0	0.8	0.2	20.0	3.0	5.0	12
Oral bulge, height	2.4	2.0	–	–	–	2.0	3.0	12

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

distinctly obovate oral bulge. The oral ciliature is as described in *E. multinucleata*, and there is no indication of oralized somatic monokinetids at the anterior end of the ciliary rows. Unfortunately, we cannot name this species because we did not observe it in vivo and the slides contain only five specimens. The rows of body extrusomes and the three-rowed dorsal brush suggest that it is even a new enchelariid genus.

Phialinides armatus **nov. spec.** (Fig. 47a–j; 327m, n; Table 38)

Diagnosis: Size in vivo 140 × 10 µm when fully extended, on average 100 × 11 µm in protargol preparations. Cylindroidal with head and oral bulge distinctly set off from body proper. On average 29 scattered macronuclear nodules and 9 ciliary rows. Extrusomes drumstick-shaped and about 30 × 1 µm in size.

Type location: Rain forest soil from a small island in the Amazon River, Brazil, about 20 km east of the town of Manaus, Janauari region, 04°S 60°W.

Etymology: The Latin adjective *armatus* (armed) refers to the extraordinary extrusomes.

Description: Size about 80–150 × 8–18 µm in vivo when fully extended, usually, however, more or less distinctly contracted and near 110 × 12 µm; contracts and extends slowly up to 30%, real size thus difficult to determine; usually, however, very slender with an average length:width ratio of 9–10:1 in protargol preparations (Table 38). Shape cylindroidal to slightly cuneate or fusiform; unflattened; head distinctly set off from body proper, appears as a minute process in swimming specimens (Fig. 47a–c, h; 327n). Most macronuclear nodules scattered in middle third of cell; individual nodules small and globular to elongate ellipsoidal, on average 4 × 3 µm in vivo and protargol preparations; nucleoli inconspicuous. Micronuclei not recognizable. Contractile vacuole in posterior body end. Most extrusomes attached to oral bulge, form a conspicuous, posteriorly diverging bundle in anterior third of cell; individual extrusomes drumstick-shaped or obclavate, about 25–30 × 1 µm in size, broadened portion 6–10 µm long (Fig. 47a, e, i, j; 327m, n). Cortex very flexible, contains rows of rather loosely spaced, colourless granules about 0.3 µm across. Cytoplasm colourless, contains many small food vacuoles with loose content and some fat globules 1–3 µm across. Likely feeds on protists. Swims rapidly, but does not dart like most congeners.

Cilia 7–8 µm long in vivo, arranged in an average of nine meridional, equidistant rows, not spiralling in contracted specimens; loosely spaced, except in anterior trunk region, where each kinety has an average of three dikinetids or trikinetids, some of which have 3 µm long bristles (Fig. 47a, f–h, j; Table 38).

Head and oral bulge rather conspicuous because about 10 µm long in vivo and distinctly set off from body proper. Head barrel-shaped, of usual structure, anteriorly limited by a dikinetidal circumoral kinety, posteriorly by a girdle of widely spaced cilia. Oral bulge discoidal to cylindroidal, contains tip of extrusomes (Fig. 47a, f–j; 327n; Table 38).

Occurrence and ecology: To date found only at type location, viz., a floodplain rainforest soil at the Amazon River (detailed site description in FOISSNER 1997d, site 22). The species is well adapted to soil life by its slender body. The large extrusomes indicate that it is an effective predator. Abundance was very low in the non-flooded Petri dish culture.

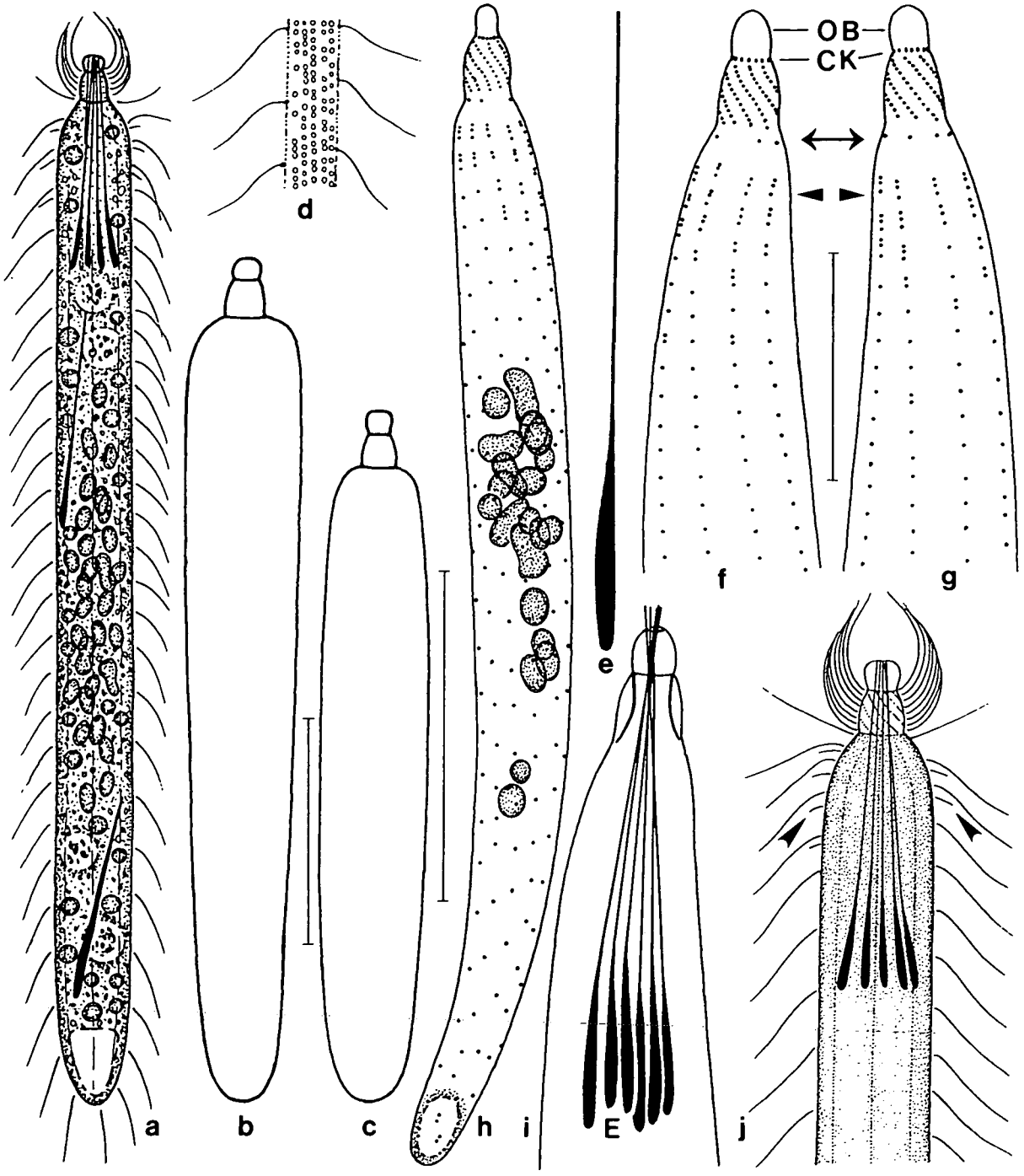

Fig. 47a–j. *Phialinides armatus* from life (a–e, j) and after protargol impregnation (f–i). **a–c:** A slender, likely completely extended specimen, slightly (b) and fully (c) contracted (drawn to scale). **d:** Surface view showing inconspicuous cortical granulation. **e:** Resting extrusome, length 30 µm. **f, g, i:** Anterior body portion of same specimen, showing oral and somatic ciliary pattern and extrusomes. Arrows mark ciliary girdle at base of head, that is, the main feature of the genus *Phialinides*. Arrowheads denote dorsal brush comprising di- and trikinetids. **h:** Ciliary and nuclear pattern of holotype specimen. **j:** Anterior body portion, slightly schematized. Arrowheads mark bristles of dorsal brush. CK – circumoral kinety, E – extrusomes, OB – oral bulge. Scale bars 30 µm (a–c, f–h).

Comparison with related species: This population belongs to *Phialinides* because it has a ciliary girdle between head and trunk (FOISSNER 1988a). *Phialinides armatus* is a very distinct species distinguished from all members of the family by the large, drumstick-shaped extrusomes and the numerous macronuclear nodules. All other described species have shorter, rod-shaped or fusiform extrusomes and less than 15 macronuclear nodules.

Table 38. Morphometric data on *Phialinides armatus* (upper line) and *Phialina minima* (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, total length	97.3	103.0	18.2	4.7	18.7	61.0	120.0	15
	75.0	74.0	10.2	3.2	13.7	58.0	95.0	10
Body, width	11.5	11.0	1.9	0.5	16.1	9.0	16.0	15
	14.9	14.0	2.1	0.7	14.0	11.0	18.0	10
Body length:width, ratio	9.0	9.6	2.3	0.6	25.7	5.5	12.0	15
	5.1	5.0	0.7	0.2	13.7	4.1	6.6	10
Oral bulge plus head, length	8.0	8.0	0.7	0.2	8.2	7.0	9.0	15
	11.4	11.0	1.1	0.3	9.4	10.0	14.0	10
Oral bulge, length	2.8	3.0	0.5	0.1	16.5	2.0	4.0	15
	4.3	4.0	0.8	0.3	19.1	3.0	6.0	10
Oral bulge, width	3.0	3.0	–	–	–	2.5	4.0	15
	5.9	6.0	0.7	0.2	12.5	5.0	7.0	10
Head, width	5.0	5.0	0.3	0.1	6.0	4.0	6.0	15
	8.4	8.0	1.1	0.3	12.8	7.0	10.0	10
Anterior body end to first macronuclear nodule, distance	30.3	33.0	9.7	2.5	32.0	9.0	43.0	15
	29.9	29.0	5.5	1.7	18.5	20.0	38.0	10
Anterior body end to somatic kineties on trunk, distance	10.7	11.0	0.7	0.2	6.6	10.0	12.0	15
	–	–	–	–	–	–	–	–
Macronuclear nodules, length	3.8	4.0	0.9	0.2	23.0	3.0	6.0	15
	19.6	20.0	1.7	0.5	8.7	17.0	22.0	10
Macronuclear nodules, width	2.4	3.0	–	–	–	2.0	3.0	15
	7.2	7.0	0.8	0.2	11.0	6.0	8.0	10
Macronuclear nodules, number	29.3	28.0	7.0	1.8	23.8	21.0	46.0	15
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10
Ciliary rows, number	9.1	9.0	1.0	0.3	10.6	8.0	11.0	15
	15.4	15.0	0.8	0.3	5.5	14.0	17.0	10
Brush pairs or triplets in a kinety, number	3.5	3.0	0.7	0.2	21.4	2.0	5.0	15
	2.8	3.0	0.8	0.2	28.2	2.0	4.0	10
Kinetids in a ciliary row, total number [b]	29.3	29.0	5.8	1.7	19.9	20.0	39.0	15
	38.0	37.0	9.3	2.9	24.5	26.0	55.0	10

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Dikinetids and trikinetids at anterior end of ciliary rows each counted as one kinetid.

Phialina minima (KAHL, 1927) **nov. comb.** (Fig. 48a–e; Table 38)

1927 *Lacrymaria minima* KAHL, Arch. Protistenk., 60: 103.

Material: Soil from the surroundings of the Mzima Springs in the Tsavo National Park West, Kenya, 03°S 38°E.

Description of Kenyan population: Size about 70–100 × 10–20 µm in vivo; length:width ratio near 6:1 in vivo and about 5:1 in protargol preparations. Elongate cylindroidal to fusiform because of gradually narrowing posterior body third. Head distinctly set off from body proper both in vivo and protargol preparations, barrel-shaped, about 11 × 8 µm in vivo. Oral bulge discoidal in vivo, conspicuously conical in protargol preparations. Acontractile, ciliary rows thus meridionally extending in prepared specimens. Macronucleus in body centre, elongate ellipsoidal (2.5–3:1), rarely ellipsoidal (2:1), with many minute nucleoli. Micronucleus attached to macronucleus, lenticular, 1.5–2 µm across. Contractile vacuole in posterior body end with short canal ending in pole area. Extrusomes mainly in centre of oral bulge and head, rod-shaped, about 15 µm long, often form conspicuous appendices when partially extruded in protargol preparations. Cytoplasm rather hyaline, contains few to many fat globules 3–5 µm across. Swims extremely rapidly, frequently changing direction.

Ordinary somatic cilia about 10 µm long, brush dikinetids associated with about 5 µm long bristles, likely originating from anterior basal body. Somatic and oral ciliary pattern as in other members of genus. Brush at anterior end of kineties frequently contains basal body triplets.

Occurrence and ecology: KAHL (1927b) discovered *P. minima* in a sapropelic pond near Hamburg, Germany. We found it at various sites of Namibia (Table 4) and in Kenya, where it occurred in an alkaline (pH 8.6) sample containing soil and litter from the forest surrounding the Mzima Springs in the Tsavo National Park West. Most samples were saline, indicating that *P. minima* is a euryhaline species.

Generic classification and comparison with related species: This species belongs to *Phialina* according to the classification by FOISSNER (1983b). Phialinas of the type described above are difficult to identify, and many species have been described over the years, mainly from limnetic and marine coastal biotopes (KAHL 1930a, VUXANOVICI 1963), but also from terrestrial habitats (FOISSNER 1998a). Although the African population is probably a new species, we identify it with *Lacrymaria minima* KAHL, 1927b, mainly because of the rather similar shape (Fig. 48e). However, we do not neotypify the species with our material because it is from a different biogeographic region (Africa vs. Europe) and habitat (soil vs. sapropelic pond), has a different size (70–100 µm vs. about 60 µm), a different location of the contractile vacuole (terminal vs. subterminal), and KAHL (1927) did not observe the nuclear apparatus.

Phialina vertens STOKES, 1885, as redescribed by FOISSNER (1983b) and SONG & WILBERT (1989), is also rather similar to the Kenyan specimens. However, the original figure, which shows a dumb-bell-shaped organism with broadly rounded posterior end (Fig. 48f), argues against conspecificity.

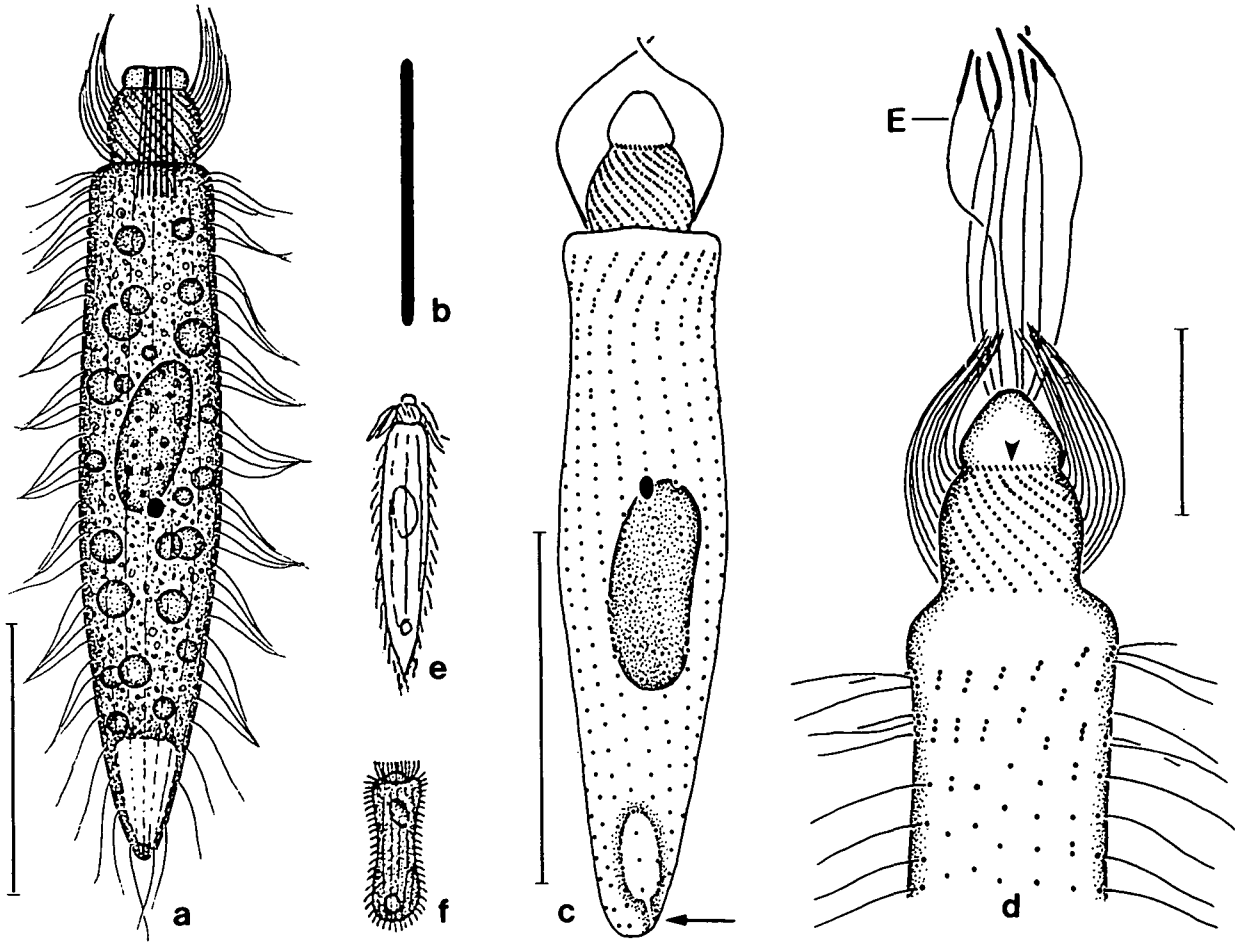

Fig. 48a–e. *Phialina minima* from life (a, b, e) and after protargol impregnation (c, d). **a:** A representative specimen with lipid droplets. **b:** Extrusome, length 15 µm. **c:** Total view of ciliary pattern and nuclear apparatus. Arrow marks canal of contractile vacuole. **d:** Anterior body portion of a specimen, with partially extruded toxicysts (E) at higher magnification. Arrowhead marks circumoral kinety composed of dikinetids. **e:** Original illustration, length 50 µm (KAHL 1927b) or 60 µm (KAHL 1930a). Scale bars 10 µm (d) and 30 µm (a, c).

Fig. 48f. *Phialina vertens*, length 85 µm (from STOKES 1885).

Spathidium seppelti PETZ & FOISSNER, 1997

Extended diagnosis (to include subspecies *etoschense*): Size about 120 × 25 µm or 150 × 30 µm in vivo. Spatulate with conspicuous, distinctly slanted, slenderly elliptical oral bulge one or two thirds longer than maximum postoral width, and with or without conical depression. About 65 or > 100 ellipsoidal macronuclear nodules. Extrusomes rod-shaped, 3–4 µm or

5–6 µm long. On average 21 or 28 ciliary rows, 3 anteriorly differentiated to moderately conspicuous dorsal brush occupying 22% or 29% of body length. Brush row 1 composed of 14 or 27 dikinetids, row 2 of 18 or 40, and row 3 of 8 or 27 dikinetids on average.

Remarks: We split this species into two subspecies for the reason discussed under *S. seppelti etoschense*.

Spathidium seppelti seppelti PETZ & FOISSNER, 1997 **nov. stat.**

Diagnosis: Size about 80–140 × 20–40 µm. Oral bulge with obconical depression and about one third longer than maximum postoral width. Approximately 100–200 macronuclear nodules. Extrusomes 3–4 µm long. On average 21 ciliary rows, with longest brush row occupying 22% of body length. Brush row 1 composed of 14 dikinetids, row 2 of 18, and row 3 of 8 dikinetids on average.

Type location: Algal ornithogenic soil near an Adelie penguin rookery, north coast of Shirley Island, Windmill Islands, continental Antarctica, 66°17'S 110°29'E.

Description: See PETZ & FOISSNER (1997).

Spathidium seppelti etoschense **nov. sspec.** (Fig. 49a–q; 322a–j; Tables 39, 40)

Diagnosis: Size about 130–200 × 25–40 µm. Oral bulge about two thirds longer than maximum postoral width, without obconical depression. Approximately 55–90 macronuclear nodules. Extrusomes 5–6 µm long. On average 28 ciliary rows, with longest brush row occupying 29% of body length. Brush row 1 composed of 27 dikinetids, row 2 of 40, and row 3 of 27 dikinetids on average.

Type location: Soil from margin (*Sporobolus* grass girdle) of Etosha Pan, Namibia, 19°10'S 15°55'E (site 60 in figures 2, 3 and chapter 2.1.2).

Etymology: Named after the site discovered.

Description: Size 130–200 × 25–40 µm in vivo, usually about 150 × 30 µm; length:width ratio highly variable, that is, 4–8:1, on average 5.4:1 in protargol preparations (Table 39), cells with just ingested prey distinctly stouter. Spatulous, oral area often conspicuously axe-shaped, flattened leaf-like and thus hyaline, more or less distinctly set off from cylindroidal, opaque trunk by slightly narrowed neck; posterior body portion slightly tapering and evenly rounded (Fig. 49a, l–p). Acontractile but very flexible, can actively curve oral region laterally by up to 90° (Fig. 49k). Macronuclear nodules scattered throughout trunk, globular to distinctly ellipsoidal (up to 10:1, on average about 2:1; Table 39), contain 1–2 globular nucleoli (Fig. 49e, h; 322i). Many micronuclei 1.5–2 µm across scattered between macronuclear nodules, exact number difficult to determine because usually hard to distinguish from similarly sized cytoplasmic fat globules. One contractile vacuole with about 6 excretory pores in centre of posterior pole. Two types of extrusomes: type I in oral bulge and cytoplasm, rod-

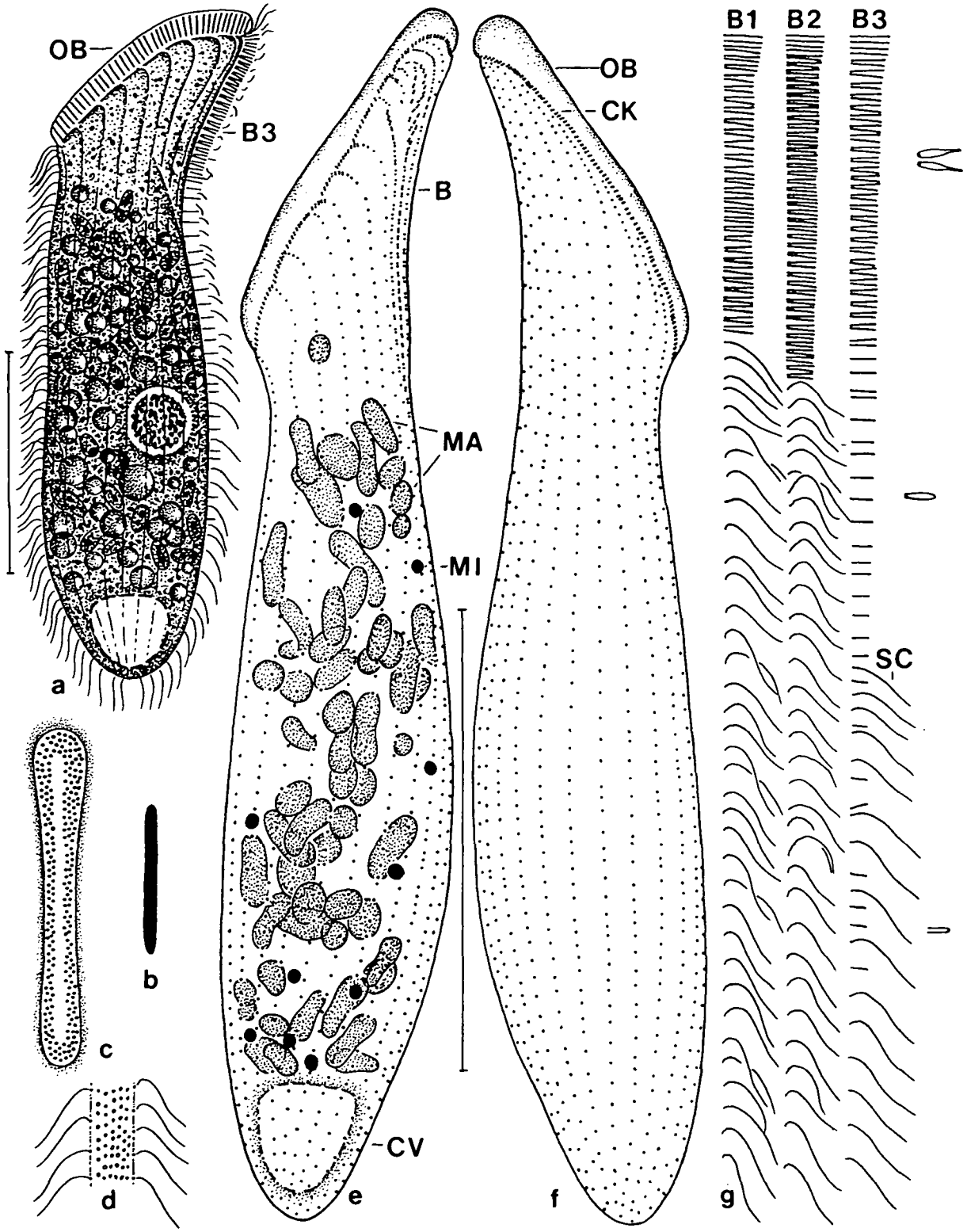

Fig. 49a–g. *Spathidium seppelti etoschense* from life (a–d, g) and after protargol impregnation (e, f). **a:** Left side view of a representative specimen. **b:** Oral bulge extrusome, 5–6 µm long. **c:** Frontal view of oral bulge studded with extrusomes. **d:** Surface view showing cortical granulation. **e, f:** Infraciliature of left and right side of holotype specimen. **g:** Structure of dorsal brush; shape of brush cilia shown at right. B(1-3) – dorsal brush (rows), CK – circumoral kinety, CV – contractile vacuole, MA – macronuclear nodules, MI – micronuclei, OB – oral bulge, SC –somatic cilia. Scale bars 50 µm.

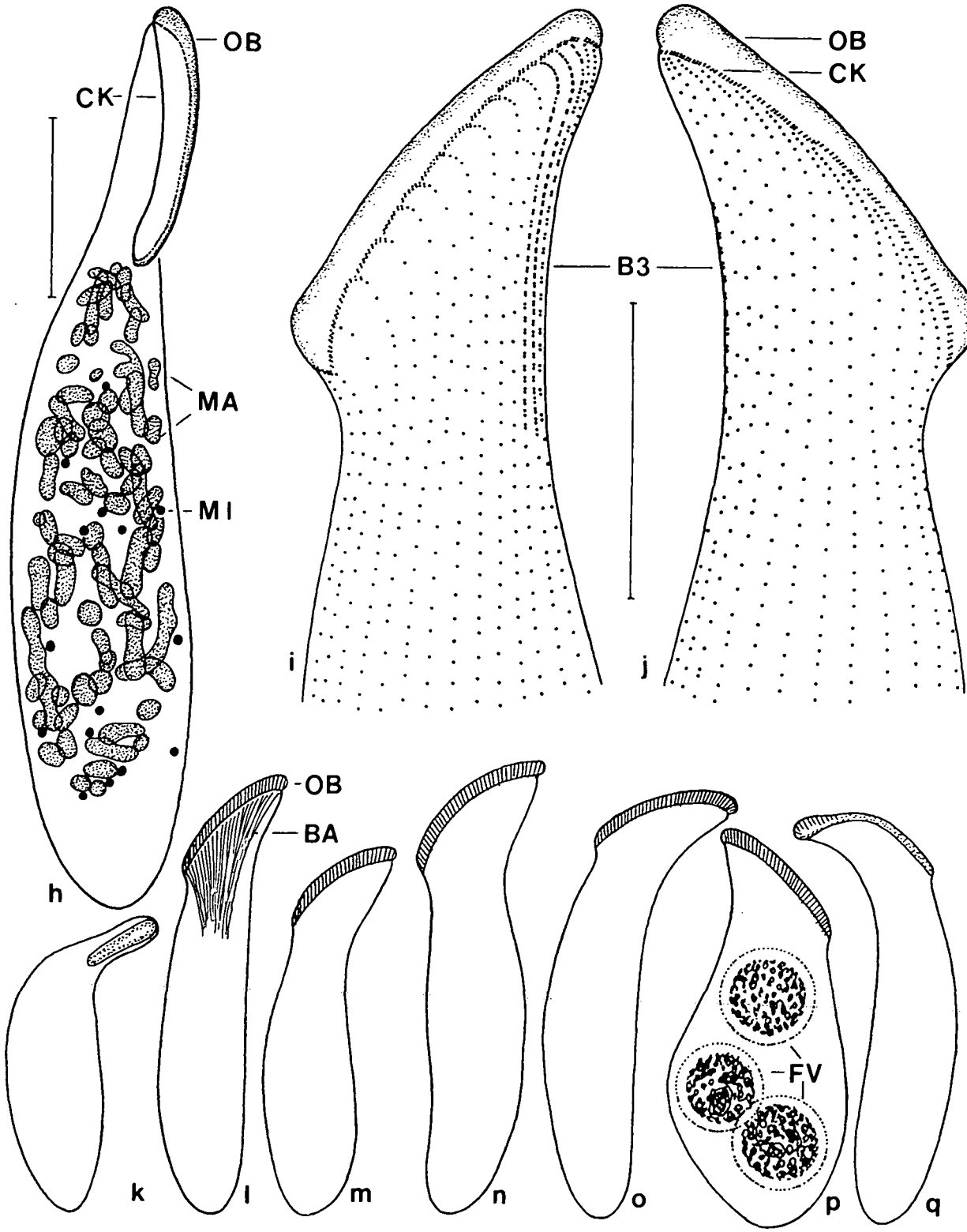

Fig. 49h–q. *Spathidium seppelti etoschense* from life (k–q, video records) and after protargol impregnation (h–j). **h:** Dorsal view. **i, j:** Infraciliature of left and right side. **k:** Specimen with oral region curved laterally by about 90°. **l–o, q:** Shape variability. **p:** Specimen with three newly formed food vacuoles. BA – oral basket, B3 – dorsal brush row, CK – circumoral kinety, FV – food vacuoles, MA – macronuclear nodules, MI – micronucleus, OB – oral bulge. Scale bars 30 µm.

shaped with slightly narrowed, rounded ends, 5–6 µm long (Fig. 49a–c; 322a–g); type II recognized only in the cytoplasm of silver carbonate-impregnated specimens, rod-shaped, about 3 µm long (Fig. 322b–d, i). Cortex very flexible, contains about 6 rows of minute (~0.3 µm), colourless granules between each two ciliary rows. Cytoplasm more or less densely packed with 1–7 µm-sized fat globules, except for flat and hyaline oral portion, depending on nutrition (Fig. 49a). Feeds on ciliates, in pure cultures mainly on *Halteria grandinella*. Swims rather clumsily but creeps versatilely on soil particles, showing great flexibility (Fig. 49k).

Somatic cilia about 12 µm long in vivo, slightly irregularly spaced, arranged in an average of 28 bipolar, equidistant rows, those of right side attached to circumoral kinety at acute angles, while those of left side, which have 2–6 closely spaced cilia at anterior end, abut at right angles (Fig. 49e, f, i, j; 322b–d, f, g). Dorsal brush three-rowed, a fourth short row occurred in 2 out of 20 specimens investigated; dikinetidal portion of all rows of about same length, but number of dikinetids distinctly higher in row 2 than in rows 1 and 3; rows 1 and 2 consist of about 5 µm long, fusiform bristles, which elongate to 6–7 µm near anterior end of cell, row 2 fragmented anteriorly in about half of specimens; row 3 like rows 1 and 2 in dikinetidal portion, but continuing as a long, monokinetidal tail to near posterior body end with 2.5–3 µm long, rod-shaped bristles irregularly alternating with ordinary somatic cilia in posterior body half; all brush kineties continue posteriorly as ordinary somatic kineties (Fig. 49a, e, g, i; 322h; Table 39).

Table 39. Morphometric data on *Spathidium seppelti etoschense*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	133.5	130.0	17.6	4.6	13.2	114.0	170.0	15
Body, width	25.1	25.0	3.8	1.0	15.1	20.0	32.0	15
Oral bulge, length	40.9	40.0	3.9	1.0	9.6	35.0	50.0	15
Macronuclear nodules, length	6.3	6.0	2.1	0.5	33.2	4.0	11.0	15
Macronuclear nodules, width	3.1	3.0	0.7	0.2	24.0	1.0	4.0	15
Micronucleus, largest diameter	1.9	2.0	–	–	–	1.6	2.0	15
Extrusomes, length	3.9	4.0	0.4	0.1	10.7	3.0	5.0	15
Brush kinety 1, length [b]	34.0	33.0	4.3	1.1	12.6	30.0	41.0	15
Brush kinety 2, length [b]	38.1	37.0	4.1	1.1	10.8	33.0	45.0	15
Brush kinety 3, length [b]	35.5	35.0	2.9	0.7	8.0	31.0	40.0	15
Dikinetids in brush row 1, number	26.8	27.0	3.7	0.9	13.8	19.0	33.0	16
Dikinetids in brush row 2, number	40.6	40.0	5.5	1.4	13.6	28.0	50.0	16
Dikinetids in brush row 3, number	26.6	27.0	2.8	0.7	10.5	20.0	31.0	16
Macronuclear nodules, number	67.3	65.0	11.1	2.9	16.5	55.0	90.0	15
Somatic ciliary rows, number	28.1	28.0	3.2	0.8	11.5	23.0	35.0	15
Basal bodies in a left kinety, number	64.7	62.0	10.8	2.8	16.7	51.0	92.0	15
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a wheat grain culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Distance between circumoral kinety and last dikinetid of row.

Oral bulge on average twice as long as maximum postoral width, inclined about 45° to ventral side, narrowly elliptical with dorsal end rather distinctly inflated, bright because packed with extrusomes; base surrounded by an elongate-elliptical circumoral kinety composed of closely spaced dikinetids, which give rise to fine nematodesmata forming rather conspicuous basket. No conical depression in bulge area (Fig. 49e, f, h–j, l; 322a, b, d, f, j; Table 39).

Occurrence and ecology: To date found only at various sites around the Etosha Pan. Euryhaline.

Table 40. Comparison of main morphometrics from multinucleate spathidiids. SE – *Spathidium seppelti etoschense* (present paper), SS – *Spathidium seppelti seppelti* (from PETZ & FOISSNER 1997), AM – *Arcuospathidium multinucleatum* (from FOISSNER 1999b), ER – *Epispathidium regium* (from FOISSNER 1984).

Characteristics [a]	Species	$\bar{x}$	CV	Min	Max	n
Body, length	SE	133.0	13.0	114.0	170.0	15
	SS	99.0	16.0	68.0	131.0	30
	AM	140.0	12.0	103.0	192.0	30
	ER	166.0	25.0	132.0	260.0	8
Body, width	SE	25.0	15.0	20.0	32.0	15
	SS	25.0	18.0	18.0	33.0	30
	AM	20.0	13.0	12.0	35.0	30
	ER	54.0	19.0	42.0	72.0	8
Body length:width, ratio	SE	5.4	–	–	–	15
	SS	4.0	–	–	–	30
	AM	7.0	–	–	–	30
	ER	3.1	–	–	–	8
Somatic ciliary rows, number	SE	28.0	12.0	23.0	35.0	15
	SS	21.0	9.0	18.0	25.0	16
	AM	15.0	10.0	11.0	19.0	30
	ER	41.0	8.0	36.0	46.0	8
Macronuclear nodules, number	SE	67.0	17.0	55.0	90.0	15
	SS	> 100	–	100.0	200.0	10
	AM	40.0	27.0	14.0	65.0	30
	ER		about 100			8
Conical depression in oral bulge	SE		absent			15
	SS		present			30
	AM		present			30
	ER		absent			8

[a] Data based on protargol-impregnated (FOISSNER's method for *S. seppelti etoschense*, *A. multinucleatum*, and *E. regium*; WILBERT's method for *S. seppelti seppelti*), mounted specimens from non-flooded Petri dish cultures. CV – coefficient of variation in %, Min – minimum, Max – maximum, n – number of individuals investigated, $\bar{x}$ – arithmetic mean.

Comparison with related species: There are three well-known spathidiids that are similar to *S. seppelti etoschense*, especially in having a similar size, shape, and many macronuclear nodules (Table 40); they are easily confused, especially in vivo. Further similar, poorly known species are discussed in PETZ & FOISSNER (1997). The population from the Etosha Pan is most similar to *S. seppelti seppelti* discovered by PETZ & FOISSNER (1997) in Antarctica, except for many morphometric features, which only slightly overlap (Table 40). However, there is also a differing morphological feature, viz., the conical depression in the dorsal third of the oral bulge, which is lacking in the Namibian population. Thus, it could also be considered as a distinct species. However, the conical depression in the oral bulge of several spathidiids is a rather new feature, whose taxonomical significance cannot yet be reliably estimated. Thus, we prefer to give the African population subspecies rank at the present state of knowledge.

Spathidium turgitorum **nov. spec.** (Fig. 50a–r, 51a–y, 52a–p; 323a–v, 324a–t; Tables 41–43)

Diagnosis: Size about 160 × 15 µm in vivo. Cylindroidal with oblique, obovate, thick oral bulge about as wide as cell. On average 56 scattered macronuclear nodules. Extrusomes slenderly rod-shaped, 3–4 µm long. On average 11 ciliary rows, 3 anteriorly differentiated to inconspicuous dorsal brush occupying 15% of body length.

Type location: Highly saline soil from Etosha Pan, Namibia, 19°S 15°50'E (site 54 in figures 2, 3 and chapter 2.1.2).

Etymology: Composite of the Latin adjective *turgidus* (thick, inflated) and the Latin noun *torus* (bulge), referring to the comparatively conspicuous oral bulge.

Description: Several populations and ontogenesis were studied. Although conspecificity is likely, the observations are kept separate and the diagnosis and description contain only data from Namibian site (54) specimens.

Size 130–200 × 10–20 µm in vivo, usually near 160 × 15 µm when well-growing; slightly smaller and stouter in declining state, viz., 100–200 × 10–25 µm, usually about 140 × 16 µm in vivo; length:width ratio also highly variable, usually, however, near 10:1 both in vivo and protargol preparations (Table 41). Shape conspicuous because like a rod or very elongate spindle, even if well-fed; indeed, swimming cells look like moving sticks; flattened only in oral region (Fig. 50a–e, j). Macronuclear nodules highly scattered, leaving blank only body ends; individual nodules globular to elongate ellipsoidal, on average about 5 × 3 µm, contain globular and lobate nucleoli (Fig. 50a, k). Micronuclei globular, exact number could be not counted because of many similarly sized and impregnated cytoplasmic inclusions. Contractile vacuole in rear end, some excretory pores in posterior pole area. Extrusomes accumulated in oral bulge and scattered in cytoplasm, rod-shaped with rounded ends, slightly curved, fine, viz. 3–4 × < 0.5 µm. Cortex inconspicuous, very flexible, contains loosely spaced, minute (~ 0.2 µm), colourless granules, which can be extruded (Fig. 323u, v). Cytoplasm colourless,

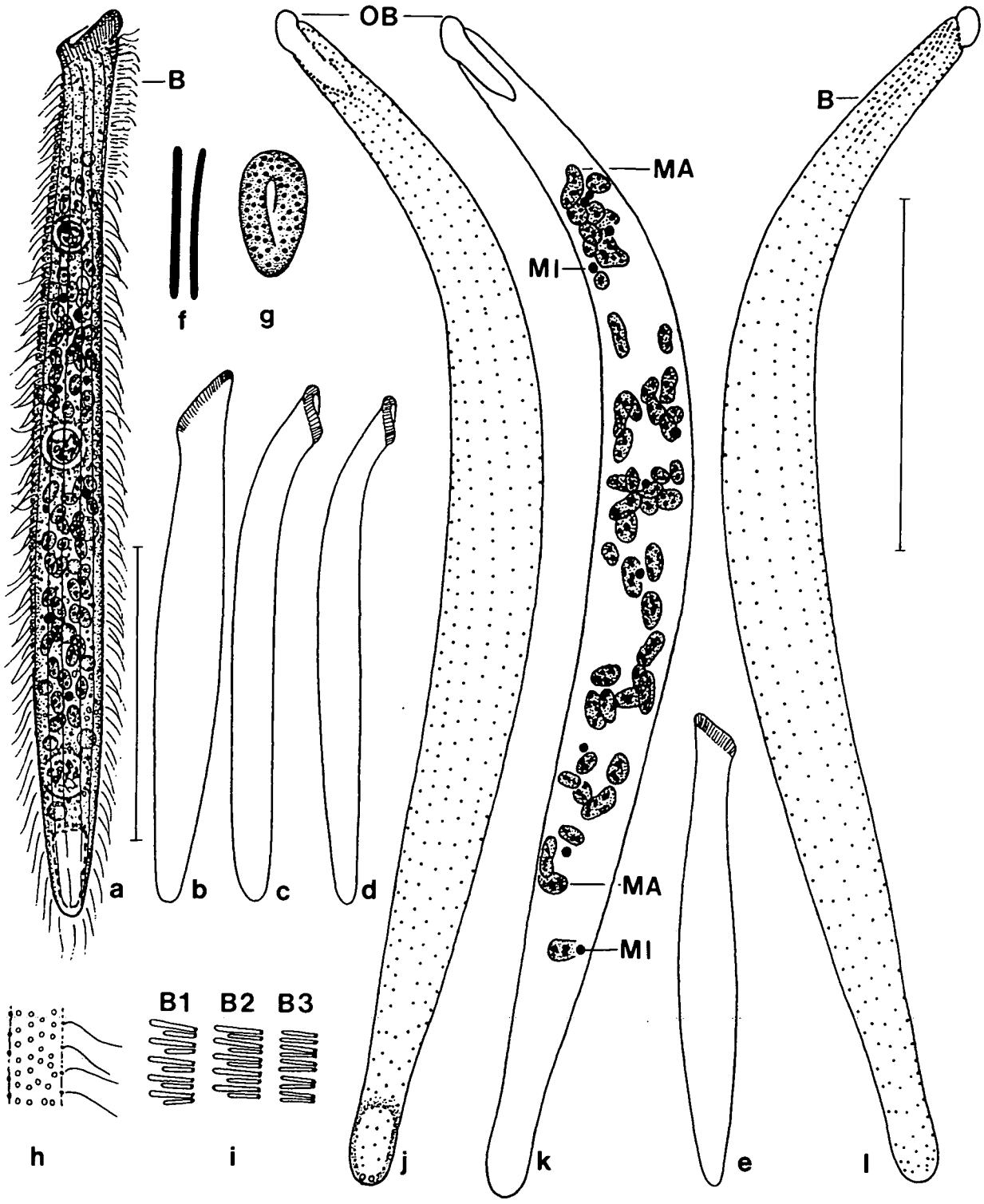

Fig. 50a–l. *Spathidium turgitorum*, Namibian site (54) specimens from life (a–i) and after protargol impregnation (j–l). **a:** Left side view. **b–e:** Shape variants, those shown in (b, e) are dark, well-nourished individuals. **f:** An extrusome seen from two sides, length 3–4 µm. **g:** Frontal view of oral bulge. **h:** Surface view showing loose cortical granulation. **i:** Middle portion of dorsal brush. **j–l:** Ciliary pattern of ventral and dorsal side and nuclear apparatus of holotype specimen. B1, 2, 3 – dorsal brush rows, MA –macronuclear nodules, MI – micronuclei, OB – oral bulge. Scale bars 50 µm (a, j–l).

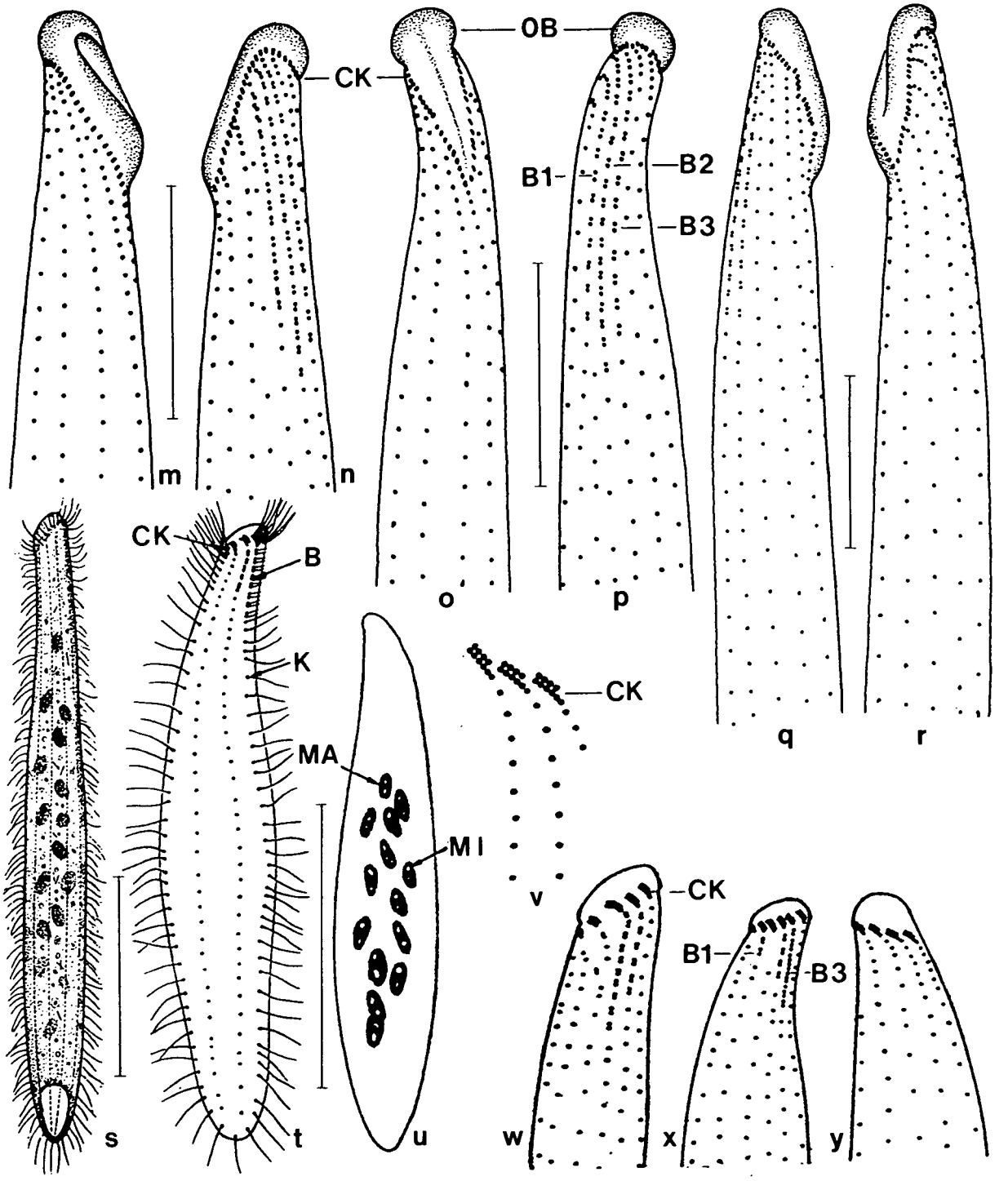

Fig. 50m–r. *Spathidium turgitorum*, somatic and oral ciliary pattern in anterior body region of Namibian site (54) specimens after protargol impregnation. **m, n:** Ventrolateral and dorsolateral view. **o, p:** Ventral and dorsal view showing the hemispherical oral bulge in optical section. **q, r:** Right and left side view. Scale bars 15 µm.

Fig. 50s–y. *Protospathidium muscicola* from life (s) and after protargol impregnation (t–y). Scale bars 30 µm (s–u). From DRAGESCO & DRAGESCO-KERNÉIS (1979). B – dorsal brush, B1, 2, 3 – dorsal brush rows, CK – circumoral kinety (fragments), K – somatic kinety, MA – macronuclear nodule, MI – micronucleus, OB – oral bulge.

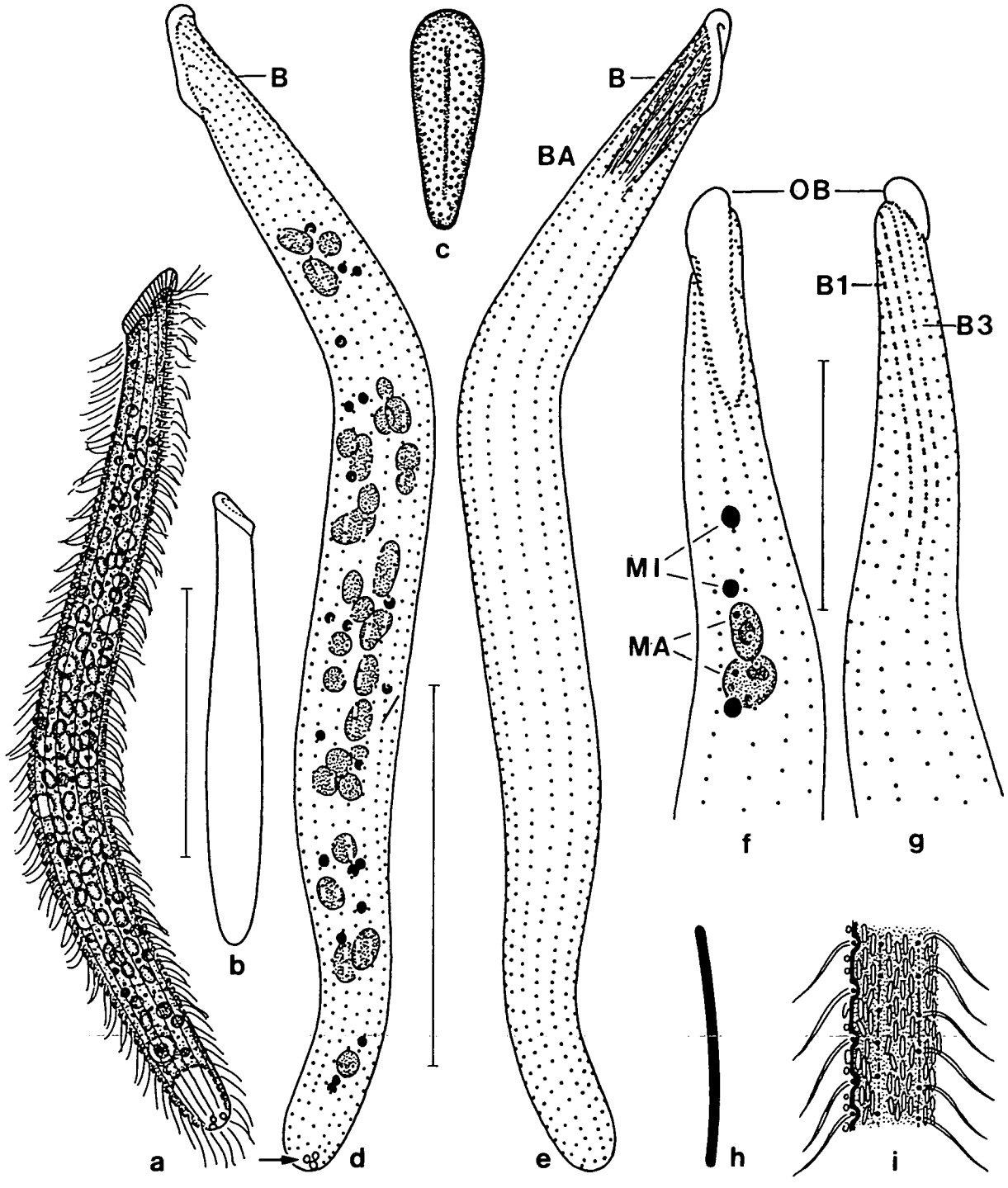

Fig. 51a–i. *Spathidium turgitorum*, Tunisian specimens from life (a–c, h, i) and after protargol impregnation (d–g). **a:** Left side view of a representative specimen. **b:** Shape variant. **c:** Frontal view of oral bulge, which is studded with extrusomes. **d, e:** Ciliary pattern of left and right side and nuclear apparatus of same specimen. Arrow marks excretory pores of contractile vacuole. **f, g:** Somatic and oral ciliary pattern of anterior ventral and dorsal side of same specimen. **h:** Extrusome, length 6 µm. **i:** Surface view showing epipellicular bacterial rods. B – dorsal brush, B1, 3 – dorsal brush rows, BA – oral basket, MA – macronuclear nodules, MI – micronuclei, OB – oral bulge. Scale bars 60 µm (a, d, e) and 20 µm (f, g).

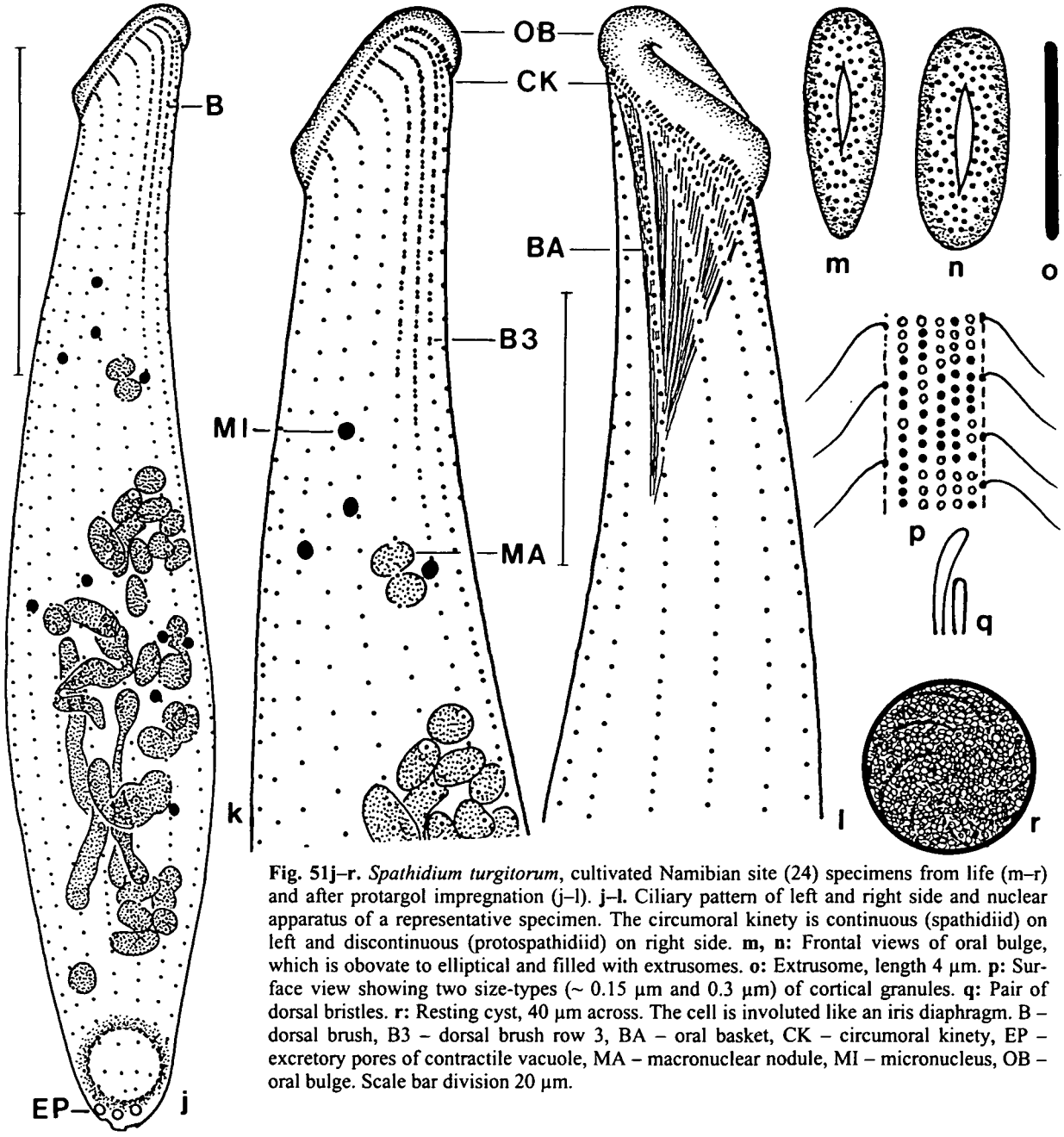

Fig. 51j–r. *Spathidium turgitorum*, cultivated Namibian site (24) specimens from life (m–r) and after protargol impregnation (j–l). **j–l.** Ciliary pattern of left and right side and nuclear apparatus of a representative specimen. The circumoral kinety is continuous (spathidiid) on left and discontinuous (protospathidiid) on right side. **m, n:** Frontal views of oral bulge, which is obovate to elliptical and filled with extrusomes. **o:** Extrusome, length 4 µm. **p:** Surface view showing two size-types (~ 0.15 µm and 0.3 µm) of cortical granules. **q:** Pair of dorsal bristles. **r:** Resting cyst, 40 µm across. The cell is involuted like an iris diaphragm. B – dorsal brush, B3 – dorsal brush row 3, BA – oral basket, CK – circumoral kinety, EP – excretory pores of contractile vacuole, MA – macronuclear nodule, MI – micronucleus, OB – oral bulge. Scale bar division 20 µm.

packed with macronuclear nodules and, in well-fed specimens, with fat globules and food vacuoles containing heterotrophic flagellates (*Polytomella*). Swims rather rapidly with anterior portion often slightly curved.

Cilia arranged in an average of 11 bipolar, equidistant, rather densely ciliated rows abutting on circumoral kinety in acute (at right side) or almost right (at left) angles, as is typical for the genus (FOISSNER 1984). Dorsal brush inconspicuous because occupying merely 15% of body length and bristles only up to 4 µm long; all rows of similar length and structure, anterior bristle of dikinetids of rows 1 and 2 slightly longer than posterior (Fig. 50a, i–r).

Table 41. Morphometric data on *Spathidium turgitorum* from Namibian site (54).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length [b]	154.3	152.0	17.5	4.0	11.3	120.0	188.0	19
Body, width [b]	13.6	13.0	1.9	0.4	13.7	10.0	16.0	19
Body length:width, ratio [b]	11.6	12.0	2.3	0.5	20.2	8.0	16.0	19
Body, length [c]	131.8	132.0	22.3	5.1	16.9	88.0	184.0	19
Body, width [c]	15.6	14.0	4.1	1.0	26.5	10.0	25.0	19
Body length:width, ratio [c]	8.9	9.0	2.5	0.6	27.7	4.0	13.0	19
Anterior body end to first macronuclear nodule, distance	21.1	21.0	6.3	1.5	30.1	10.0	36.0	19
Circumoral kinety to last dikinetid of brush row 1, distance	18.8	19.0	2.1	0.5	11.2	15.0	23.0	19
Circumoral kinety to last dikinetid of brush row 2, distance	22.5	23.0	2.3	0.5	10.4	18.0	26.0	19
Circumoral kinety to last dikinetid of brush row 3, distance	18.4	19.0	2.3	0.5	12.3	13.0	22.0	19
Oral bulge (circumoral kinety), length	10.8	11.0	1.8	0.4	16.8	8.0	15.0	19
Nuclear figure, length	104.6	100.0	15.8	3.6	15.1	80.0	140.0	19
Macronuclear nodules, length	5.3	5.0	1.7	0.4	31.4	3.0	10.0	19
Macronuclear nodules, width	2.6	3.0	0.6	0.1	22.5	2.0	4.0	19
Macronuclear nodules, number	56.0	52.0	14.3	3.3	25.5	40.0	97.0	19
Somatic kineties, number	11.4	12.0	1.2	0.3	10.7	10.0	15.0	19
Ciliated kinetids in a right side kinety, number	73.0	74.0	17.6	4.7	24.2	48.0	107.0	14
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
Dikinetids in brush row 1, number	13.5	13.0	1.9	0.4	14.1	11.0	18.0	19
Dikinetids in brush row 2, number	17.7	18.0	2.2	0.5	12.7	11.0	21.0	19
Dikinetids in brush row 3, number	13.1	13.0	2.9	0.7	22.2	9.0	22.0	18

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] From flourishing culture.

[c] From declining culture.

Oral bulge about as wide as widest trunk region, slanted approximately 45° to main body axis, conspicuous because rather thick and bright due to the extrusomes contained; obovate to cuneate in frontal view, ∞-like curved when viewed laterally. Circumoral kinety cuneate, composed of dikinetids occasionally rather irregularly arranged or forming distinct fragments, like in *Protospathidium* (Fig. 50a, j, k, m–r). Oral basket rods not impregnated.

Observations on Namibian site (24) population (Fig. 51j–r; 323a–v; Tables 42, 43): Specimens from the non-flooded Petri dish culture ("field material") and pure cultures (Eau de Volvic enriched with some crushed wheat grains to stimulate growth of small food organisms, such as *Colpoda* and *Polytomella*) were studied in vivo and the scanning electron microscope. The field specimens are highly similar to those from type location (Fig. 323a–h; Table 43), while the cultivated cells are considerably stouter, thus looking rather different (Fig. 323i–v; Tables 42, 43). However, all main cytological features (macronuclear nodules, extrusomes, number and arrangement of ciliary rows, structure of dorsal brush) are unchanged. The following additional observations should be mentioned

(Fig. 51j–r; 323a–v; Tables 42, 43): (i) The extrusomes are simple, straight rods with a size of about 4 × 0.3 μm; (ii) Usually, the oral bulge is cuneate, rarely obovate or elliptical; (iii) The dorsal brush bristles are slightly inflated and the posterior bristle of the dikinetids is slightly shorter than the anterior, except for row 3; (iv) The last and/or penultimate dikinetid of brush row 1 has an ordinary cilium associated with the posterior basal body in the six specimens investigated (Fig. 323c, d, g, h, k, l); (v) The monokinetidal tail of brush row 3 extends to the second third of the cell and is composed of single, rod-shaped bristles; (vi) The protospathidiid circumoral ciliary pattern is even more distinct than in field specimens, but only at the left side (Fig. 51j–l); (vii) The oral basket is of ordinary structure (Fig. 51l); (viii) Resting cysts are globular ($\bar{x}$ = 41.8 μm, M = 41 μm, SD = 4.5 μm, SE = 1.2 μm, CV = 10.8%, Min = 36 μm, Max = 52 μm, n = 15) and have a smooth, 1–1.5 μm thick wall with a bluish shimmer (not an optical artefact because recognizable also under interference contrast optics). The cell is involuted like an iris diaphragm within the cyst.

Observations on a Tunisian population (Fig. 51a–i; 324 l; Tables 42, 43): The Tunisian specimens match the type population in all main features, such as the number of ciliary rows and macronuclear nodules; the length:width ratio; the thick, ∞-shaped oral bulge; the extrusome shape; and the structure of the dorsal brush. Thus, conspecificity is beyond reasonable doubt. Differences occur in body length (longer by 18%), extrusome length (6 μm), and the shape of the oral bulge (more cuneate). Most Tunisian specimens were covered by epicortical bacteria (Fig. 51i).

Table 42. Morphometric data on *Spathidium turgitorum* from Namibian site 24 (upper line; pure culture) and Tunisia (lower line; ordinary non-flooded Petri dish culture).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	148.6	150.0	16.4	3.8	11.1	118.0	184.0	19
	182.8	190.0	31.9	9.6	17.5	147.0	243.0	11
Body, width	25.8	25.0	3.7	0.9	14.4	21.0	35.0	19
	16.5	17.0	2.7	0.8	16.1	11.0	20.0	11
Body length:width, ratio	5.9	6.0	0.9	0.2	15.0	3.8	7.1	19
	11.2	11.0	1.8	0.6	16.3	8.3	14.5	11
Circumoral kinety to last dikinetid of brush row 1,	–	–	–	–	–	–	–	–
distance	25.0	24.0	7.3	2.2	29.4	13.0	38.0	11
Circumoral kinety to last dikinetid of brush row 2,	27.8	27.0	3.7	0.9	13.4	23.0	36.0	19
distance	29.2	30.0	7.0	2.1	24.1	20.0	43.0	11
Circumoral kinety to last dikinetid of brush row 3,	–	–	–	–	–	–	–	–
distance	25.5	26.0	6.3	1.9	24.7	18.0	36.0	11
Oral bulge, length	14.7	15.0	2.3	0.5	15.7	11.0	19.0	19
	16.8	17.0	3.5	1.1	21.1	10.0	22.0	11
Macronuclear nodules, length	6.2	5.0	2.6	0.6	42.4	3.0	12.0	19
	5.6	6.0	0.9	0.3	16.4	4.0	7.0	11
Macronuclear nodules, width	3.4	3.0	0.8	0.2	22.5	3.0	6.0	19
	3.2	3.0	0.8	0.2	23.6	2.0	4.0	11
Macronuclear nodules, number	49.2	50.0	10.4	2.4	21.2	25.0	75.0	19
	48.1	42.0	14.4	4.3	30.0	26.0	80.0	11
Micronuclei, largest diameter	–	–	–	–	–	–	–	–

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	1.9	2.0	–	–	–	1.0	2.0	11
Somatic kineties, number	15.1	15.0	1.2	0.3	7.9	13.0	18.0	19
	13.3	13.0	1.6	0.5	11.7	11.0	16.0	11
Ciliated kinetids in a right side kinety, number	–	–	–	–	–	–	–	–
	83.5	80.0	32.2	9.7	38.5	50.0	160.0	11
Dikinetids in brush row 1, number	–	–	–	–	–	–	–	–
	17.3	16.0	5.4	1.6	31.3	7.0	27.0	11
Dikinetids in brush row 2, number	23.7	24.0	2.8	0.6	11.7	20.0	30.0	19
	22.3	20.0	6.2	1.9	27.8	15.0	33.0	11
Dikinetids in brush row 3, number	–	–	–	–	–	–	–	–
	16.3	18.0	4.5	1.4	27.9	10.0	24.0	11

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Ontogenesis (Fig. 52a–p; 324a–k, m–t; Table 43): *Spathidium turgitorum* from Namibian site (24) has been cultivated as described above. Thus, we could study ontogenesis in detail. The genesis of the ciliary pattern is as in other members of the family (BERGER et al. 1983, 1984) and group (FOISSNER 1996c), while important new observations will be reported about body and nuclear division. Generally, division of *S. turgitorum* is homothetogenic, holotelokinetal, occurs in freely motile (non-encysted) condition, and most main events occur very early. No changes are recognizable in the parental oral structures and brush rows. All basal bodies develop intrakinetally without any special anlagen fields.

Body shape and contractile vacuole: Early and middle dividers are slightly smaller and stouter than interphase specimens. Curious blebs of unknown function develop in the prospective division furrow and above the forming circumoral kinety fragments (Fig. 52e–g; 324b, d). The blebs become very conspicuous in middle to late dividers (Fig. 324e, i), but disappear in very late dividers (Fig. 324j, k). Middle to late dividers are fusiform, that is, inflated in the prospective fission area, and elongate to the ordinary length (Fig. 52h). Furrowing commences in late dividers and produces two sister cells of equal size (Fig. 52i, j; 324m). Proter post-dividers look like small, stout ordinary specimens, while opisthe post-dividers are cylindroidal, slowly developing the species-specific body and oral bulge shape (Fig. 52k, o, p; 324n–p, t). The opisthe obtains the parental contractile vacuole, while the proter very soon forms a new contractile vacuole and excretory pores close above the prospective fission area (Fig. 52b–d, 324g).

Infraciliature: The genesis of the ciliary pattern commences with an intense, intrakinetal production of basal bodies in all kineties underneath the prospective division furrow (Fig. 52a). The newly formed basal bodies soon become dikinetidal and separate from the parental ciliary rows, producing small kinetofragments each composed of 4–8 dikinetids having only one basal body ciliated (Fig. 52b; 324a, c). The opisthe's dorsal brush also develops very early within the same rows as in the parent. In the brush area, the parental somatic cilia are obviously resorbed, while new, paired bristles grow out. At the anterior end of the new brush rows is an ordinary kinetofragment each (Fig. 52b; 324f–h). In middle dividers, the newly

formed kinetofragments curve right and have cilia of almost ordinary length. Furthermore, intrakinetal proliferation of ordinary somatic kinetids (basal bodies) continues, producing more or less distinct pairs (Fig. 52b, c; 324b, d). Production of ordinary somatic kinetids likely continues throughout the life cycle because unciliated basal bodies are found in front of ciliated ones in most interphase specimens (Fig. 323u). These basal bodies could be a reservoir for somatic kinetids during division. Nematodesmata (oral basket rods) develop from the newly formed kinetofragments when the division furrow becomes recognizable, that is, in late and very late dividers (Fig. 52d). The opisthe circumoral kinety is formed from the kinetofragments only during post-divisional shaping of the oral bulge.

Nuclear apparatus: When proliferation of basal bodies commences in mid-body, the macronuclear nodules begin to fuse, sometimes showing fibrous connections or elongations (Fig. 52a, b, e, f). This indicates that the nodules could be connected by very fine fibres and/or the nuclear membrane. In middle dividers, all nodules have fused to a globular mass in mid-body and the micronuclei commence to divide in the usual manner (Fig. 52c, g). In late and very late dividers, the macronuclear mass elongates to a rod-shaped strand that usually shows some small branches (Fig. 52d, h–j; 324m). Thus, early post-dividers have a single, more or less tortuous macronuclear strand (Fig. 52k, 324n). The interphase nuclear pattern is obtained by a special process only in post-dividers (Fig. 52k–p; 324n–t): the macronuclear strand begins to elongate and ramify until a three-dimensional reticulum is achieved which eventually breaks into many nodules. This process likely takes several hours because many specimens with incomplete macronuclear fragmentation can be found in preparations from exponentially growing cultures. The individual strands of the reticulum are thinner than the single strand of the post-dividers, indicating that elongation and ramification of the macronucleus is caused both by thinning of the post-divider strand and production of new nuclear material.

In about 1% of specimens, the macronucleus consists of three to six, usually four rather large globules. Such a pattern is found both in seemingly normal and dwarf individuals. We could not clear how this pattern originates, but such individuals may even divide, whereby the macronuclear globules flatten and occasionally break into up to ten pieces, which fuse to an elongate mass in middle dividers.

Ontogenetic comparison: The genesis of body shape and infraciliature of *S. turgitorum* is very similar to that of other *Spathidium* species (BERGER et al. 1983, 1984, FYDA 1989, MOODY 1912) and haptorid gymnostomes in general (FOISSNER 1996c). The species investigated by the above authors have a single macronuclear strand, which condenses in middle dividers. Later, the globular mass elongates and divides once or several times (in *Homalozoon*; LEIPE et al. 1992). Few data are available on nuclear division in multinucleate haptorid gymnostomes (FOISSNER 1996c). However, each nodule divides individually in multinucleate *Dileptus* spp. (JONES 1951, VINNIKOVA 1974), a genus traditionally considered to be rather closely related to *Spathidium* (CORLISS 1979, FOISSNER & FOISSNER 1988). Thus, it was a great surprise that *S. turgitorum* behaves entirely different: the nodules fuse to a globular mass in mid-dividers. The mass elongates and divides once in late and very late dividers. In post-dividers, the single macronuclear strand transforms to a reticular structure which eventually breaks into many pieces. This mode of nuclear division is highly reminiscent of that found in most multinucleate hypotrichs, for instance, *Bakuella pampinaria* (EIGNER & FOISSNER 1992).

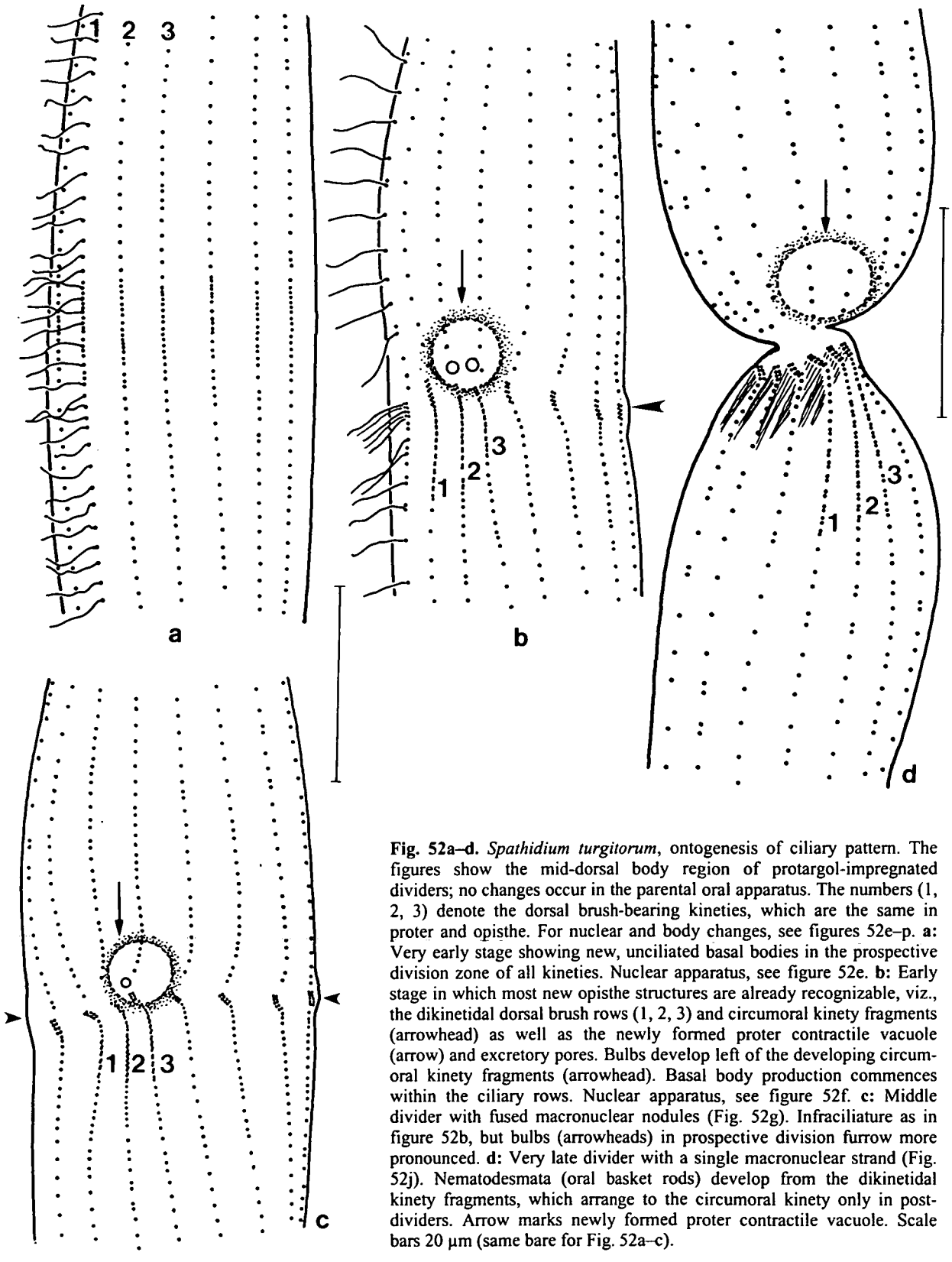

Fig. 52a–d. *Spathidium turgitorum*, ontogenesis of ciliary pattern. The figures show the mid-dorsal body region of protargol-impregnated dividers; no changes occur in the parental oral apparatus. The numbers (1, 2, 3) denote the dorsal brush-bearing kineties, which are the same in proter and opisthe. For nuclear and body changes, see figures 52e–p. **a:** Very early stage showing new, unciliated basal bodies in the prospective division zone of all kineties. Nuclear apparatus, see figure 52e. **b:** Early stage in which most new opisthe structures are already recognizable, viz., the dikinetidal dorsal brush rows (1, 2, 3) and circumoral kinety fragments (arrowhead) as well as the newly formed proter contractile vacuole (arrow) and excretory pores. Bulbs develop left of the developing circumoral kinety fragments (arrowhead). Basal body production commences within the ciliary rows. Nuclear apparatus, see figure 52f. **c:** Middle divider with fused macronuclear nodules (Fig. 52g). Infraciliature as in figure 52b, but bulbs (arrowheads) in prospective division furrow more pronounced. **d:** Very late divider with a single macronuclear strand (Fig. 52j). Nematodesmata (oral basket rods) develop from the dikinetidal kinety fragments, which arrange to the circumoral kinety only in post-dividers. Arrow marks newly formed proter contractile vacuole. Scale bars 20 μm (same bare for Fig. 52a–c).

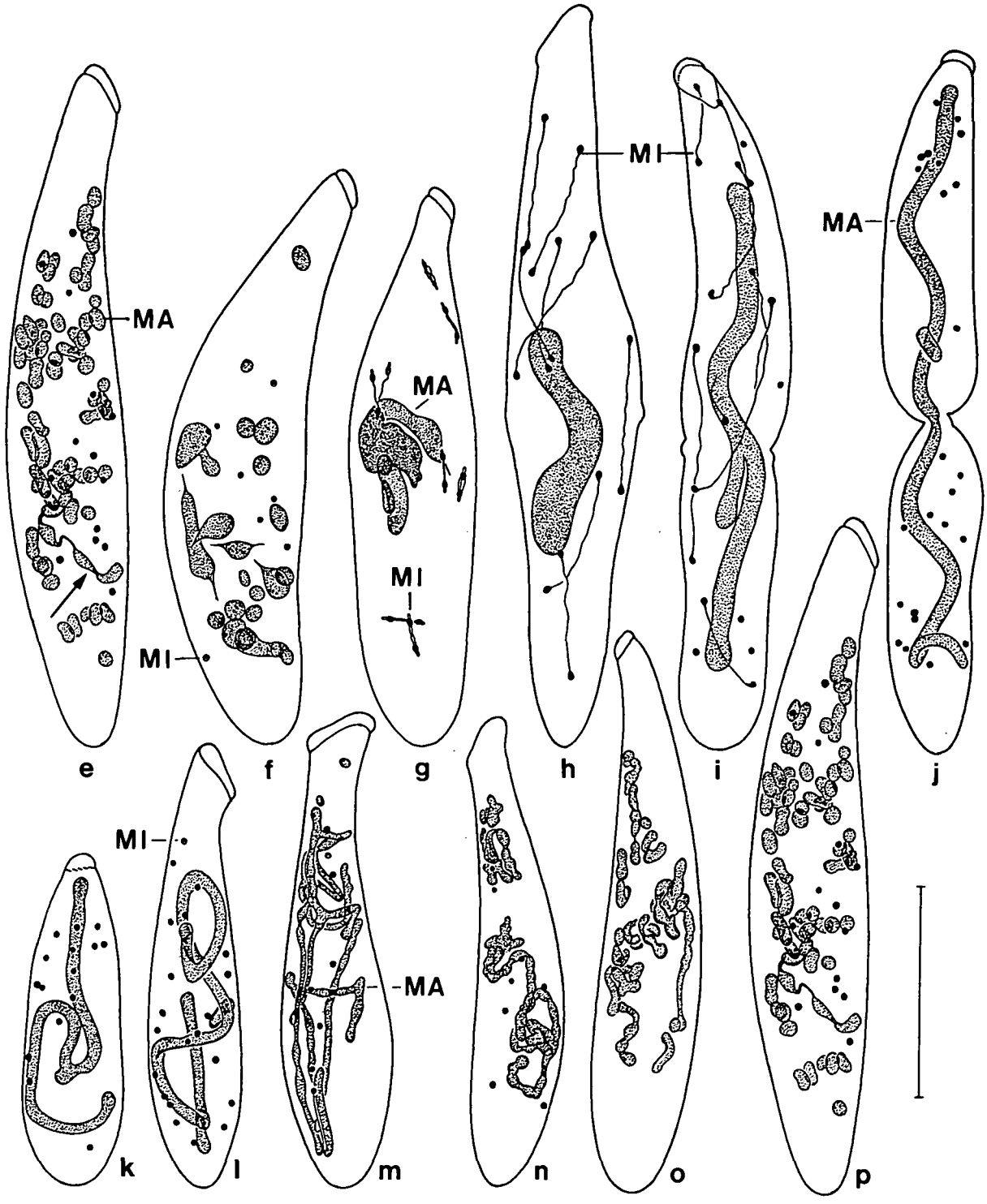

Fig. 52e–p. *Spathidium turgitorum*, nuclear and body changes in dividers (e–j) and post-dividers (k–p) after protargol impregnation, drawn to scale (bar 50 µm). **e:** Very early stage. The macronuclear nodules begin to fuse (arrow). **f:** Early stage. Most macronuclear nodules fused. **g:** Middle stage. The macronuclear nodules fused and the micronuclei commence to divide. Specimens became smaller during early to middle ontogenesis. **h:** Middle-late stage showing elongation of body and macronuclear mass, micronuclear fission, and inflated fission area. **i, j:** Late and very late stage showing elongation of macronucleus and division furrow. Nematodesma develop (Fig. 52d). **k–p:** Post-dividers grow slowly and develop a reticular macronuclear mass, which eventually breaks into many nodules. Ma – macronucleus, MI – micronuclei.

Typically, multinucleate *Spathidium* species have a rather variable nuclear pattern, that is, there are usually some specimens with a mixture of ordinary nodules and more or less long strands or even only a single, tortuous strand among, say, 100 individuals. Now it is clear that such cells are post-dividers, which are often difficult to distinguish from small, ordinary specimens, especially late post-dividers. Actually, the multinucleate pattern of *S. turgitorum* is entirely constant if only fully grown individuals are analyzed: all 25 very early dividers (= fully grown cells) studied have only nodules. Thus, if in doubt about the macronuclear pattern, early dividers must be investigated.

Table 43. Body length and width and length:width ratio in three populations and varying states of *Spathidium turgitorum*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Namibian site (54), flourishing NFP [b]								
Body, length	154.3	152.0	17.5	4.0	11.3	120.0	188.0	19
Body, width	13.6	13.0	1.9	0.4	13.7	10.0	16.0	19
Body length:width, ratio	11.6	12.0	2.3	0.5	20.2	8.0	16.0	19
Namibian site (54), declining NFP [b]								
Body, length	131.8	132.0	22.3	5.1	16.9	88.0	184.0	19
Body, width	15.6	14.0	4.1	1.0	26.5	10.0	25.0	19
Body length:width, ratio	8.9	9.0	2.5	0.6	27.7	4.0	13.0	19
Namibian site (24), NFP [b], SEM [c]								
Body, length	144.8	144.0	22.2	9.9	15.3	117.0	179.0	5
Body, width	18.6	20.0	2.6	1.2	14.0	14.0	20.0	5
Body length:width, ratio	7.9	7.2	1.7	0.8	21.0	6.2	10.3	5
Namibian site (24), cultivated and randomly selected [d]								
Body, length	132.7	135.0	16.1	3.5	12.1	105.0	170.0	21
Body, width	26.7	25.0	3.4	0.7	12.6	21.0	32.0	21
Body length:width, ratio	5.0	5.1	0.8	0.2	16.0	4.0	6.4	21
Namibian site (24), cultivated and selected for nicely impregnated cells [d]								
Body, length	148.6	150.0	16.4	3.8	11.1	118.0	184.0	19
Body, width	25.8	25.0	3.7	0.9	14.4	21.0	35.0	19
Body length:width, ratio	5.9	6.0	0.9	0.2	15.0	3.8	7.1	19
Namibian site (24), cultivated, very early dividers [d]								
Body, length	152.9	150.0	12.6	2.8	8.2	130.0	183.0	21
Body, width	28.4	28.0	2.3	0.5	8.0	23.0	33.0	21
Body length:width, ratio	5.4	5.4	0.6	0.1	10.3	4.5	6.7	21
Tunisia, flourishing NFP [b]								
Body, length	182.8	190.0	31.9	9.6	17.5	147.0	243.0	11
Body, width	16.5	17.0	2.7	0.8	16.1	11.0	20.0	11
Body length:width, ratio	11.2	11.0	1.8	0.6	16.3	8.3	14.5	11

[a] Data based, if not otherwise stated, on mounted, protargol-impregnated (FOISSNER's method), randomly selected specimens. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] From ordinary non-flooded Petri dish culture (NFP).

[c] From scanning electron micrographs (SEM).

[d] Pure culture with mainly flagellates (*Polytomella*) as food.

Occurrence and ecology: To date found at several sites in Namibia (Table 4) and in Tunisia (detritus-rich sand dune from the Grand Erg Oriental near the town of Ksar Rhilane). *Spathidium turgitorum* is a slender species and thus well-adapted to live in soil pores. Furthermore, it is euryhaline.

Comparison with related species: Taking into consideration field and cultivated specimens as well as various populations, *S. turgitorum* shows a high variability in size (about 90–250 × 10–35 µm) and ratio of body length:width (4–16; averages about 5–12), while the extrusome shape and the averages of macronuclear nodules (about 50) and ciliary rows (11–15) are fairly similar and thus the most important features of the species. *Spathidium turgitorum* is closely related to *S. procerum* and *S. anguilla*, as redescribed by FOISSNER (1984). It differs from *S. procerum* mainly by the macronucleus (many small nodules vs. long, tortuous strand) and the shorter extrusomes (3–4 µm vs. 6–10 µm), and from *S. anguilla* by the shape of the extrusomes (rod-like vs. fusiform), the thinner body (9–12:1 vs. 8:1), and shorter oral bulge (about as wide vs. one and a half as wide as body). *Spathidium metabolicum* POMP & WILBERT, 1988, discovered in saline soil from Australia, is also similar to *S. turgitorum*. Unfortunately, the description of *S. metabolicum* lacks detailed morphometrics and, especially, live observations on the extrusomes, which are "elongated oval, pointed on one side" in protargol preparations, indicating synonymy with *S. anguilla*, as does the small number (13) of macronuclear nodules. The extreme individuals of *S. turgitorum* overlap with *Protospathidium muscicola* DRAGESCO & DRAGESCO-KERNÉIS, 1979 in all main features (Fig. 50s–y). However, average values are distinctly different (154 × 13 µm vs. 75 × 13 µm), and *P. muscicola* has dorsal brush row 1 reduced to a few, indistinct bristles. Furthermore, the circumoral kinety fragments are more distinct in *P. muscicola* than *S. turgitorum* (Fig. 50v–y). For separation from → *Epispathidium polynucleatum*, see that species. Certainly, all these species look rather similar, especially when the considerable variability is taken into account (Tables 41–43), but at population level they can be reliably distinguished by the shape of the extrusomes and macronucleus, the dorsal brush, and morphometric details, such as the length of the oral bulge and the ratio of body length:width.

Spathidium namibicola nov. spec. (Fig. 53a–w; 325a–r; Table 44)

Diagnosis: Size about 130 × 30 µm in vivo. Cylindroidal or club-shaped with oral region conspicuously curved rightwards and dorsally. Oral bulge massive, elliptical to obovate, about 20 µm long. Macronucleus a long, tortuous strand. Extrusomes rod-shaped, about 5 × 0.5 µm. On average 17 ciliary rows, 3–6, usually 4 anteriorly differentiated to indistinct dorsal brush occupying 10% of body length.

Type location: Slightly saline litter and sand from centre of Sossus Vlei, southern Namib Desert, 25°50'S 15°20'E (site 23 in figure 2 and chapter 2.1.2).

Etymology: Composite of *Namib* (Desert) and the Latin verb *colere* (dwelling), referring to the area where it was discovered.

Description: Size 100–160 × 20–50 µm, usually about 130 × 30 µm in vivo; length:width ratio also considerably variable, namely 2.9–6.0:1, usually 4.5:1 (Table 44). Shape conspicuous, but only partially preserved in protargol and scanning electron microscope preparations, because like a curved rod or club with oral region usually distinctly curved dorsally and right laterally, exposing front of oral bulge more or less distinctly to the observer when seen right laterally; cross-section circular, except for distinctly flattened neck region and oral bulge (Fig. 53a, c, d, g, n–u; 325a, e, f, l). Macronucleus a tortuous, indistinctly moniliform strand in main body portion; if artificially extended about as long as body; nucleoli branched, rarely globular (Fig. 53c, n–q, s, u; 325c). Several globular micronuclei attached to macronucleus, number highly variable and counted in lightly impregnated specimens with unstained cytoplasmic inclusions. Contractile vacuole in rear body end; excretory pores not recognizable in protargol preparations. Extrusomes accumulated in oral bulge and scattered in cytoplasm, slenderly rod-shaped and slightly curved with ends inconspicuously narrowed and rounded, about 5 × 0.5 µm in vivo (Fig. 53f; 325b–d, m, o–r). Cortex almost smooth, except for furrowed neck region extending to oral bulge, forming minute ribs separating the individual kinetofragments of the circumoral kinety; contains about eight rows of approximately 0.2 µm-sized granules between each two kineties (Fig. 53e, g; 325b, g, l, m, o–r). Cytoplasm colourless, contains innumerable fat globules 1–7 µm across and food vacuoles with crystals and remnants of ciliates and the heterotrophic flagellate *Polytomella*. Swims rather rapidly.

Cilia arranged in an average of 17 equidistant, mostly bipolar, rather densely ciliated rows abutting with several very closely spaced cilia on circumoral kinety in acute (at right side) or almost right (at left) angles, as is typical for *Spathidium* (FOISSNER 1984). Dorsal brush inconspicuous because dikinetidal portion occupies merely 10% of body length on average and bristles only up to 2.5 µm long; rather irregular, that is, comprises three to six, usually four rows, of which one or two are occasionally broken with ends overlapping. Brush rows in distinct furrows, variable in length, with rather long portion of ordinary cilia anteriorly and continuing as somatic kineties posteriorly; composed of paired bristles closely spaced in anterior portion of rows and rather widely in posterior; last and often also penultimate row have a monokinetidal tail of up to 12 bristles extending to second third of cell. Bristles longer in anterior portion of rows (2–2.5 µm) than in posterior (0.5–1 µm); pairs of right brush rows consist of a longer anterior and a shorter posterior bristle, while vice versa in the left rows (Fig. 53c, d, h–m, v, w; 325a, f–j, l–n; Table 44).

Oral bulge, although shorter than widest trunk region, conspicuous because 3–5 µm high and packed with extrusomes, slightly to distinctly (45°) inclined to main body axis, obovate to broadly elliptical when seen frontally, central portion distinctly depressed. Circumoral kinety at base of slightly projecting oral bulge, obovate to broadly elliptical, composed of dikinetidal fragments slightly separated, especially in scanning electron micrographs, by minute, somatic cortical ribs merging into the oral bulge (Fig. 53g, h–m, w; 325b, i, j, n–r). Circumoral dikinetids almost equidistant, each associated with a cilium as long as ordinary somatic cilia and a fine, short (~ 6 µm) fibre contributing to the inconspicuous oral basket recognizable only in protargol preparations.

Occurrence and ecology: To date found only in two samples from the Sossus Vlei in the southern Namib Desert. The samples were circumneutral (pH 6.2–7.7) and comprised mainly plant remnants sieved off the sand.

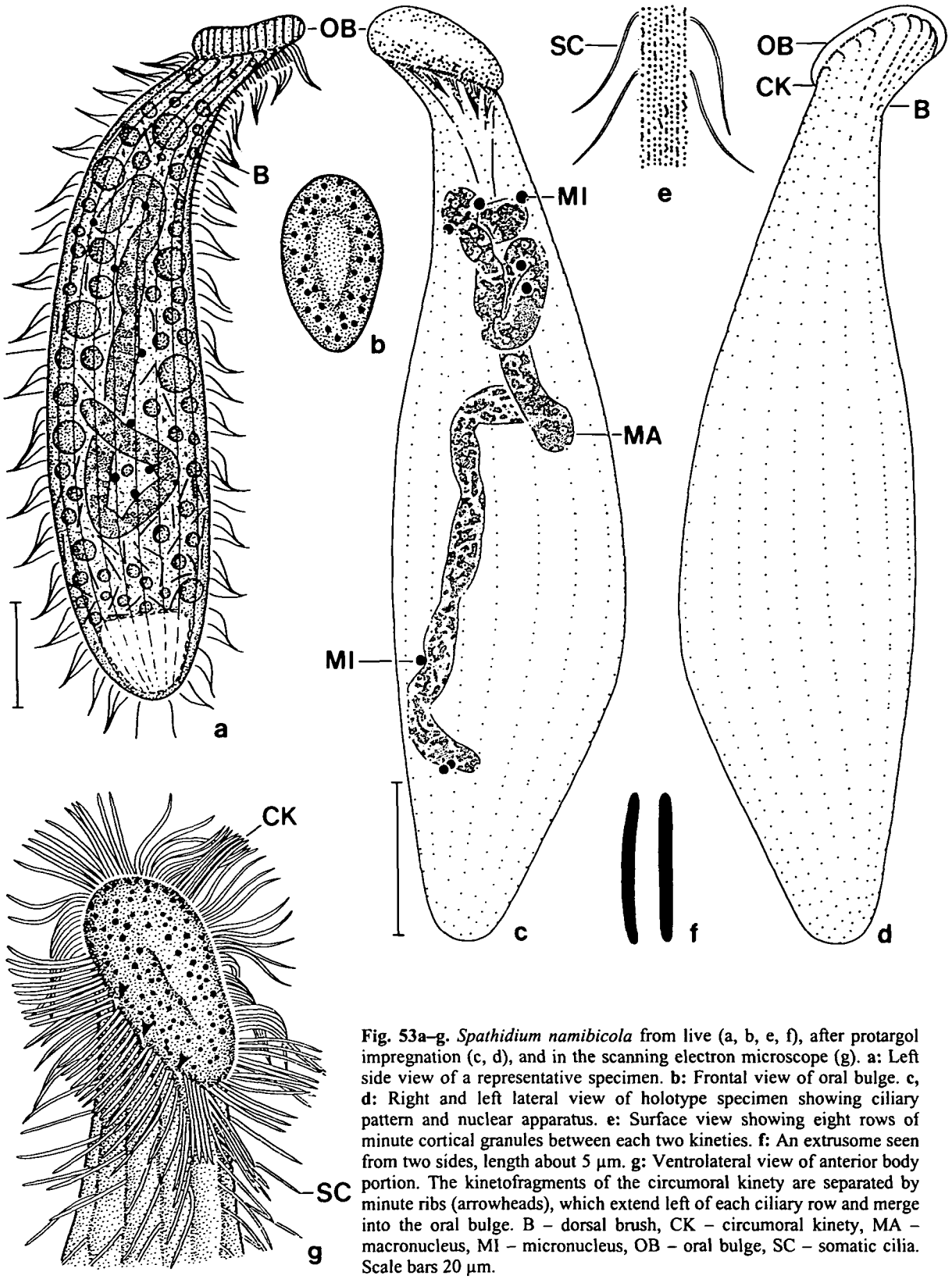

Fig. 53a–g. *Spathidium namibicola* from live (a, b, e, f), after protargol impregnation (c, d), and in the scanning electron microscope (g). **a:** Left side view of a representative specimen. **b:** Frontal view of oral bulge. **c, d:** Right and left lateral view of holotype specimen showing ciliary pattern and nuclear apparatus. **e:** Surface view showing eight rows of minute cortical granules between each two kineties. **f:** An extrusome seen from two sides, length about 5 μm. **g:** Ventrolateral view of anterior body portion. The kinetofragments of the circumoral kinety are separated by minute ribs (arrowheads), which extend left of each ciliary row and merge into the oral bulge. B – dorsal brush, CK – circumoral kinety, MA – macronucleus, MI – micronucleus, OB – oral bulge, SC – somatic cilia. Scale bars 20 μm.

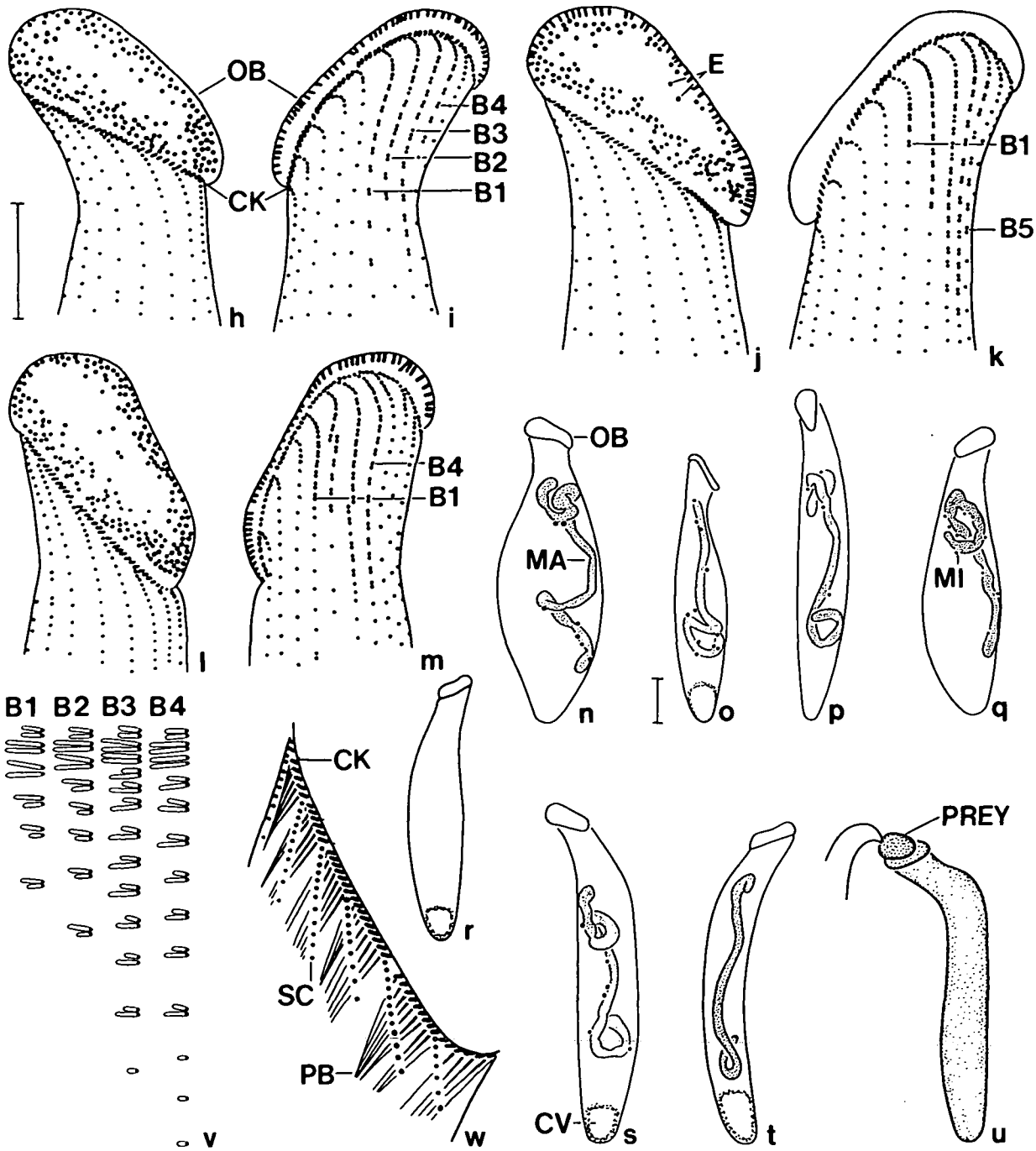

Fig. 53h–w. *Spathidium namibicola* after protargol impregnation (h–q, s, w) and from live (r, t, u, v). **h–m:** Right (h, j, l) and left (i, k, m) lateral views of three specimens showing ciliary pattern of anterior body portion. The dorsal brush is rather variable, comprising three to six, usually four rows of different length, of which one or two may be interrupted (m). **n–s:** Right lateral (n, o, s), ventral (p), and left lateral (q, r) views showing variability of body shape and macronuclear figure. **t, u:** Same specimen swimming and engulfing a heterotrophic flagellate (*Polytomella*). **v:** Slightly schematized dorsal brush. **w:** Ciliature along right side of oral bulge. The ciliary rows abut with some closely spaced kinetids on the circumoral kinety in acute angles. The pharyngeal basket is composed of short fibres originating from the circumoral dikinetids. B1-5 – dorsal brush rows, CK – circumoral kinety, CV – contractile vacuole, E – extrusome tips, MA – macronucleus, MI – micronucleus, OB – oral bulge, PB – fibres of oral basket, SC – somatic cilia. Scale bars 10 µm (h–m) and 20 µm (n–u).

Table 44. Morphometric data on *Spathidium namibicola* from Namibian site (23).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	118.4	119.0	19.9	4.6	16.8	86.0	154.0	19
Body, width	27.3	26.0	6.9	1.6	25.2	18.0	47.0	19
Body length:width, ratio	4.5	4.5	0.9	0.2	20.2	2.9	6.0	19
Oral bulge, length	18.3	18.0	2.0	0.5	11.0	15.0	21.0	15
Anterior body end to macronucleus, distance	28.9	28.0	4.8	1.2	16.4	24.0	41.0	15
Nuclear figure, length	60.4	59.0	21.5	5.6	35.6	26.0	103.0	15
Macronucleus, estimated total length [b]	107.1	98.0	–	–	–	70.0	154.0	15
Macronucleus, width	4.5	4.0	–	–	–	4.0	5.0	15
Micronuclei, diameter	1.2	1.0	–	–	–	1.0	2.0	15
Cytoplasmic extrusomes, length	4.7	5.0	0.7	0.2	14.3	3.0	6.0	15
Dorsal brush row 1, length [c]	9.8	9.0	2.5	0.6	25.3	6.0	14.0	15
Dorsal brush row 2, length [c]	12.5	14.0	3.4	0.9	27.5	7.0	19.0	15
Dorsal brush row 3, length [c]	17.7	18.0	3.1	0.8	17.4	10.0	21.0	15
Dorsal brush row 4, length [c]	17.7	18.5	3.6	1.0	20.5	9.0	24.0	14
Dorsal brush row 5, length [c]	–	–	–	–	–	5.0	16.0	2
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Micronuclei, number [d]	8.3	8.0	2.3	0.6	27.2	5.0	13.0	15
Somatic ciliary rows, number	17.1	18.0	2.9	0.7	16.9	12.0	23.0	15
Basal bodies in a left side ciliary row, number	63.4	59.0	13.2	3.4	20.8	44.0	88.0	15
Dorsal brush rows, number	4.2	4.0	0.7	0.2	16.6	3.0	6.0	20
Dorsal brush row 1, number of dikinetids	6.3	6.0	2.6	0.7	41.6	2.0	13.0	15
Dorsal brush row 2, number of dikinetids	8.6	9.0	3.6	0.9	42.3	3.0	17.0	15
Dorsal brush row 3, number of dikinetids	12.1	13.0	2.3	0.6	19.2	8.0	16.0	15
Dorsal brush row 4, number of dikinetids	9.9	9.5	2.5	0.7	25.4	5.0	16.0	14
Dorsal brush row 5, number of dikinetids	–	–	–	–	–	3.0	8.0	2

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Approximations from uncoiled nuclei.

[c] Measured as distance between circumoral kinety and last dikinetid of row.

[d] Counted in lightly impregnated specimens with unstained cytoplasmic inclusions.

Comparison with related species: *Spathidium namibicola* has a particular body shape different from all *Spathidium* taxa described previously (e.g. FOISSNER, GELEI, KAHL, LEPSI, VUXANOVICI), except for two species now considered to belong to *Protospathidium* DRAGESCO & DRAGESCO-KERNÉIS, 1979, viz., *P. serpens* (KAHL, 1930a) FOISSNER, 1981b and *P. terricola* FOISSNER, 1998a. The latter has an elongate ellipsoidal macronucleus (~ 33 × 13 µm; FOISSNER 1998a, PETZ & FOISSNER 1997) and is thus easily distinguished from *S. namibicola*. *Protospathidium serpens* matches *S. namibicola* in many features, but has, of

course, a discontinuous circumoral kinety composed of short kinetofragments usually comprising only four kinetids (FOISSNER 1981b, 1996a). The difference in the circumoral pattern becomes indisputable when comparing appropriate micrographs (Fig. 325i–k). Interestingly, the three species mentioned have a rather variable dorsal brush consisting not of the usual three rows, but of three to six with an average of four rows in *S. namibicola* and *P. serpens*. Thus, *S. namibicola* and *P. serpens* are difficult to distinguish in vivo; however, the latter is usually smaller (≤ 100 µm vs. > 100 µm in vivo), especially as concerns the oral bulge (≤ 10 µm vs. about 20 µm in vivo).

Spathidium rusticanum FOISSNER, 1981 (Fig. 54a–m; 327e; Tables 45, 46)

Description of Namibian site (5) population: Size 90–160 × 15–30 µm in vivo, usually about 120 × 25 µm; length:width ratio 3.4–6.6:1, on average 4.4:1in protargol preparations (Table 45). Elongate spatulate with distinctly narrowed neck; oral bulge about as long as widest trunk region, neck and bulge distinctly flattened (Fig. 54a, e, l). Macronucleus in middle quarters of cell, basically a more or less distinctly moniliform rod with ends frequently curved and coiled, usually as shown in figures 54e and 327e; nucleoli large and in centre of nodes; becomes a globular mass in middle dividers. Several globular micronuclei, exact number could not be counted because of similarly sized and impregnated cytoplasmic inclusions. Contractile vacuole in rear end, several excretory pores in posterior pole area. Extrusomes rather conspicuous because compact and comparatively thick, accumulated in ends and right half of oral bulge, scattered in cytoplasm; individual extrusomes about 5–6 × 0.4 µm, basically rod-shaped, but when investigated carefully somewhat fusiform and slightly curved (Fig. 54a–c). Cortex very flexible, contains several rows of minute (~ 0.2 µm), colourless granules between each two kineties. Trunk usually packed with up to 10 µm-sized fat inclusions, so that macronucleus stands out as whitish rod. Swims and creeps rather rapidly.

Somatic cilia about 9 µm long in vivo, arranged in an average of 15 equidistant, mostly bipolar rows loosely ciliated in oral and neck region, where some rows may be slightly shortened; kineties abut, although rather indistinctly, on circumoral kinety, as is typical for the genus (FOISSNER 1984). Dorsal brush inconspicuous because occupying only 10% of body length on average, dikinetidal part of row 3 distinctly shortened, that is, about half as long as rows 1 and 2 (Table 45); bristles similar in all rows, that is, anterior bristle of dikinetids slightly inflated and about 3 µm long in anterior half of rows decreasing to 2 µm posteriorly, posterior bristle slightly shorter than anterior, rod-shaped; row 3 continues to near body end with 1–1.5 µm long, conical, monokinetidal bristles (Fig. 54a, i–m).

Oral bulge 3–4 µm high and slanted roughly 45° to main body axis, about as long as widest trunk region, mid portion slightly depressed in half of specimens; elongate elliptical with ventral half slightly narrowed, bulge ends bright due to the extrusome accumulations. Circumoral kinety elongate elliptical, consists of rather loosely spaced and irregularly arranged dikinetids, each associated with a cilium and a fine nematodesma. Oral basket inconspicuous (too distinctly illustrated in original description, according to the type slides), rods slightly concentrated in dorsal third (Fig. 54a, i, j, l, m).

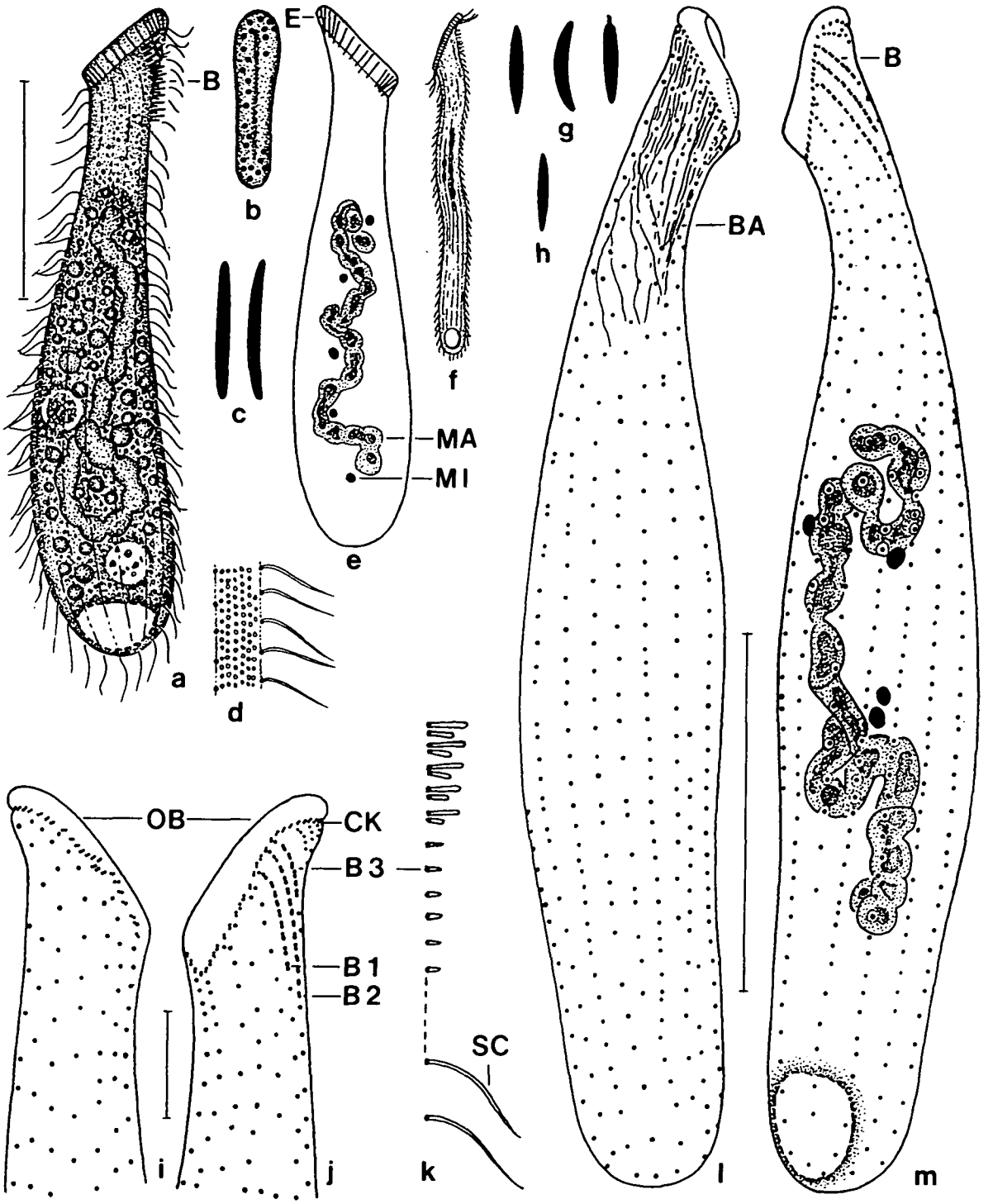

Fig. 54a–m. *Spathidium rusticanum* (a–e, i–m) and *S. anguilla* (f–h) from life (a–h, k) and after protargol impregnation (i, j, l, m). **a:** Left side view. **b:** Frontal view of oral bulge. **c:** Two views of same extrusome. **d:** Cortical granulation. **e:** Shape variant with nuclear apparatus from a protargol-impregnated specimen. **f:** Left side view, length 89 µm (VUXANOVICI 1962a). **g, h:** Extrusomes from activated sludge and soil specimens (from AUGUSTIN & FOISSNER 1992 and FOISSNER 1984). **i, j:** Ciliary pattern in oral region. **k:** Dorsal brush row 3. **l, m:** Ciliary pattern of right and left side and nuclear apparatus. B(1, 2, 3) – dorsal brush (rows), BA – oral basket, CK – circumoral kinety, CV – contractile vacuole, E – extrusomes, MA – macronucleus, MI – micro-nucleus, OB – oral bulge, SC – somatic cilia. Scale bars 40 µm (a, l, m) and 10 µm (i, j).

Table 45. Morphometric data on *Spathidium rusticanum* from Namibian site 5 (upper line) and *Spathidium etoschense* from site 57 (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	114.9	115.0	16.0	4.1	13.9	83.0	140.0	15
	145.0	145.0	15.9	5.3	10.9	123.0	180.0	9
Body, width	26.0	26.0	4.1	1.1	15.6	17.0	35.0	15
	22.7	22.0	4.9	1.6	21.8	17.0	32.0	9
Body length:width, ratio	4.5	4.4	0.9	0.2	19.6	3.4	6.8	15
	6.7	6.7	1.4	0.5	20.3	4.1	8.2	9
Oral bulge, length	17.5	17.0	2.1	0.5	11.8	15.0	22.0	15
	22.7	23.0	4.1	1.4	17.9	16.0	29.0	9
Circumoral kinety to last dikinetid of brush row 1, distance	10.6	11.0	1.9	0.5	17.8	7.0	14.0	15
	8.0	7.0	3.8	1.4	54.7	4.0	14.0	7
Circumoral kinety to last dikinetid of brush row 2, distance	11.5	12.0	2.2	0.6	18.8	7.0	16.0	15
	18.1	17.0	3.0	1.1	16.4	14.0	23.0	7
Circumoral kinety to last dikinetid of brush row 3, distance	5.2	5.0	0.9	0.2	18.1	3.0	7.0	15
	13.3	13.0	4.0	1.5	30.0	7.0	20.0	7
Nuclear figure, length	56.5	57.0	13.9	3.6	24.7	33.0	80.0	15
	42.7	39.0	14.5	4.8	33.9	24.0	76.0	9
Macronucleus, estimated total length [b]	79.7	70.0	–	–	–	50.0	110.0	15
	57.1	55.0	–	–	–	44.0	90.0	9
Body length:macronucleus total length, ratio	1.5	1.4	0.3	0.1	17.5	1.1	2.0	15
	2.6	2.7	0.5	0.2	18.6	2.0	3.3	9
Macronucleus, width	5.0	5.0	0.7	0.2	13.1	4.0	6.0	15
	6.4	6.0	0.7	0.2	11.3	6.0	8.0	9
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	9
Micronuclei, number				several				
	3.1	3.0	1.1	0.4	34.3	2.0	5.0	7
Somatic kineties, number	15.2	15.0	0.9	0.2	6.2	14.0	17.0	15
	10.4	11.0	1.1	0.4	10.9	9.0	12.0	9
Ciliated kinetids in a right lateral kinety, number	38.4	38.0	8.9	2.4	23.2	25.0	52.0	15
	64.0	68.0	9.1	3.7	14.2	46.0	70.0	6
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
	3.1	3.0	–	–	–	3.0	4.0	7
Dikinetids in brush row 1, number	9.6	9.0	1.8	0.5	18.4	7.0	14.0	15
	5.4	6.0	2.1	0.7	39.8	3.0	8.0	7
Dikinetids in brush row 2, number	12.3	12.0	2.0	0.5	16.4	7.0	15.0	15
	17.6	19.0	3.9	1.5	22.0	12.0	21.0	7
Dikinetids in brush row 3, number	5.0	5.0	1.3	0.3	25.1	3.0	7.0	15
	12.3	12.0	2.0	0.7	16.1	9.0	15.0	7

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Approximations from uncoiled nuclei.

Occurrence and ecology: *Spathidium rusticanum* is a common species in Namibia, but abundances are often low (Table 4). The type population was discovered in an alpine grassland soil of Austria.

Comparison with original description and related species: The original description of *S. rusticanum* is rather incomplete. The Namibian site (5) population matches the Austrian type in all main features, although the macronucleus is less distinctly monili form. However, a reinvestigation of the type slides showed that FOISSNER's (1981b) figure is

Table 46. Comparison of main morphometrics in *Spathidium rusticanum* (RNA – Namibian site 5), *S. rusticanum* (RAU – Austrian type population; from FOISSNER 1984), *S. anguilla* (AAS – from soil in Austria; from FOISSNER 1984), and *S. anguilla* (AAA – from activated sludge in Austria; from AUGUSTIN & FOISSNER 1992).

Characteristics [a]	Population	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	RNA	114.9	115.0	16.0	4.1	13.9	83.0	140.0	15
	RAU	122.8	124.0	7.1	3.5	5.8	113.0	130.0	4
	AAS	119.9	122.0	15.4	4.0	12.9	94.0	140.0	15
	AAA	112.8	109.0	20.6	4.0	18.3	67.0	139.0	27
Body, width	RNA	26.0	26.0	4.1	1.1	15.6	17.0	35.0	15
	RAU	24.0	24.0	2.6	1.3	10.8	21.0	27.0	4
	AAS	14.5	15.0	2.3	0.6	16.0	10.0	18.0	15
	AAA	17.3	16.0	3.6	0.7	20.8	13.0	29.0	28
Oral bulge, length	RNA	17.5	17.0	2.1	0.5	11.8	15.0	22.0	15
	RAU	18.3	18.0	–	–	–	17.0	20.0	3
	AAS	22.1	20.0	4.8	1.3	21.8	17.0	34.0	15
	AAA	19.1	19.0	3.0	0.6	15.9	12.0	26.0	28
Somatic ciliary rows, number	RNA	15.2	15.0	0.9	0.2	6.2	14.0	17.0	15
	RAU	17.8	17.0	1.5	0.8	8.5	17.0	20.0	4
	AAS	10.9	11.0	1.1	0.3	10.1	9.0	13.0	15
	AAA	12.0	12.0	0.7	0.2	5.5	11.0	13.0	15
Dikinetids in brush row 1, number	RNA	9.6	9.0	1.8	0.5	18.4	7.0	14.0	15
	RAU [b]	13.0	–	–	–	–	–	–	1
	AAS [b]	19.0	–	–	–	–	15.0	22.0	2
	AAA	17.4	17.0	1.5	0.5	8.7	15.0	20.0	10
Dikinetids in brush row 2, number	RNA	12.3	12.0	2.0	0.5	16.4	7.0	15.0	15
	RAU [b]	19.0	–	–	–	–	–	–	1
	AAS [b]	18.0	–	–	–	–	14.0	22.0	2
	AAA	26.3	26.0	2.2	0.7	8.4	23.0	30.0	10
Dikinetids in brush row 3, number	RNA	5.0	5.0	1.3	0.3	25.1	3.0	7.0	15
	RAU [b]	8.0	–	–	–	–	–	–	1
	AAS [b]	12.0	–	–	–	–	–	–	1
	AAA	20.2	20.0	2.4	0.8	12.1	17.0	24.0	10

[a] Data from mounted, protargol-impregnated specimens (FOISSNER's method). Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] From figures.

too schematic in this respect, that is, the macronucleus is very similar to that of the Namibian specimens. Thus, we are convinced that the Austrian and Namibian population belong to the same morphospecies.

FOISSNER (1984) recognized a high similarity of *S. rusticanum* and *S. anguilla* VUXANOVICI, 1962a, which was redescribed by FOISSNER (1984) and AUGUSTIN & FOISSNER (1992). This is emphasized by the present investigations, which, however, indicate that both are distinct taxa, perhaps subspecies (Table 46). The most significant difference is the length:width ratio, which is about 7.6:1 in *S. anguilla* (14:1 according to the original figure, Fig. 54f) and about 4.7:1 in *S. rusticanum*; thus, *S. anguilla* is much more slender than *S. rusticanum*. Another important feature are the extrusomes, which are almost rod-shaped in *S. rusticanum*, while fusiform in *S. anguilla* (Fig. 54g, h). Furthermore, the number of ciliary rows does not overlap in two populations each (Table 46).

Generally, *S. rusticanum* is difficult to identify because it has hardly any prominent feature, that is, looks like an ordinary "typical" *Spathidium*. The following combination of features seems to be important: size, about 120 × 25 µm, and shape, that is, spatulate with distinctly narrowed neck; macronucleus moniliform; extrusomes fairly conspicuous, that is, about 5 µm long, rather thick, and almost rod-shaped; about 16 ciliary rows.

Late remarks: Observations on other Namibian populations showed that the nodulate macronucleus is, indeed, highly characteristic and thus the most important feature of this species. Accordingly, *S. anguilla*, as redescribed by FOISSNER (1984), is another species because it has many scattered macronuclear nodules. It may be considered as the neotype of *S. anguilla*. *Spathidium anguilla*, as redescribed by AUGUSTIN & FOISSNER (1992), has a tortuous macronuclear strand and is thus another, likely new species. Obviously, the situation is bewildering and must be cleared by a revision of the genus.

Spathidium etoschense nov. spec. (Fig. 55a–j; 327j–l; Table 45)

Diagnosis: Size about 160 × 25 µm in vivo. Spatulate with oblique, slightly cuneate oral bulge about as long as widest trunk region. Macronucleus slightly tortuous and approximately 60 µm long; several micronuclei circa 4 µm across. Extrusomes acicular, about 8 × 1 µm. On average 10 ciliary rows, 3 anteriorly differentiated to inconspicuous dorsal brush occupying 12% of body length.

Type location: Highly saline soil from margin of Etosha Pan, lookout site "Pan", Namibia, 19°10'S 15°55'E (site 57 in figures 2, 3 and chapter 2.1.2).

Etymology: Named after the area discovered.

Description: Size 130–200 × 20–30 µm in vivo, usually near 160 × 25 µm; length:width ratio 4–8:1, on average 6.7:1, that is, slenderly spatulate with anterior body end obliquely truncate and posterior narrowly rounded, but never tail-like (Fig. 55a, e; Table 45). Macronucleus in middle third of cell, usually a slightly tortuous rod distinctly shorter than body (1:2.6 on average; Table 45), in one specimen circular; contains many large and small nucleoli. Micronuclei difficult to identify because of many similarly-sized and impregnated

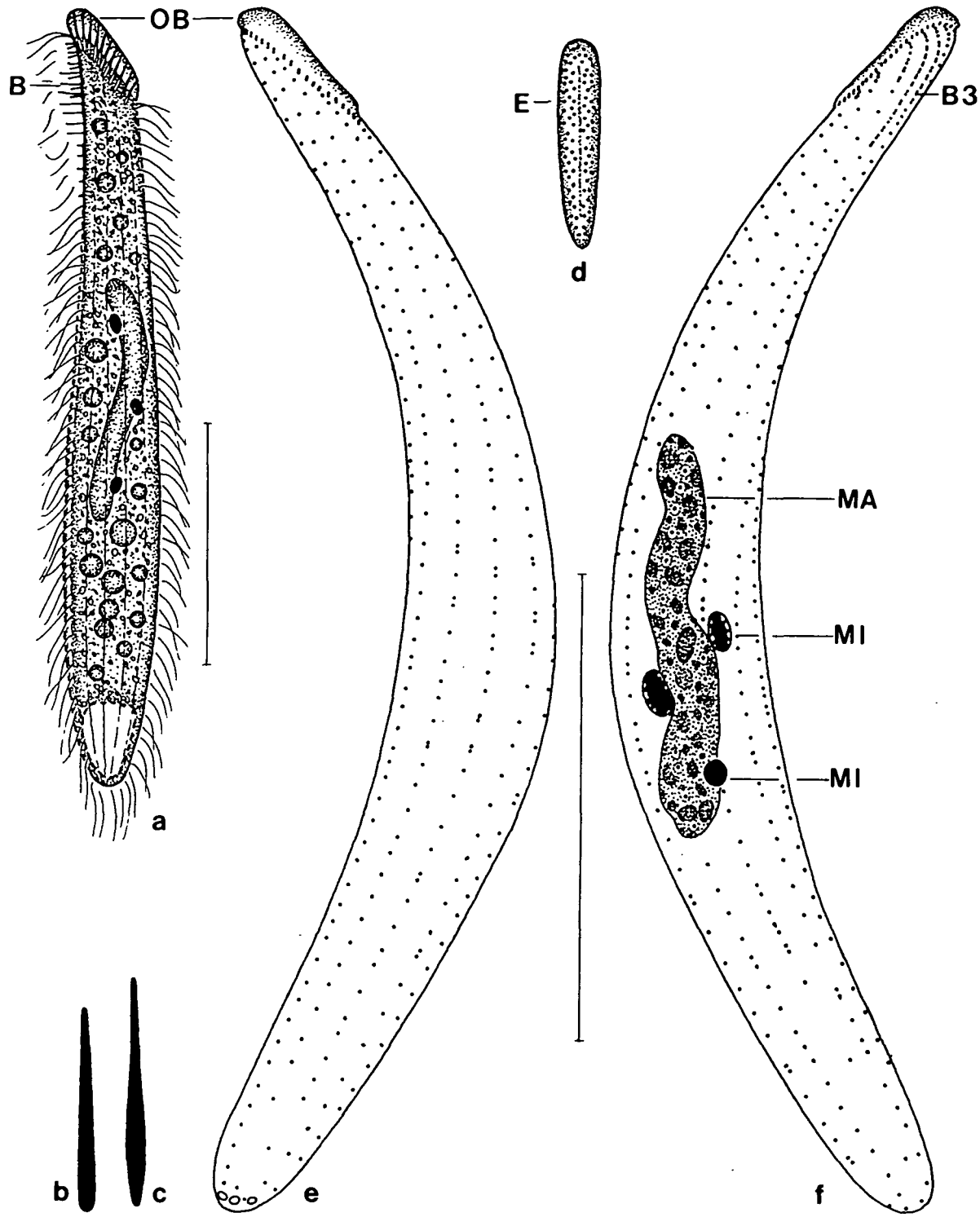

Fig. 55a–f. *Spathidium etoschense* from life (a–d) and after protargol impregnation (e, f). **a:** Right side view of a representative specimen. **b:** Resting oral extrusome, length 7 µm. **c:** Extrusome before explosion, length 8 µm. **d:** Frontal view of oral bulge packed with extrusomes. **e, f:** Oral and somatic ciliary pattern of right and left side and nuclear apparatus of holotype specimen. Two of the three micronuclei are enlarged, indicating preparation for division. B – dorsal brush, B3 – dorsal brush row 3, MA – macronucleus, MI – micronucleus, OB – oral bulge. Scale bars 50 µm.

cytoplasmic inclusions; fortunately, two dividers each unequivocally show three micronuclei. Contractile vacuole in rear end, some excretory pores in posterior pole area. Extrusomes accumulated in oral bulge and scattered in cytoplasm, acicular and 6–8 µm long and thus fairly conspicuous in vivo (Fig. 45a, b, d; 327j–l). Cortex very flexible, contains rows of colourless granules. Cytoplasm colourless, packed with fat globules up to 8 µm across. Food not observed. Glides and swims rather rapidly.

Cilia arranged in an average of ten equidistant, bipolar, rather densely ciliated rows abutting to circumoral kinety in acute (at right side) or almost right angles (at left), as is typical for *Spathidium* (FOISSNER 1984). Dorsal brush three-rowed (four in one out of ten specimens), rather inconspicuous because occupying only 12% of body length and bristles merely up to 4 µm long; all rows have some ordinary cilia anteriorly and continue as somatic kineties posteriorly; row 1 composed of five, row 2 of eighteen, and row 3 of twelve dikinetids on average (Fig. 55a, f, g, i; Table 45); details of bristles studied in only one specimen (Fig. 55j).

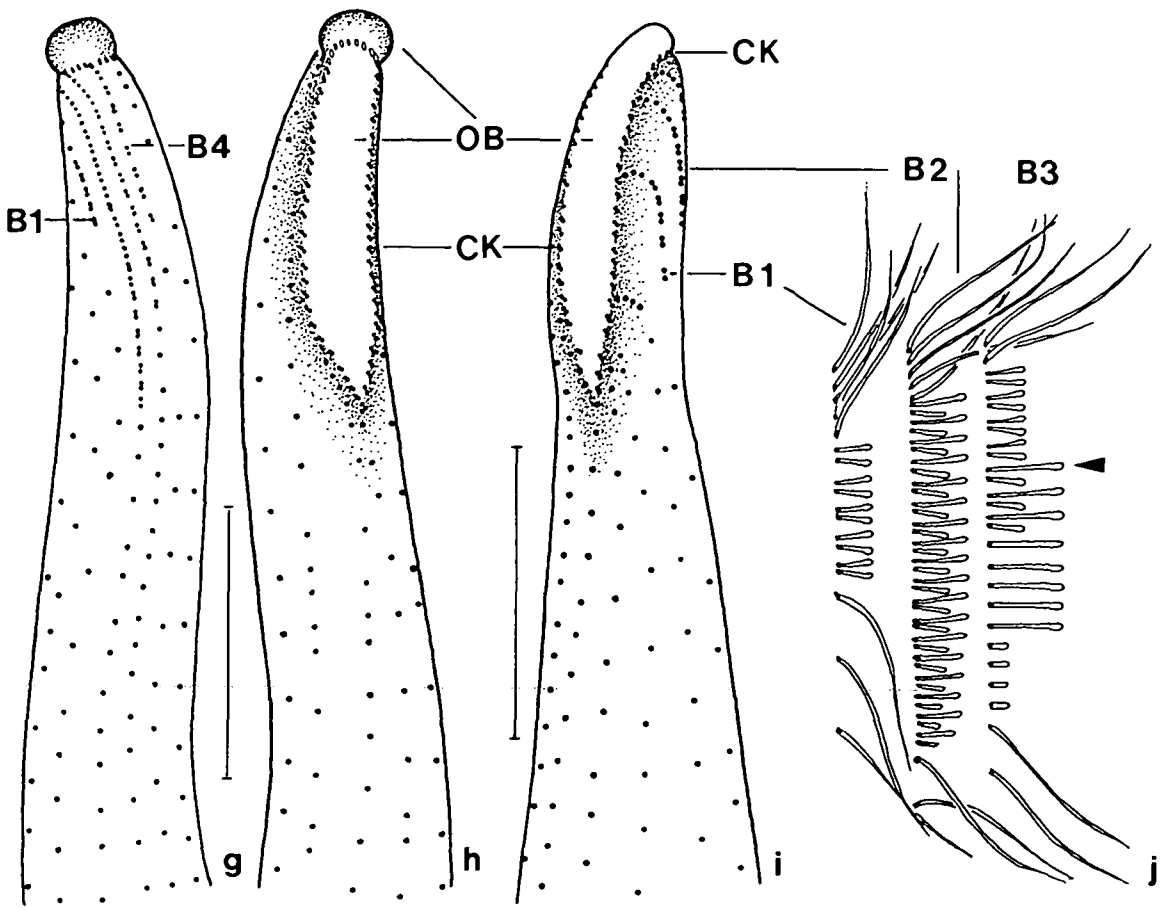

Fig. 55g–j. *Spathidium etoschense* from life (j) and after protargol impregnation (g–i). **g, h:** Dorsal and ventral anterior body portion of a specimen with four dorsal brush rows. **i:** Ventrolateral view showing the spathidiid organization of the left side ciliary rows. **j:** Dorsal brush of a single specimen, variability thus unknown. Bristles drawn to scale and up to 4 µm long (arrowhead). Some ordinary somatic cilia are at the anterior end of the rows, whose bristles have very different lengths; the rows continue posteriorly as ordinary somatic kineties. B1-4 – dorsal brush rows, CK – circumoral kinety, OB – oral bulge. Scale bars 15 µm.

Oral bulge short, that is, about as long as widest trunk region, higher dorsally than ventrally, obliquely truncate and slightly cuneate in frontal view. Circumoral kinety also cuneate and composed of comparatively widely spaced dikinetids forming continuous row. Oral basket rods not impregnated (Fig. 55a, d–i; Table 45).

Occurrence and ecology: To date found only at the highly saline type location, where it was very rare (13 specimens in 14 slides). However, two dividers were among the 13 specimens, indicating that the population was growing when the sample was fixed for preparation.

Comparison with related species: *Spathidium etoschense* resembles *S. procerum*, *S. anguilla*, *S. piliforme*, → *S. extensum*, and → *S. rusticanum*. It differs from these species, all described in FOISSNER (1984) or the present monograph, by the extrusomes (acicular vs. rod-shaped or fusiform) and the macronucleus (conspicuously short vs. long, that is, body length:nucleus length ratio 2.6:1 vs. < 2:1 on average; Table 47). The latter feature resembles → *Apospathidium atypicum*, which has fine, rod-shaped extrusomes and a distinctly narrowed posterior body portion region. *Spathidium elmenteitanum* DIETZ, 1965 has a similar nucleus as *S. etoschense*, but is only 65-80 x 12-18 µm in size and has very fine, 3 µm long extrusomes. For separation from → *S. aciculare*, see table 48.

Spathidium aciculare nov. spec. (Fig. 56a–l; 332e–h; Tables 47, 48)

Diagnosis: Size about 150 × 30 µm in vivo. Spatulate with oblique oral bulge about two thirds as long as widest trunk region. Macronucleus long and tortuous; several globular micronuclei. Extrusomes acicular, about 8 × 1 µm. On average 19 ciliary rows, 3 anteriorly differentiated to dorsal brush occupying 26% of body length.

Type location: Grassland soil from the Botanical Garden in the town of Darwin, Northern Territory, Australia, 12°S 131°30'E.

Etymology: The Latin adjective *acicularis* (needle-shaped) refers to the acicular extrusomes.

Description: Size 100–200 × 25–40 µm in vivo, usually near 150 × 30 µm, length:width ratio 2.9–6.6:1, on average 4.4:1, that is, slenderly spatulate with anterior body end obliquely truncate and posterior narrowly rounded, but never tail-like; laterally flattened up to 2:1 (Fig. 56a, b, h; Table 47). Macronucleus in posterior two body thirds, highly tortuous, straightened about as long as body (Table 47). Micronuclei attached and near to macronucleus, broadly ellipsoidal, often difficult to distinguish from similarly sized and impregnated cytoplasmic inclusions. Contractile vacuole in rear body end, about five excretory pores in posterior pole area. Extrusomes accumulated in oral bulge and scattered in cytoplasm, acicular and 7–8 × 1 µm in size and thus fairly conspicuous in vivo; do not impregnate with the protargol method used (Fig. 56a, b, e, f; 332b–d). Exploded toxicysts drumstick-shaped, 15–20 µm long (Fig. 56g). Cortex very flexible and rather conspicuous because forming an about 1.5 µm thick, gelatinous layer containing compact and thus bright, ellipsoidal granules in dense rows (Fig. 56c, d; 332a). Cytoplasm colourless, often packed with fat globules up to 7 µm across and food vacuoles containing small and medium-sized ciliates (hypotrichs, *Nassula*, *Pseudochilo-*

donopsis mutabilis, *Leptopharynx costatus*), whose pharyngeal baskets remain in the cytoplasm for a long time becoming conspicuous "teeth". Glides and swims moderately fast.

Cilia about 8 µm long in vivo, arranged in an average of 19 equidistant, bipolar, densely ciliated rows abutting to circumoral kinety in acute (at right side) or almost right angles (at left), as is typical for *Spathidium* (FOISSNER 1984). Dorsal brush dikinetidal and three-rowed, rarely a fourth, minute row occurs right of row 1, rather conspicuous because occupying 26% of body length on average; all rows have some ordinary cilia anteriorly and continue as somatic kineties posteriorly; anterior bristle of dikinetids about 3 µm long in anterior portion of rows, decreasing to 1.5 µm in posterior portion; posterior bristle about 2.5 µm anteriorly, decreasing to 1 µm posteriorly. Brush row 1 is the shortest of the three and composed of an average of 23 dikinetids; row 2 is the longest and composed of an average of 34 dikinetids; row 3 is composed of 27 dikinetids on average and continues with a monokinetidal bristle tail to mid-body, rarely to near body end (Fig. 56a, i, k, l; Table 47).

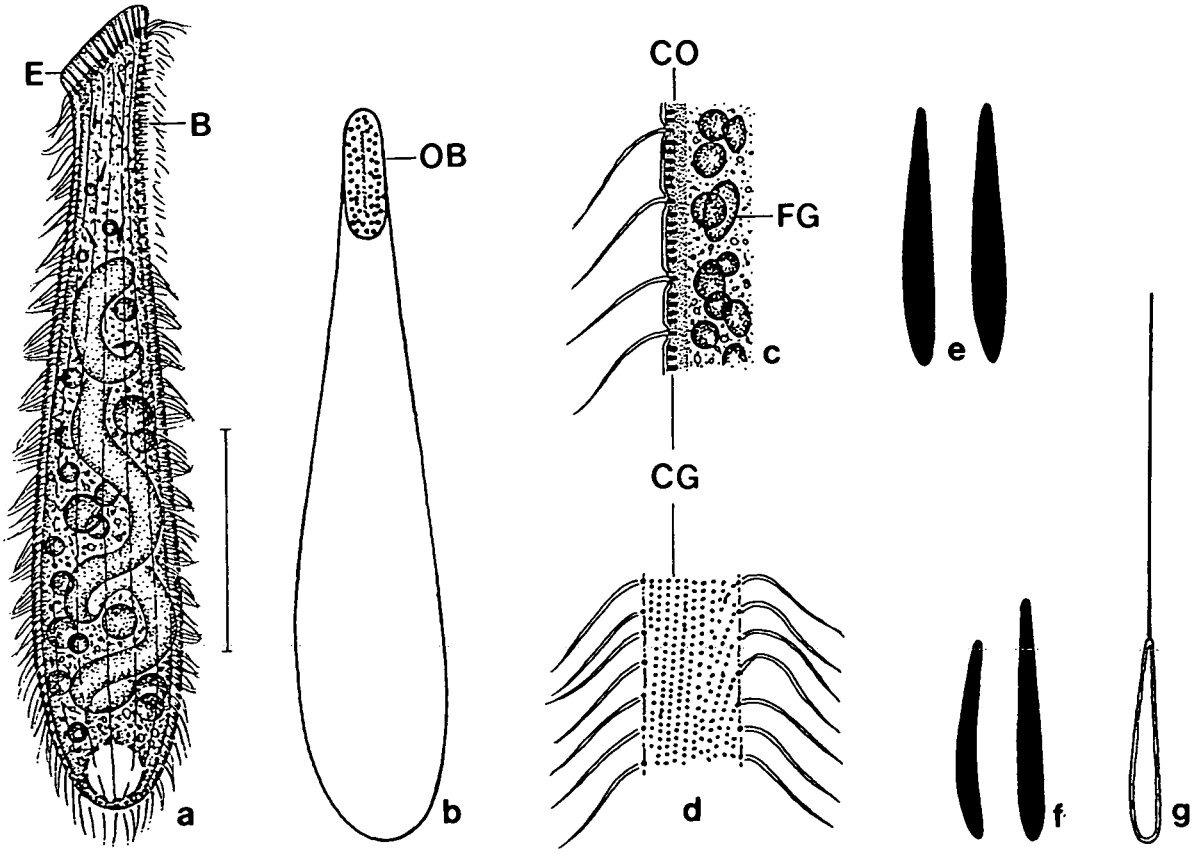

Fig. 56a–g. *Spathidium aciculare* from life. **a:** Left side view of a representative specimen. **b:** Ventral view showing the oblong oral bulge packed with extrusomes. **c, d:** The cortex is about 1.5 µm thick, gelatinous, and contains rows of compact and thus bright granules (cp. figure 332a). **e:** Extrusomes of a specimen from Australian site (128), size about 8 × 1 µm. **f:** Resting extrusomes of specimens from Australian type population, length about 7 µm. **g:** Exploded toxicyst from Australian type population, length 15–20 µm. B – dorsal brush, CG – cortical granules, CO – cortex, E – extrusomes, FG – fat globules, OB – oral bulge. Scale bar 40 µm.

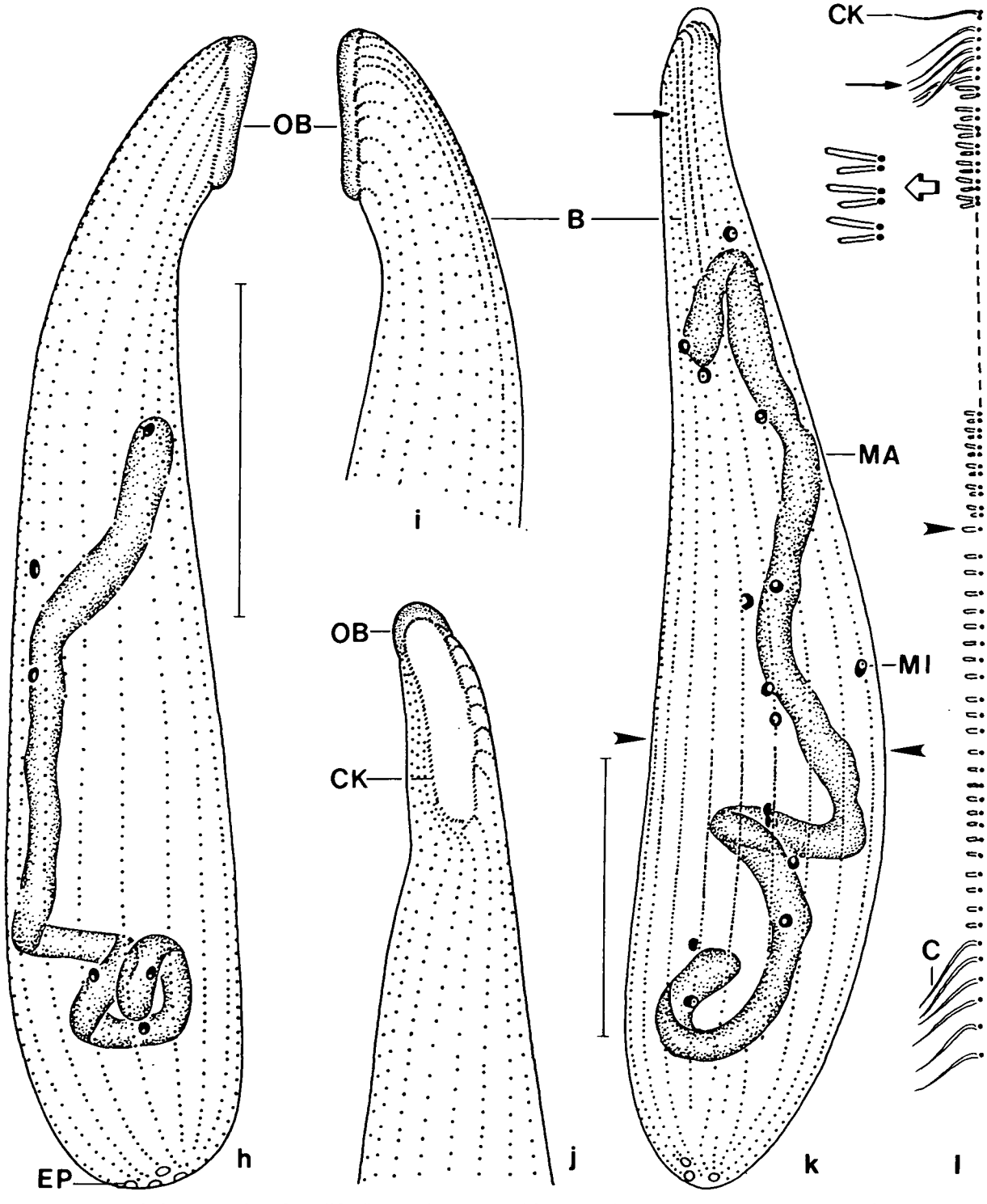

Fig. 56h–l. *Spathidium aciculare* from life (l) and after protargol impregnation (h–k). **h, i:** Ciliary pattern of right and left side of holotype specimen. Note the short oral bulge. **j, k:** Ciliary pattern of ventral and dorsal side and nuclear apparatus of a very early divider (prospective division furrow marked by arrowheads). Note the elliptical circumoral kinety (CK) and two dikinetids right of dorsal brush row 1 (arrow). **l:** Fine structure of dorsal brush row 3, which has an anterior tail of ordinary cilia (arrow) and a posterior tail of minute, monokinetidal bristles (arrowhead). B – dorsal brush, C – somatic cilia, CK – circumoral kinety, EP – excretory pores, MA – macronucleus, MI – micronucleus, OB – oral bulge. Scale bars 40 μm.

Oral bulge short compared to body size, that is, about two thirds as long as widest trunk region; dorsally slightly higher than ventrally, obliquely truncate and elongate elliptical in frontal view, surface flat to slightly convex, ends never inflated. Circumoral kinety at base of oral bulge, oblong, composed of dikinetidal kinetofragments adhering to the somatic kineties and frequently recognizable by minute gaps in between. Oral basket hardly recognizable in vivo and very lightly impregnated with protargol, individual rods originate from circumoral dikinetids (Fig. 56a, b, h–j; Table 47).

Occurrence and ecology: The soil (pH 7.1) from the type location is probably not native; however, we found *S. aciculare* also at another site in Australia, viz., in rain forest soil (pH 5.1) near Cairns. In Namibia, this species occurred only at site (48). Interestingly, *S. aciculare* was accompanied by *Enchelyodon armatides*, both at the type location and in Namibia.

Table 47. Morphometric data on *Spathidium aciculare* from Australian type population.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	137.3	140.0	25.5	5.9	18.6	85.0	185.0	19
Body, width	31.5	32.0	3.4	0.8	10.9	26.0	38.0	19
Body length:width, ratio	4.4	4.3	0.9	0.2	20.2	2.9	6.6	19
Oral bulge, length	18.4	19.0	2.6	0.6	14.2	12.0	22.0	19
Oral bulge, width between circumoral kinety	5.5	6.0	0.7	0.2	12.9	4.0	6.0	10
Oral bulge, height	3.1	3.0	0.5	0.1	15.6	2.0	4.0	19
Circumoral kinety to last dikinetid of brush row 1, distance	26.0	25.0	3.8	0.9	14.6	18.0	33.0	19
Circumoral kinety to last dikinetid of brush row 2, distance	33.3	35.0	6.8	1.6	20.5	18.0	45.0	19
Circumoral kinety to last dikinetid of brush row 3, distance	31.2	31.0	7.9	1.8	25.4	9.0	45.0	19
Anterior body end to macronucleus, distance	40.3	35.0	12.4	2.9	30.9	23.0	66.0	19
Macronuclear figure, length	78.5	77.0	23.1	5.3	29.4	45.0	123.0	19
Macronucleus, length (spread) [b]	129.7	140.0	–	–	–	60.0	190.0	19
Macronucleus, width	5.5	5.0	0.8	0.2	15.2	5.0	8.0	19
Micronucleus, length	2.2	2.0	–	–	–	1.2	3.0	19
Micronucleus, width	1.8	1.8	–	–	–	1.2	3.0	19
Somatic kineties, number	18.8	19.0	1.5	0.4	8.2	16.0	23.0	19
Ciliated kinetids in a right side kinety, number	93.1	91.0	13.7	3.1	14.7	65.0	120.0	19
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
Dikinetids in brush row 1, number	22.8	23.0	4.2	1.0	18.2	17.0	34.0	19
Dikinetids in brush row 2, number	34.3	36.0	6.1	1.4	17.8	19.0	43.0	19
Dikinetids in brush row 3, number	26.7	27.0	5.1	1.2	19.2	12.0	38.0	19

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Approximations.

Generic assignment and comparison with related species (Table 48): This population belongs to *Spathidium*, as defined by FOISSNER (1984), because the somatic kineties adhere to the circumoral kinetofragments, especially on the left side. As concerns the species, *S. aciculare* is most similar to *Epispathidium ascendens*, as redescribed by FOISSNER (1987b), but differs in the shape of the extrusomes (acicular vs. rod-shaped) and the oral bulge (oblong vs. dumb-bell-shaped) as well as the oral ciliary pattern (*Spathidium* vs. *Epispathidium* pattern). Admittedly, the individual differences might be considered inconspicuous, but together they are a firm constellation suggesting species rank, especially since the differences were confirmed in several populations from various biogeographic regions. Of the three features mentioned, the extrusome shape is the most important. In this respect, but also in body size and shape, *Spathidium aciculare* resembles → *S. etoschense* which, however, has a comparatively short, rod-shaped macronucleus and only ten ciliary rows; furthermore, the dorsal brush rows are distinctly shorter (Table 48).

Table 48. Comparison of main morphometrics of *Spathidium aciculare* (upper line), *Epispathidium ascendens* (middle line; from FOISSNER 1987b), and → *Spathidium etoschense* (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	137.3	140.0	25.5	5.9	18.6	85.0	185.0	19
	143.4	144.0	17.2	4.5	12.0	100.0	168.0	13
	145.0	145.0	15.9	5.3	10.9	123.0	180.0	9
Body, width	31.5	32.0	3.4	0.8	10.9	26.0	38.0	19
	30.1	31.0	3.2	0.9	10.7	24.0	36.0	13
	22.7	22.0	4.9	1.6	21.8	17.0	32.0	9
Oral bulge, length	18.4	19.0	2.6	0.6	14.2	12.0	22.0	19
	25.7	27.0	3.3	0.9	12.8	20.0	30.0	13
	22.7	23.0	4.1	1.4	17.9	16.0	29.0	9
Somatic kineties, number	18.8	19.0	1.5	0.4	8.2	16.0	23.0	19
	21.6	21.0	1.6	0.4	7.2	20.0	25.0	13
	10.4	11.0	1.1	0.4	10.9	9.0	12.0	9
Dikinetids in middle brush row, number	34.3	36.0	6.1	1.4	17.8	19.0	43.0	19
	30.5	30.0	5.6	1.7	18.3	20.0	40.0	11
	17.6	19.0	3.9	1.5	22.0	12	21	7

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Spathidium contractile nov. spec. (Fig. 57a–l; 328g; Table 49)

Diagnosis: Size about 160 × 40 µm in vivo; contractile by about 20%. Spatulate with distinctly slanted, convex, cuneate oral bulge about as long as widest trunk region. Macronucleus long and tortuous, usually composed of 10 fairly distinct nodules. Two types of extrusomes: type I slightly curved, rather thick rods with bluntly pointed ends, about 5 × 0.5 µm in size; type II 1.5 µm long, thin rods. On average 17 ciliary rows, 3 anteriorly differentiated to inconspicuous dorsal brush occupying 15% of body length.

Type location: Mud and soil from road puddles in the Bambatsi Guest Farm, Namibia, 20°10'S 15°25'E (site 49 in figure 2 and chapter 2.1.2).

Etymology: The Latin adjective *contractilis* (to be able to contract) refers to a main feature of the species.

Description: This species was not very abundant, but present in the non-flooded Petri dish culture for several weeks. Thus, cells from three sampling occasions were used for morphometry, which increased variability coefficients to 20% and more because of several small specimens found in the last samplings; in spite of this, we included them in the analysis because they showed the minimum range and were well-impregnated. Ordinary variability coefficients between 10% and 20% were obtained when the small cells were excluded (shown for length and width in Table 49).

"Typical" size difficult to estimate due to contractility and the small cells mentioned above; however, when growing well often near to 160 × 40 µm, with a range from 130–200 × 30–55 µm; if the small specimens and one extraordinarily large cell are included, the range is somewhere between 80–280 × 30–60 µm! Likewise, length:width ratio varies considerably, on average it is near 3.2:1 in protargol preparations and 4:1 in vivo (Table 49). Shape basically spatulate with convex oral bulge distinctly slanted ventrally, main body axis slightly curved ventrally shifting posterior pole dorsally; flattened only in hyaline oral area. Contracted cells bluntly obclavate, contracts and extends slowly and not very distinctly, but shows conspicuous ridges with minute conical processes, which do not contain extrusomes (checked with oil immersion), mainly in posterior body half (Fig. 49a, c, d, j; 328g). Macronucleus on average in posterior two thirds of body and tortuous, when spread almost as long as cell; rather distinctly moniliform in 32 out of 41 specimens investigated, with an average of ten nodules connected by broad bridges and containing many ellipsoidal and globular nucleoli. On average nine ellipsoidal, slightly flattened micronuclei scattered throughout body. Contractile vacuole in rear end, 11 (n = 4) excretory pores in posterior pole area. Two types of extrusomes scattered in oral bulge and cytoplasm (Fig. 57a, b; 328g): type I conspicuous because comprising slightly curved, rather thick rods with bluntly pointed ends, about 5–6 × 0.5 µm in size, only those in cytoplasm lightly impregnate with protargol; type II rod-shaped, very inconspicuous because only 1.5 µm long, impregnates more or less distinctly with protargol both in oral bulge and cytoplasm. Cortex very flexible, contains rows of minute granules about 0.5 µm across in protargol preparations. Cytoplasm colourless, in well-fed specimens packed with extrusomes and globular inclusions up to 10 µm across, leaving blank flattened, hyaline oral area; two cells contained up to 35 µm large, fibrous

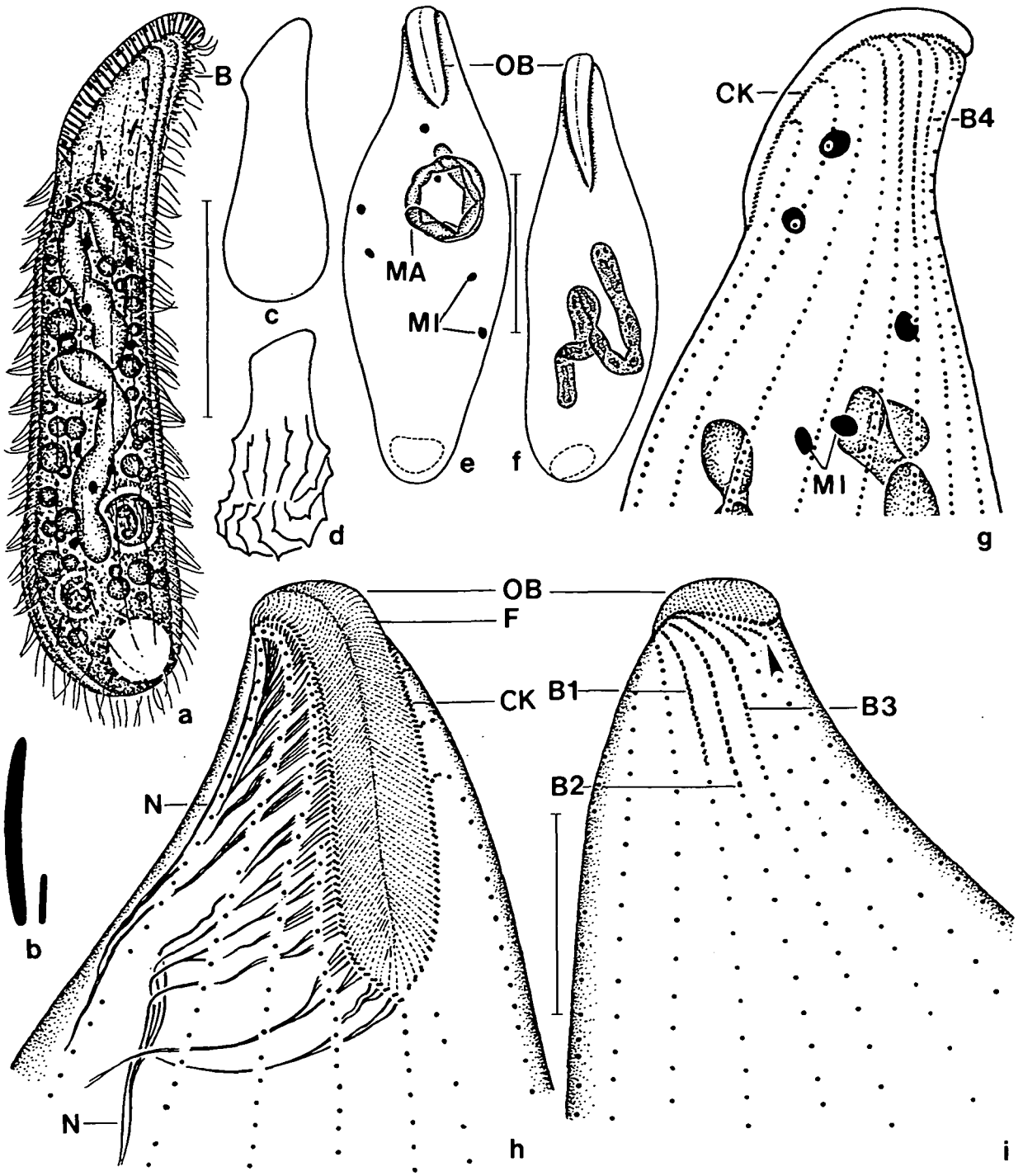

Fig. 57a–i. *Spathidium contractile* from life (a–d) and after protargol impregnation (e–l). **a:** Left side view of a representative specimen. **b:** Type I (length 5 µm) and type II (length 1.5 µm) oral extrusomes, drawn to scale. **c:** Same specimen as shown in (a), but contracted. **d:** Another contracted cell. **e, f:** Ventral views showing the cuneate oral bulge and the nuclear apparatus. **g:** Anterior left side region of holotype specimen, which has four dorsal brush rows (see figures 57j, k). **h, i:** Ventral and dorsal view of a broken specimen with slightly broadened oral bulge (cp. figures 57e, f). Arrowhead marks a supernumerary kinetofragment. B(1-4) – dorsal brush (rows), CK – circumoral kinety, F – fibres, MA – macronucleus, MI – micronucleus, N – nematodesmata, OB – oral bulge. Scale bars 50 µm (a, e, f) and 20 µm (h, i).

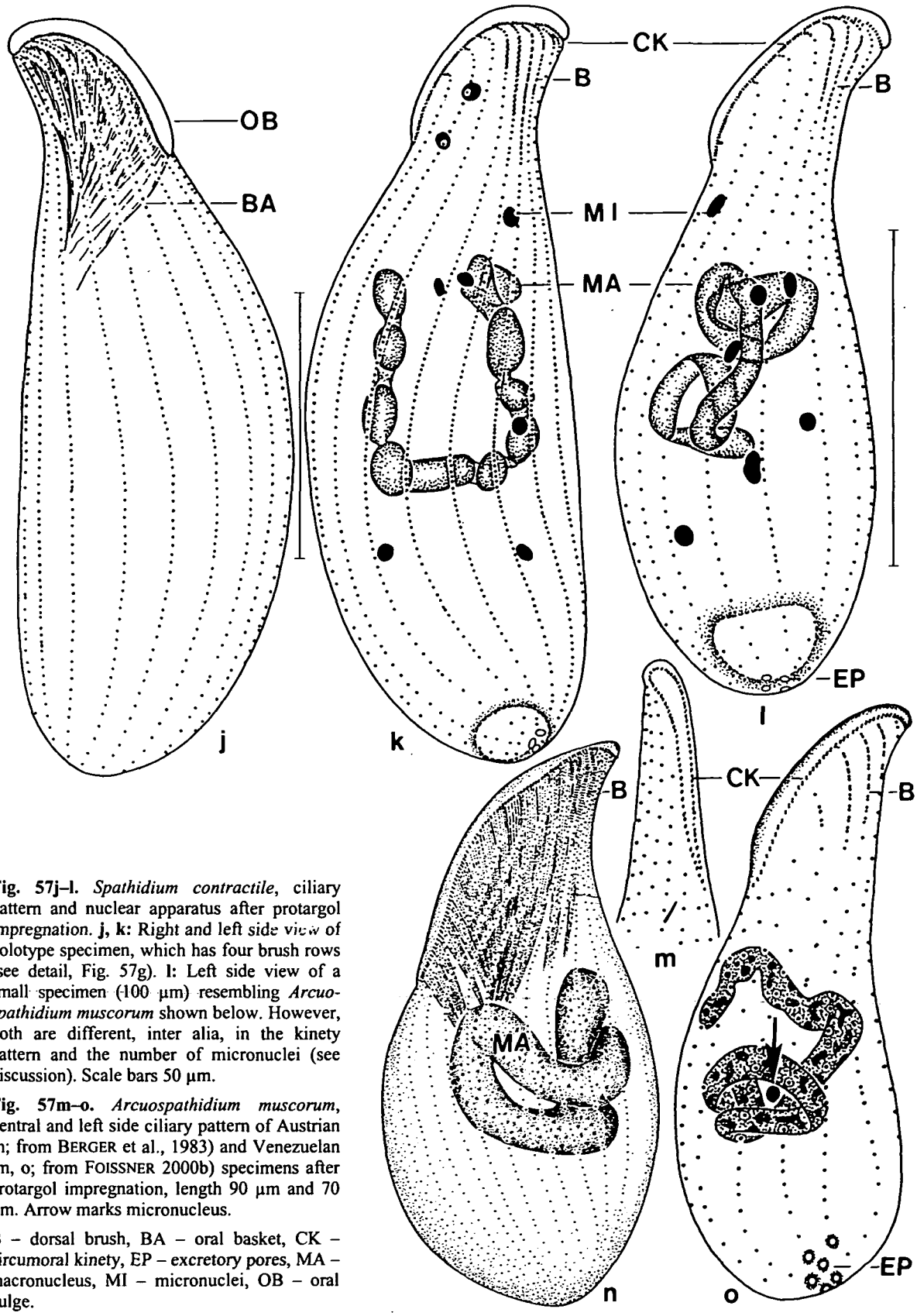

Fig. 57j–l. *Spathidium contractile*, ciliary pattern and nuclear apparatus after protargol impregnation. **j, k:** Right and left side view of holotype specimen, which has four brush rows (see detail, Fig. 57g). **l:** Left side view of a small specimen (100 µm) resembling *Arcuospathidium muscorum* shown below. However, both are different, inter alia, in the kinety pattern and the number of micronuclei (see discussion). Scale bars 50 µm.

Fig. 57m–o. *Arcuospathidium muscorum*, ventral and left side ciliary pattern of Austrian (n; from BERGER et al., 1983) and Venezuelan (m, o; from FOISSNER 2000b) specimens after protargol impregnation, length 90 µm and 70 µm. Arrow marks micronucleus.

B – dorsal brush, BA – oral basket, CK – circumoral kinety, EP – excretory pores, MA – macronucleus, MI – micronuclei, OB – oral bulge.

Table 49. Morphometric data on *Spathidium contractile.*

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	135.0	131.0	38.3	8.4	28.4	77.0	250.0	21
Body, width	44.7	45.0	8.5	1.9	19.0	29.0	57.0	21
Body length:width, ratio	3.2	3.2	0.8	0.2	24.7	2.1	4.7	21
Body, length [b]	142.9	137.0	17.0	4.4	11.9	120.0	170.0	15
Body, width [b]	47.0	49.0	7.5	1.9	15.9	32.0	57.0	15
Body length:width, ratio [b]	3.3	3.1	0.7	0.2	20.8	2.2	4.6	15
Oral bulge (circumoral kinety), length	40.7	40.0	8.0	1.7	19.7	26.0	60.0	21
Oral bulge (circumoral kinety), width near dorsal end	8.0	8.0	1.6	0.4	19.6	6.0	10.0	14
Circumoral kinety to last dikinetid of brush row 1, distance	14.6	15.0	5.6	1.2	38.3	7.0	28.0	21
Circumoral kinety to last dikinetid of brush row 2, distance	19.7	19.0	5.2	1.1	26.3	10.0	30.0	21
Circumoral kinety to last dikinetid of brush row 3, distance	13.3	12.0	4.6	1.0	34.2	8.0	25.0	21
Circumoral kinety to last dikinetid of brush row 4, distance	10.5	11.0	3.6	1.5	34.4	5.0	15.0	6
Anterior body end to macronucleus, distance	50.8	44.0	23.9	5.2	47.1	27.0	132.0	21
Nuclear figure, length	50.2	47.0	17.7	3.9	35.2	27.0	85.0	21
Macronucleus, length (spread)	116.9	110.0	36.6	7.9	31.1	70.0	200.0	21
Macronucleus, width	6.8	7.0	1.4	0.3	20.7	5.0	11.0	21
Macronuclear nodules, number [c]	10.2	10.0	2.1	0.5	20.5	6.0	13.0	21
Micronuclei, length	3.7	4.0	–	–	–	3.0	4.5	12
Micronuclei, width	3.3	3.0	–	–	–	2.5	3.5	12
Micronuclei, number	8.8	9.0	2.4	0.7	27.8	5.0	13.0	12
Somatic kineties, number	17.0	16.0	5.0	1.1	29.4	15.0	26.0	21
Ciliated kinetids in a right kinety, number	58.2	60.0	10.4	4.2	17.9	40.0	70.0	6
Dorsal brush rows, number	3.4	3.0	–	–	–	3.0	5.0	21
Dikinetids in brush row 1, number	15.9	17.0	4.4	1.0	27.7	8.0	24.0	21
Dikinetids in brush row 2, number	20.8	22.0	3.7	0.8	17.8	16.0	30.0	21
Dikinetids in brush row 3, number	12.6	11.0	4.2	0.9	33.5	8.0	21.0	21
Dikinetids in brush row 4, number	7.6	10.0	3.8	1.7	49.8	3.0	11.0	5

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Small specimens from declining population excluded.

[c] Of 41 specimens investigated, 32 have a distinctly moniliform nucleus, in 4 it is indistinctly nodulated, and in 5 it is not nodulated. Morphometry contains only specimens with nodulated macronucleus.

aggregates, possibly parasitic bacteria. Feeds mainly on ciliates, for instance, *Vorticella astyliformis*, which could be identified in the food vacuoles. Movement conspicuous because slowly creeping showing slight, spontaneous contractions.

Somatic cilia about 8 µm long in vivo, ordinarily spaced, arranged in an average of 17 equidistant, bipolar rows, which is few compared to similar-sized species, such as → *Spathidium seppelti etoschense* (28) and → *Epispathidium polynucleatum* (23). Right side kineties anteriorly strongly curved dorsally and distinctly separated from circumoral kinety in

ventral half of cell; left side kineties anteriorly with some narrowly spaced cilia and curved ventrally to abut to circumoral kinety at roughly right angles (Fig. 57a, h–l; Table 49). Dorsal brush inconspicuous because short, that is, longest middle row occupies only 15% of body length on average, and having only 1–3 µm long bristles; basically three-rowed, but a fourth or even fifth row occurs in almost one third of specimens; row 3 with a monokinetidal bristle tail; all brush kineties continue posteriorly as normal ciliary rows (Fig. 57a, g, i, k, l; Table 49).

Oral bulge about as long as widest postoral region, conspicuous because inclined to main body axis by about 45° and containing many thick and thus refractive extrusomes; distinctly convex, ventral outline cuneate to bluntly cuneate and rather massive because up to 10 µm wide dorsally; contains rather thick, lightly impregnated fibres originating from circumoral dikinetids and extending obliquely dorsally, forming an arrowhead-like pattern (Fig. 57a, e–l; Table 49). Circumoral kinety cuneate to bluntly cuneate, composed of oblique dikinetids associated with bulge fibres described above and comparatively thick and long nematodesmata, forming conspicuous bundles assembling to a large oral basket (Fig. 49g, h–l).

Occurrence and ecology: To date found only at type location, where it was moderately abundant two weeks after rewetting the sample. Considering the habitat, it is impossible to know whether *S. contractile* is a limnetic or terrestrial species.

Generic classification and comparison with related species: *Spathidium contractile* has several unusual features, suggesting that it might be the representative of a new subgenus or genus. First, it is sole contractile *Spathidium*; second, the oral bulge highly resembles *Arcuospathidium*; third, the macronucleus is nodulated, a rare feature in the genus; and fourth, *S. contractile* has only an average of 17 ciliary rows, which is few compared to similar-sized congeners, as listed above.

There are several species which are similar to *S. contractile*, viz., *Spathidium moniliforme* BATHIA, 1920; *S. truncatum* STOKES, 1885; *S. scalpriforme* KAHL, 1930a; → *S. extensum* KAHL, 1933; and *S. longinucleatum* GELEI, 1954. However, all are acontractile, most of them have at least twice the number of ciliary rows, and many have different extrusomes, if known at all. The small specimens from the declining population look highly similar to *Arcuospathidium muscorum* (DRAGESCO & DRAGESCO-KERNÉIS, 1979), as evident from figures 57l–o. The three (sophisticated) features separating them unequivocally are the minute type II extrusomes, lacking in *A. muscorum*; the micronuclei (many vs. one); and the left side kineties, which are connected with the circumoral kinety in *S. contractile*.

Spathidium lanceoplites nov. spec. (Fig. 58a–l; Table 50)

Diagnosis: Size about 80 × 15 µm in vivo. Oblong to indistinctly spatulate with distinctly slanted, obovate, minute oral bulge about 1/3 as long as widest trunk region. Macronucleus elongate ellipsoidal. Extrusomes lanceolate to ovate, about 2 × 0.8 µm in size. On average 7 ciliary rows, 3 anteriorly differentiated to inconspicuous dorsal brush occupying 16% of body length.

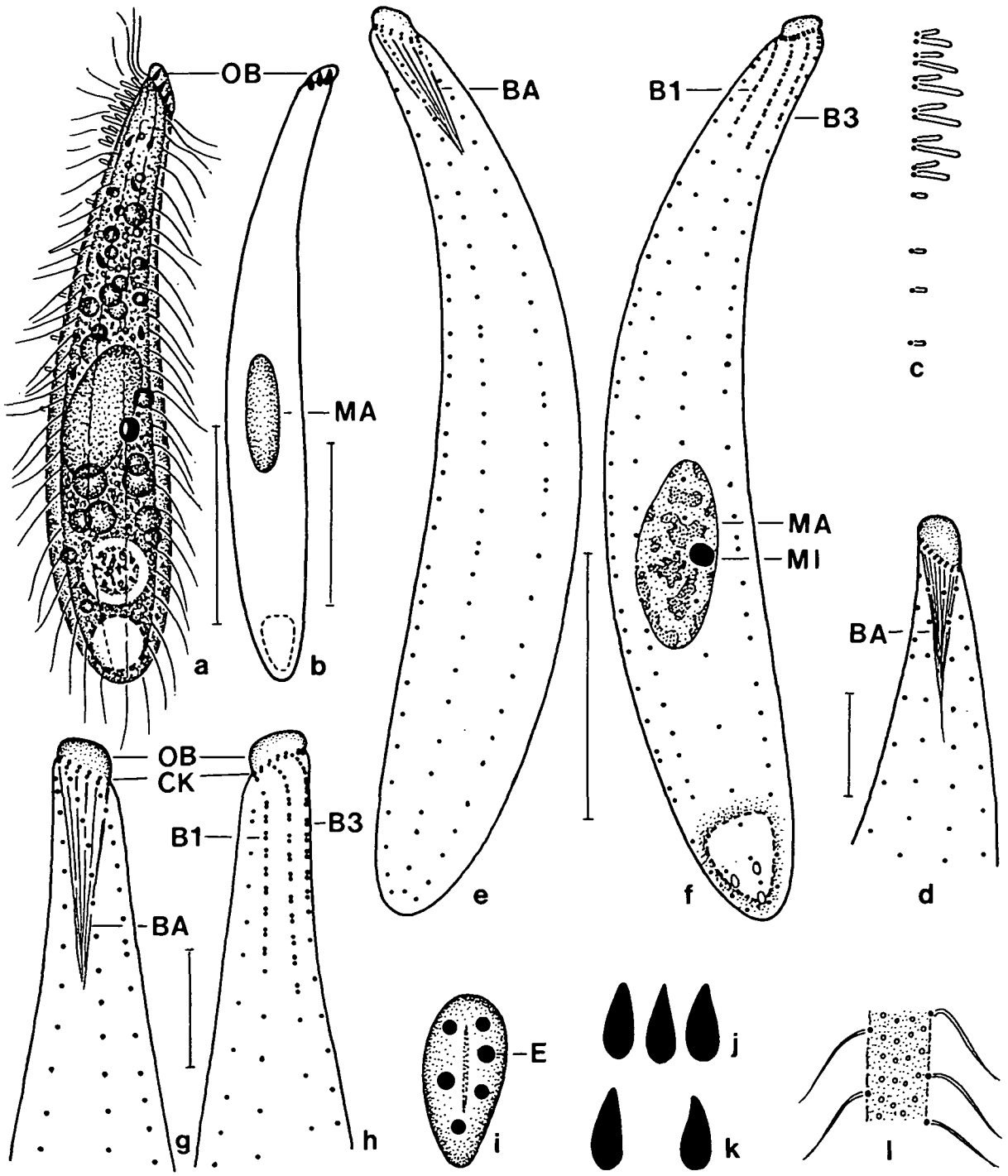

Fig. 58a–l. *Spathidium lanceoplites* from life (a–c, i–l) and after protargol impregnation (d–h). **a:** Right side view of a representative specimen. **b:** A slender specimen. **c:** Posterior portion of brush row 3, which has a tail of about eight 1 µm long, monokinetidal bristles. **d:** Ventrolateral view of anterior body region. **e, f:** Ciliary pattern of right and left side and nuclear apparatus of holotype specimen. **g, h:** Ciliary pattern in right and left anterior region. The brush is laterally located. **i:** Frontal view of oral bulge. **j, k:** Oral bulge extrusomes of specimens from Namibian sites 49 (j) and 33 (k), 1.5–2 × 0.8 µm. **l:** Loose cortical granulation. B1-3 – dorsal brush rows, BA – oral basket, CK – circumoral kinety, E – extrusome, MA – macronucleus, MI – micronucleus, OB – oral bulge. Scale bars 25 µm (a, b, e, f) and 10 µm (d, g, h).

Type location: Mud and soil from road puddles in the Bambatsi Guest Farm, Namibia, 20°10'S 15°25'E (site 49 in figure 2 and chapter 2.1.2).

Etymology: Composite of the Latin noun *lancea* (lance) and the Greek noun *hoplites* (soldier ~ extrusome), referring to the lanceolate extrusomes.

Description: Size 45–130 × 10–20 µm in vivo, usually near 80 × 15 µm; length:width ratio also highly variable, viz., 3.5–6.5:1, on average 5.2:1 in protargol preparations, up to 8:1 in vivo (Fig. 58b; Table 50). Shape inconspicuous, that is, oblong to indistinctly spatulate, rarely almost cylindroidal, slightly flattened only in oral area (Fig. 58a, e). Nuclear apparatus on average slightly underneath mid-body, consists of an ellipsoidal (2:1) to elongate ellipsoidal (3:1) macronucleus with lobate nucleoli and a broadly ellipsoidal micronucleus attached to macronucleus. Contractile vacuole in rear end, several excretory pores subterminal on left side. Extrusomes scattered in oral bulge and cytoplasm; bulge extrusomes slightly asymmetrical, lanceolate to ovate, although minute, that is, about 1.5–2 × 0.8 µm, rather distinct because strongly refractive in vivo; posterior half occasionally impregnates with the protargol method used (Fig. 58a, b, i–k). Cortex flexible, contains comparatively widely spaced

Table 50. Morphometric data on *Spathidium lanceoplites*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	74.2	72.0	16.9	3.9	22.8	42.0	120.0	19
Body, width	14.4	14.0	2.9	0.7	20.5	10.0	23.0	19
Body length:width, ratio	5.2	4.8	1.0	0.2	19.0	3.5	6.5	19
Oral bulge, length	4.1	4.0	0.8	0.2	19.0	3.0	6.0	19
Oral bulge, height	1.9	2.0	–	–	–	1.5	2.5	19
Circumoral kinety to last dikinetid of brush row 1, distance	9.1	9.0	2.0	0.5	22.1	6.0	14.0	19
Circumoral kinety to last dikinetid of brush row 2, distance	11.6	11.0	2.2	0.5	18.8	8.0	18.0	19
Circumoral kinety to last dikinetid of brush row 3, distance	7.5	7.0	2.6	0.6	34.2	4.0	15.0	19
Anterior body end to macronucleus, distance	34.7	35.0	8.8	2.0	25.3	20.0	57.0	19
Macronucleus, length	16.1	16.0	2.0	0.4	12.4	13.0	20.0	19
Macronucleus, width	6.4	6.0	1.0	0.2	15.9	5.0	8.0	19
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
Micronucleus, length	2.9	3.0	–	–	–	2.0	4.0	8
Micronucleus, width	2.3	2.5	–	–	–	1.7	3.0	8
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	8
Somatic kineties, number	7.3	7.0	0.7	0.2	10.2	7.0	10.0	19
Ciliated kinetids in a right kinety, number	31.6	32.0	3.6	0.8	11.5	22.0	37.0	19
Dorsal brush rows, number [b]	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
Dikinetids in brush row 1, number	7.7	8.0	1.1	0.3	14.3	6.0	9.0	19
Dikinetids in brush row 2, number	10.1	10.0	1.4	0.3	13.6	6.0	12.0	19
Dikinetids in brush row 3, number	6.1	6.0	1.6	0.4	25.6	4.0	11.0	19

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Only two rows in one out of 30 specimens.

rows of loosely arranged, minute granules about 0.3 µm across. Cytoplasm colourless, in well-fed specimens packed with lipid droplets up to 6 µm across, leaving blank oral area, which is thus hyaline. Likely feeds on protists, as indicated by the fatty inclusions. Movement without peculiarities.

Somatic cilia about 7 µm long in vivo and ordinarily spaced, arranged in an average of only seven equidistant, bipolar kineties anteriorly forming a *Spathidium*-pattern (FOISSNER 1984), which, however, is rather indistinct due to the low number of rows. Dorsal brush occupies anterior left side of cell, of usual structure, inconspicuous because occupying only 16% of body length and bristles merely up to 4 µm long. Brush row 1 composed of an average of eight bristles; middle row 2 slightly longer than row 1 and distinctly longer than dikinetidal portion of row 3, composed of an average of ten dikinetids; anterior portion of row 3 composed of an average of six dikinetids, followed by about eight 1 µm long bristles forming a tail extending to mid-body (Fig. 58a, c–h; Table 50).

Oral bulge minute because less than half as long as widest trunk region, but rather conspicuous due to the refractive and thus bright extrusomes contained; moderately convex in lateral view and distinctly obovate when viewed ventrally. Circumoral kinety also obovate, composed of few, comparatively loosely spaced dikinetids associated with fine nematodesmata forming a conspicuously conical oral basket (Fig. 58a, b, d–i; Table 50).

Occurrence and ecology: To date found at type location, i.e., a semiterrestrial biotope, and at site (33), that is, a sand dune in the Namib Escarpment, indicating that it prefers terrestrial habitats. *Spathidium lanceoplites* is well adapted to soil life by the small, slender body.

Comparison with related species: *Spathidium lanceoplites* has the same size, shape, and nuclear apparatus as *S. claviforme* and *Protospathidium terricola*, as described by FOISSNER (1987b) and FOISSNER (1998a). In spite of this, in vivo it is easily separated from these species by the minute extrusomes (lanceolate and 1.5–2 µm vs. 4–6 µm long, fine rods) and the small number of ciliary rows (on average 7 vs. 12, respectively, 21).

Spathidium lanceoplites is also rather similar to *S. vermiculus*, which KAHL (1926, 1930a) discovered in a moorland drain filled with decaying leaves. However, *S. vermiculus* is smaller (50 µm) and has rod-shaped, 3.3 µm long extrusomes and a longer oral bulge about as wide as the broadest trunk region.

Spathidium extensum KAHL, 1933 (Fig. 59a–n; Table 51)

Improved diagnosis: Size about 220 × 30 µm in vivo. Spatulate with steep, massive, elliptical oral bulge slightly longer than widest trunk region. Macronucleus in about 10 irregular pieces or in one or more tortuous strands. Extrusomes rod-shaped, thick, about 5 × 1 µm. On average 17 ciliary rows, 3 to 4 anteriorly differentiated to distinct dorsal brush occupying 23% of body length.

Description of Namibian site (54) population: Size 150–250 × 20–40 µm in vivo, usually about 220 × 30 µm, rarely over-sized specimens of up to 330 µm occur, and early

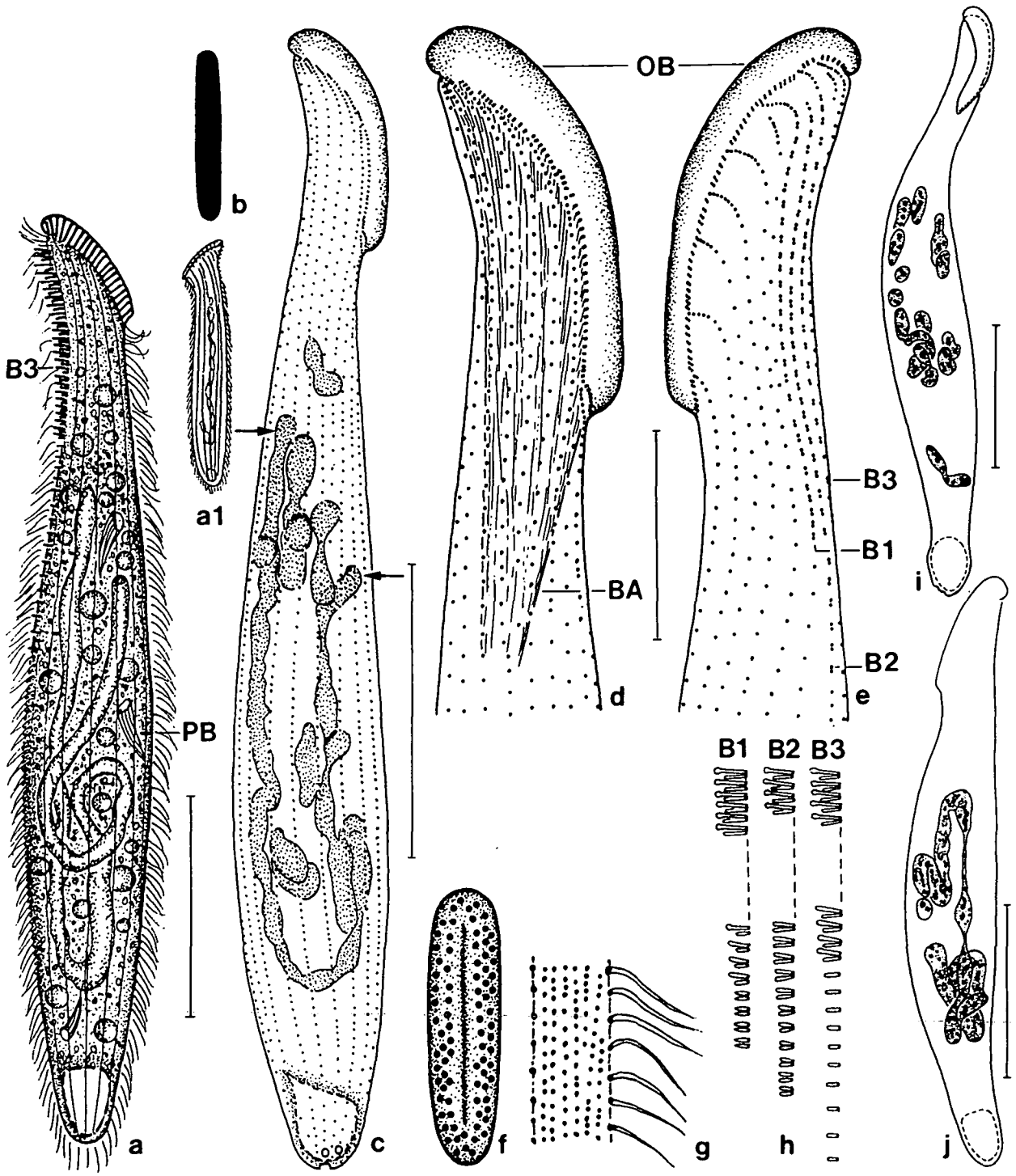

Fig. 59a–j. *Spathidium extensum* from life (a, b, f–h) and after protargol impregnation (c–e, i, j). **a, a1:** Right side view of a post-divider from Namibia (a) and left side view of German type specimen (a1), likely also a post-divider (length 200–250 µm; from KAHL 1933). The monokinetidal bristle tail of brush row 3 extends to mid-body. **b:** Extrusome, 5–6 µm long. **c–e:** Ciliary pattern of right side and of right and left anterior body portion of same specimen. Arrows mark anterior and posterior end of a long, tortuous macronuclear fragment. **f:** Frontal view of oral bulge studded with extrusomes. **g:** Cortical granulation. **h:** Brush structure, longest bristles 5 µm. **i, j:** Variability of macronucleus. B1, 2, 3 – dorsal brush rows, BA – oral basket, CK – circumoral kinety, MA – macronucleus, OB – oral bulge. Scale bars 50 µm (a, c, i, j) and 20 µm (d, e).

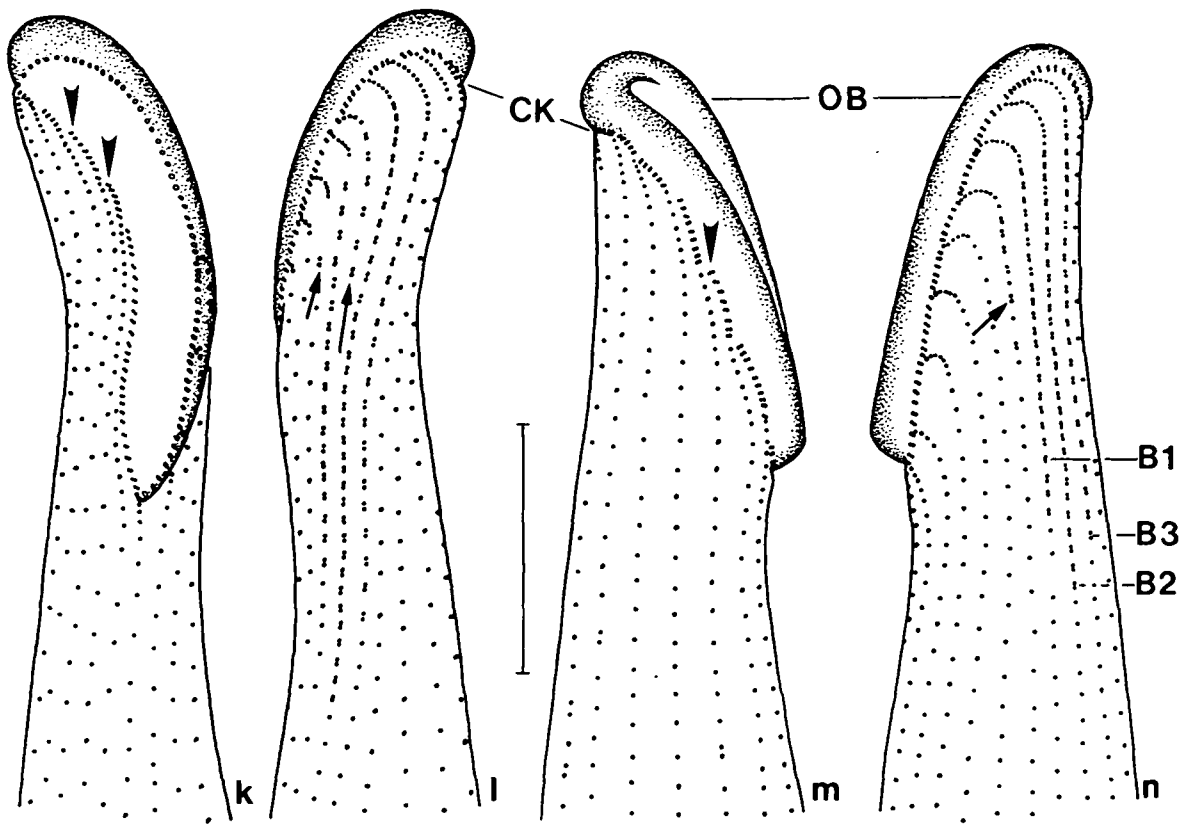

Fig. 59k–n. *Spathidium extensum*, oral and somatic ciliary pattern of anterior body region after protargol impregnation. Arrows mark short, supernumerary dorsal brush rows. Arrowheads denote dikinetidal kinety fragments, which build the circumoral kinety at the anterior end of the ciliary rows. **k, l:** Ventral and dorsal view of specimen shown in figure (i). **m, n:** Ventrolateral and dorsolateral view of specimen shown in figure (j). B1, 2, 3, – dorsal brush rows, CK – circumoral kinety, OB – oral bulge. Scale bar 20 μm for all figures.

to middle dividers may reach up to 400 μm; length: width ratio also highly variable, viz. 5–10:1, on average 7:1. Shape inconspicuous, that is, more or less distinctly spatulate or fusiform with neck usually narrowed and oral bulge distinctly slanted; acontractile and flattened only in oral and neck region (Fig. 59a, c). Macronucleus highly variable, a single or two tortuous strands in about one third of specimens, 3 to 21 globular to very elongate pieces in the others; pieces frequently in more or less distinct series, indicating that they arise by fragmentation of a tortuous strand (Fig. 59a, c, i, j). See discussion for an explanation. Many globular micronuclei, exact number could not be counted because of many similarly sized and impregnated cytoplasmic inclusions. Contractile vacuole in rear end, some excretory pores in posterior pole area. Extrusomes accumulated in oral bulge and scattered in cytoplasm, rod-shaped or slightly fusiform with rounded ends, conspicuous because about 5–6 × 1 μm, that is, rather thick (Fig. 59a, b, f). Cortex very flexible, contains about six rows of minute (< 0.5 μm) but compact, colourless granules between each two ciliary rows. Cytoplasm colourless, packed with fat globules up to 5 μm across and pharyngeal baskets of ingested microthoracid ciliates in well-nourished specimens. Glides and swims rather rapidly.

Cilia arranged in an average of 17 equidistant, mostly bipolar, densely ciliated rows abutting on circumoral kinety in acute (at right side) to almost right angles (at left), as is typical for

Spathidium (but see discussion). Dorsal brush rather conspicuous because occupying about 23% of body length and having up to 5 µm long bristles; all rows with rather long, monokinetidal portion anteriorly; rather irregular, that is, consisting of three ordinary rows and one or two additional short rows right of row 1 or between rows 1 to 3. Anterior basal body of row 1 dikinetids associated with an about 5 µm long, distally spherically inflated bristle in anterior quarter of row; bristles decrease in length and become tongue-shaped posteriorly. Brush row 2 like row 1, bristles however not tongue-shaped but slightly inflated in posterior portion of row; continues, like row 1, as an ordinary somatic kinety posteriorly. Brush row 3 anteriorly like row 1, posteriorly with a monokinetidal bristle tail extending to mid-body (Fig. 59a, e, h, k–n; Table 51).

Oral bulge comparatively short, that is, only slightly longer than widest trunk region, but massive and packed with extrusomes making it conspicuous both in vivo and protargol preparations, where the oral body portion is axe-shaped in specimens with distinctly narrowed neck; conspicuously slanting, ventral half occasionally even parallel to main body axis; elongate elliptical in frontal view. Circumoral kinety also elongate elliptical, but with ventral portion narrowed and bluntly pointed; comprising dikinetidal fragments frequently incompletely aligned, especially at right side, producing a → *Protospathidium* pattern. Oral basket composed of many fine fibres impregnating only faintly with the protargol method used (Fig. 59a, c–f, k–n; Table 51).

Table 51. Morphometric data on *Spathidium extensum*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	186.7	185.0	35.2	7.7	18.8	133.0	300.0	21
Body, width	26.3	27.0	3.4	0.8	13.0	19.0	33.0	21
Body length:width, ratio	7.1	7.0	1.1	0.2	16.0	5.0	10.0	21
Oral bulge (circumoral kinety), length	32.1	30.0	5.7	1.2	17.8	22.0	40.0	21
Circumoral kinety to last dikinetid of brush row 1, distance	35.1	33.0	8.0	1.8	22.9	25.0	60.0	21
Circumoral kinety to last dikinetid of brush row 2, distance	43.5	44.0	7.4	1.6	17.0	31.0	65.0	21
Circumoral kinety to last dikinetid of brush row 3, distance	39.4	38.0	9.0	2.0	22.8	25.0	62.0	21
Anterior body end to first macronuclear nodule, distance	55.4	53.0	15.7	3.4	28.3	33.0	107.0	21
Nuclear figure, length	89.1	91.0	21.9	4.8	24.6	50.0	135.0	21
Macronuclear pieces, width	4.5	4.0	1.0	0.2	21.9	3.0	7.0	21
Macronuclear pieces, number	up to 21, usually about 10; see discussion							21
Somatic kineties, number	17.2	17.0	1.3	0.3	7.3	15.0	20.0	21
Ciliated kinetids in a right side kinety, number	87.7	80.0	24.6	5.8	28.0	50.0	140.0	18
Dorsal brush rows, number	basically three, see text							
Dikinetids in brush row 1, number	23.8	24.0	6.0	1.3	25.3	15.0	38.0	21
Dikinetids in brush row 2, number	34.1	32.0	5.6	1.2	16.3	24.0	47.0	21
Dikinetids in brush row 3, number	25.5	24.0	4.6	1.0	18.2	20.0	37.0	21

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Occurrence and ecology: See next chapter.

Generic assignment and comparison with original description and related species: The dikinetidal fragments comprising the circumoral kinety of *S. extensum* are often not fully aligned, producing a pattern typical for *Protospathidium*. However, the general organization, especially the distinct dorsal brush and the massive oral bulge indicate that the Namibian population belongs to *Spathidium*.

Spathidium extensum is highly variable in two important features which are usually fairly constant, viz. the macronuclear pattern and the number of dorsal brush rows (Fig. 59c, i, j; Table 51). Often, such variability is found in declining cultures or associated with weak populations. However, the *S. extensum* culture was in good condition and contained a fairly high number of individuals as well as some dividers. The latter suggests that *S. extensum* basically has scattered macronuclear nodules, and specimens with one or more tortuous macronuclear strands are post-dividers, as shown in → *Spathidium turgitorum*. Possibly, full post-divisional macronuclear fragmentation needs more time in *S. extensum* than → *S. turgitorum*, and thus such specimens are more frequent in the population. KAHL (1935) also mentioned the high variability of the macronucleus.

The most important features of the Namibian specimens, viz., the large size and slender shape (220 × 30 µm), the short but massive extrusomes (5–6 × 1 µm), and the comparatively short oral bulge (one sixth of body length) match the description of *S. extensum* (Fig. 59a, l), which KAHL (1933, 1935) discovered in a ditch with sea-water at Sylt, Germany. Later, VUXANOVICI (1959) reported it from a freshwater lake (Herastrau) in Romania. Both descriptions are brief and lack reliable details, but KAHL (1933) mentions that the extrusomes are short (4 µm) and thin, while those of the Namibian specimens are thick. However, thin and thick are relative if not substantiated by measurements or figures. Thus, it would be difficult to find reliable differences between the Namibian and German populations at the present state of knowledge. This is emphasized by the biotopes: a sea-water filled ditch and highly saline soil from a flooded part of the Etosha Pan. In spite of this, we do not neotypify the species with the Namibian material because marine spathidiids are so poorly known.

The features listed above, especially the short extrusomes, separate *S. extensum* from several similar soil spathidiids, such as *S. muscicola* KAHL, 1930b, *Epispathidium terricola* FOISSNER, 1987b, and *E. ascendens*, as redescribed by FOISSNER (1987b). The most similar species are probably → *S. rusticanum* (stouter, dorsal brush short) and its relatives, especially *S. anguilla*, as redescribed by FOISSNER (1984). Further, all these species have a different oral infraciliature.

Supraspathidium etoschense nov. spec. (Fig. 60a–j, m, o; 326a–i; Table 52)

Diagnosis: Size about 200 × 70 µm in vivo. Spatulate to bursiform with elliptical, oblique oral bulge about half as wide as broadest postoral region; unflattened. Macronucleus tortuous and up to twice as long as cell. Contractile vacuole row right of dorsal brush. Oral bulge extrusomes elongate clavate, about 7 µm long. On average 44 ciliary rows.

Type location: Highly saline soil from margin of Etosha Pan, Namibia, 18°50'S 16°30'E (site 67 in figures 2, 3 and chapter 2.1.2).

Etymology: Named after the region discovered.

Description: This species is difficult to impregnate because it is large and usually packed with food inclusions. Thus, the type slides are mediocre, and especially the excretory pores of the contractile vacuoles are very faintly impregnated. The vacuoles proper, however, are well recognizable under interference contrast illumination. Accordingly, the occurrence of several contractile vacuoles in dorsolateral position is recognizable in the type slides.

Size 140–250 × 50–90 µm in vivo, usually near 200 × 70 µm; length:width ratio about 3:1 in vivo and 2.5:1 in protargol preparations, indicating that specimens became inflated and/or shrunk considerably during preparation (Table 52). Shape also very variable, obviously highly dependent on nutrition condition, viz., spatulate, bursiform, elongate bursiform, or cylindroidal (Fig. 60a, f, g); oral region flattened up to 2:1, postoral portion cylindroidal. Macronucleus in main body axis and highly tortuous, at least as long as to up to twice as long as cell, occasionally slightly nodulated. Several micronuclei, exact number difficult to assess because of many similarly sized and impregnated cell inclusions (Fig. 60a, m; 326a, b). One large terminal contractile vacuole and three to six small contractile vacuoles, each with usually several excretory pores, in dorsolateral position, that is, about ten kineties right of dorsal brush (Fig. 60a, f, o). Extrusomes packed in oral bulge and scattered in cytoplasm, 6–8 µm long, rod-shaped with fusiform subterminal inflation when attached to oral bulge (Fig. 60c, f); inflation almost disappears in preparations (Fig. 326c, e, h) and, in vivo, when extrusomes become detached from bulge (Fig. 60d; 326g), a peculiar feature observed in three carefully studied specimens; do not impregnate with protargol, but stain heavily with silver carbonate and become rod-shaped or elongate cuneate. Many minute rods (1.5–2 µm), very likely also extrusomes, scattered in oral bulge and cytoplasm, impregnate with silver carbonate (Fig. 60e; 326c, e, h). Cortex very flexible and rather thick, contains closely spaced rows of colourless granules (mucocysts ?) about 1 µm across (Fig. 60h). Cytoplasm usually packed with food vacuoles and lipid droplets up to 10 µm across, often colourful due to ingested, cyanobacteria feeding nassulids and colpodids (e.g., *Nassula granata, Kuklikophrya ougandae*). Swims rather rapidly by rotation about main body axis.

Somatic cilia about 10 µm long in vivo, form rather closely spaced, equidistant rows commencing around circumoral kinety and extending meridionally to posterior body end. Cilia closely spaced within rows (about 1 µm; Table 52), especially at anterior end, where short "perioral" fragments are produced. All ciliary rows abut on circumoral kinety, those on right side in very steep angles, those on left conspicuously curved with anterior portion directed ventrally (Fig. 60a, j, m; 326c, d, f, h). Three dorsal rows anteriorly differentiated to an about 45 µm long dorsal brush composed of paired, about 3 µm long, rod-shaped bristles; row 3 extends to mid-body with about 2 µm long, monokinetidal bristles and then continues, as the other brush rows usually do, as an ordinary somatic ciliary row (Fig. 60a, i, o; 326i).

Oral area flattened and usually set off from body proper by a slight constriction. Oral bulge obliquely (about 45°) truncate, oblong and bright in frontal view due to the refractive extrusomes contained, inconspicuous compared to size of cell because only about 3 µm high; ciliary rows thus extend almost to anterior body end, producing the pattern characteristic for this kind of spathidiids. Circumoral kinety at base of oral bulge and thus oblong, composed of very closely spaced dikinetids (Fig. 60a, b, j, m; 326b, c, d, f, h).

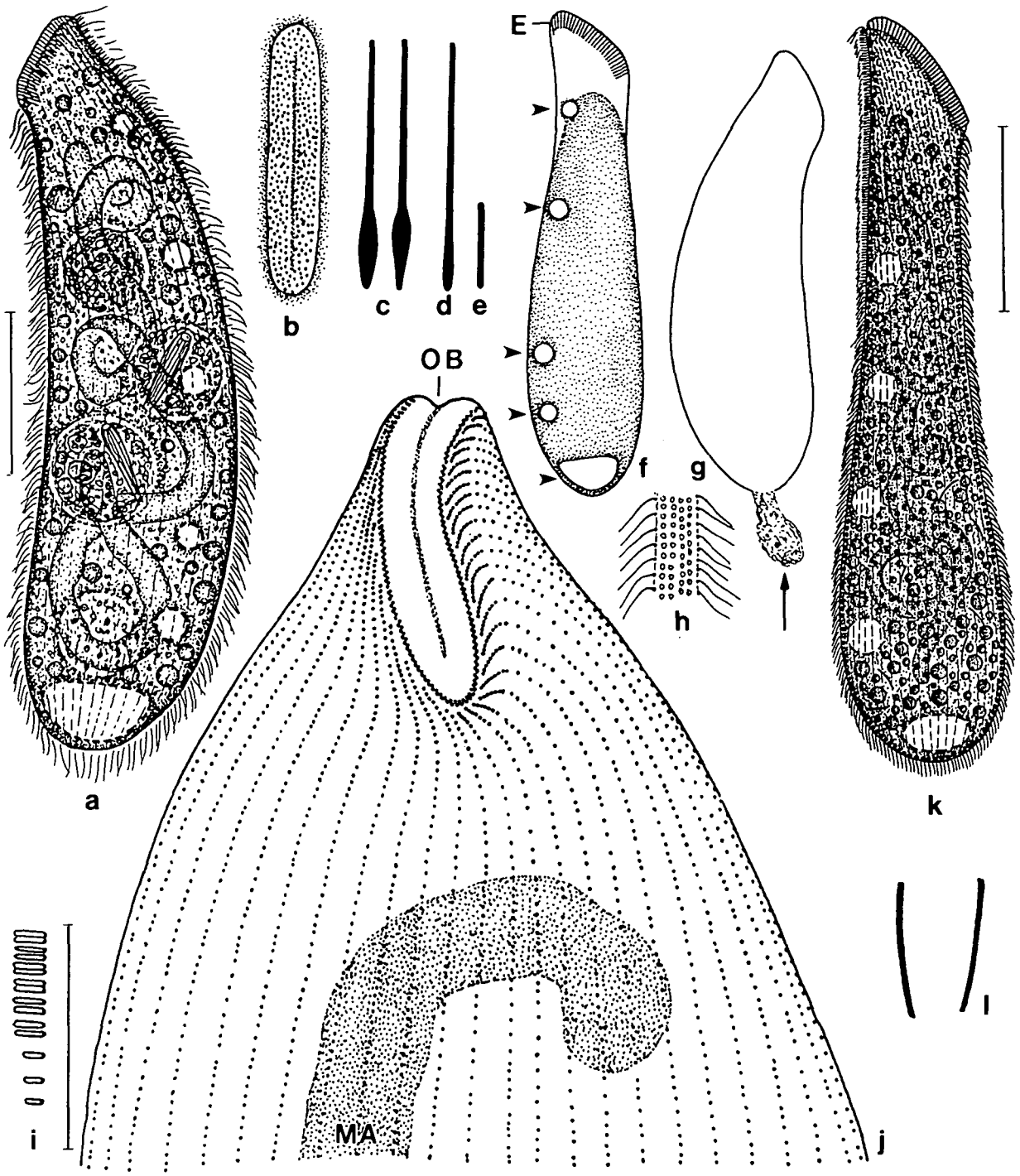

Fig. 60a–l. *Supraspathidium etoschense* (a–j) and *S. multistriatum* (k, l; from FOISSNER & DIDIER 1981) from life (a–i, k, l) and after protargol impregnation (j). **a:** Left side view of a specimen with large food vacuoles containing oral baskets from nassulids. **b:** Frontal view of oral bulge studded with extrusomes. **c:** Shape of extrusomes when attached to oral bulge, length 6–8 µm. **d:** Shape of an extrusome detached from oral bulge. **e:** Minute extrusome, length 1.5–2 µm. **f:** An ordinarily fed, spatulate specimen with five contractile vacuoles (arrowheads). **g:** Bursiform, dark specimen packed with food vacuoles and lipid droplets. Arrow marks slimy faecal mass leaving cell. **i:** Brush row 3 in the transition zone of dikinetidal and monokinetidal bristles. **j:** Ciliary pattern of ventral anterior region. **k:** Right side view of a representative specimen. **l:** Extrusomes. E – extrusomes, MA – macronucleus, OB – oral bulge. Scale bars 20 µm (j), 50 µm (a), 100 µm (k).

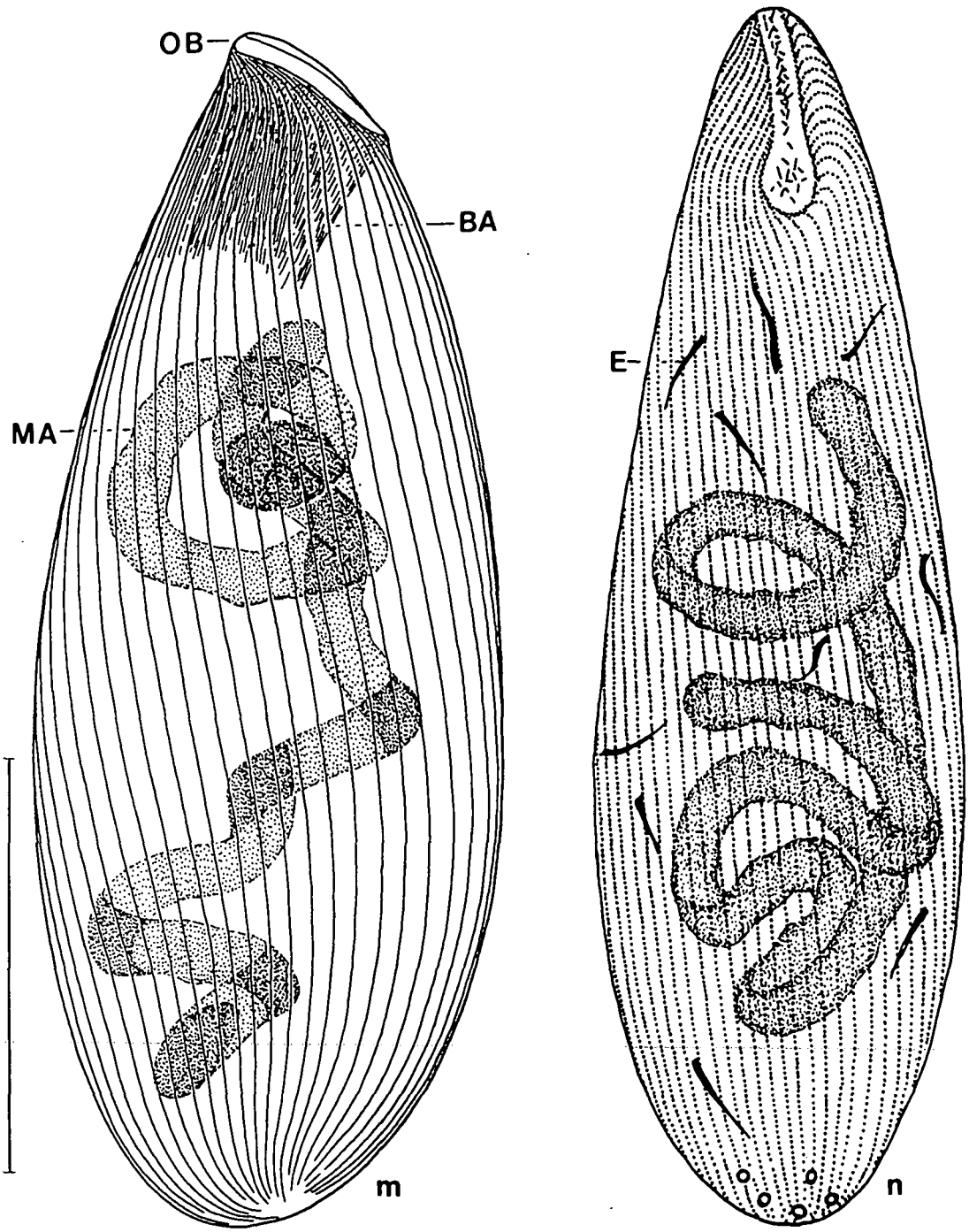

Fig. 60m, n. *Supraspathidium etoschense* (m) and *S. multistriatum* (n; from FOISSNER & DIDIER 1981) after protargol impregnation. The ciliary pattern and the macronucleus are very similar in both species. However, *S. multistriatum* is larger and thus has more ($\bar{x}$ = 74) ciliary rows than *S. etoschense* ($\bar{x}$ = 44). **m:** Right side view. **n:** Ventral view. Note the different course of the ciliary rows right and left of the oral bulge, where the basal bodies are very closely spaced producing some sort of perioral kinety fragments (cp. figure 60j). BA – oral basket, E – extrusomes or oral baskets from food organisms, MA – macronucleus, OB – oral bulge. Scale bars 60 µm.

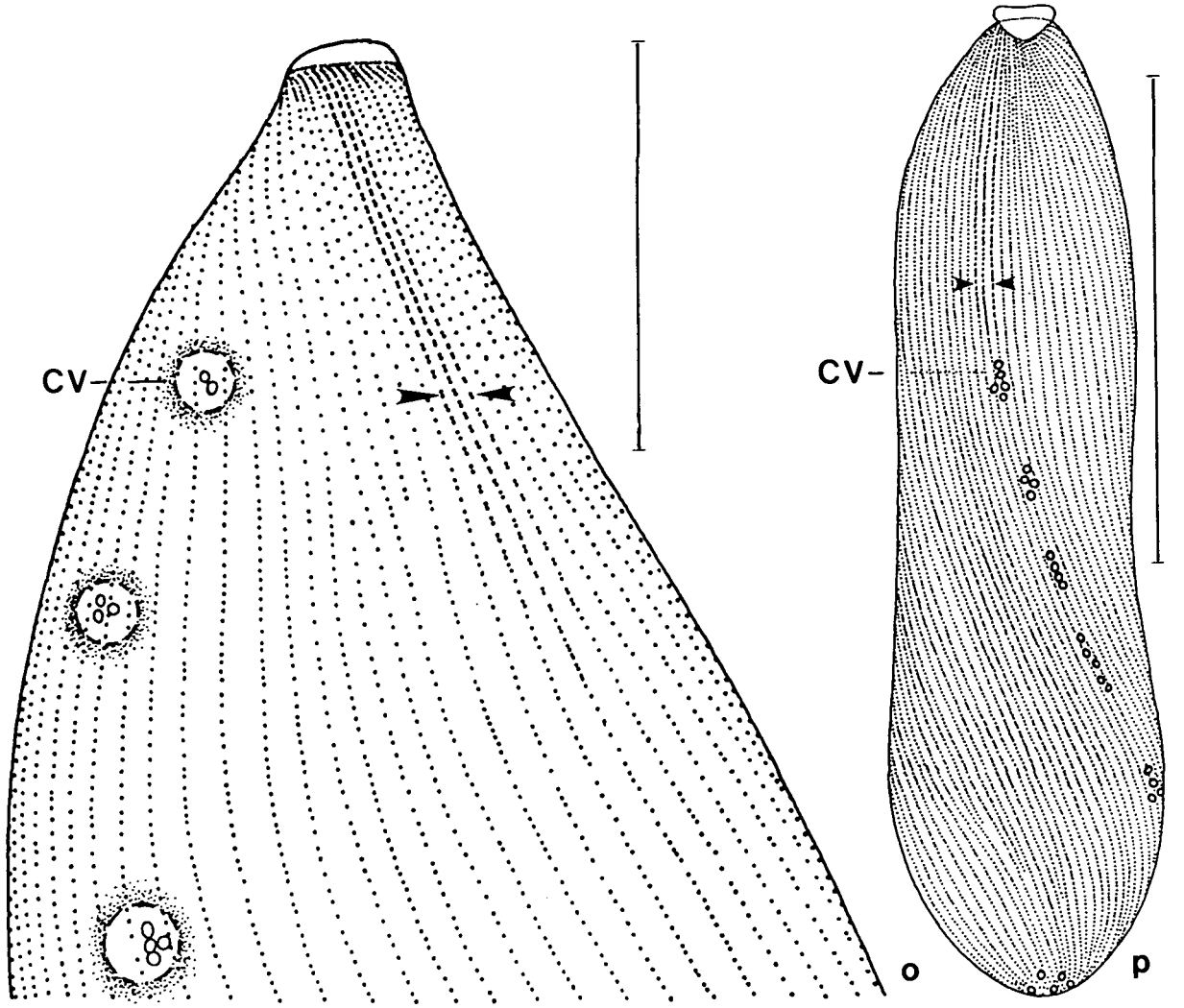

Fig. 60o, p. *Supraspathidium etoschense* (o) and *S. multistriatum* (p; from FOISSNER & DIDIER 1981), dorsal views after protargol impregnation. The ciliary pattern is very similar in both species, that is, they have three brush rows composed of dikinetids (arrowheads). In contrast, the location of the contractile vacuoles, respectively, their excretory pores, is very different and thus an important distinguishing feature: far right of the brush in *S. etoschense*, in line with the brush in *S. multistriatum*. **o:** Ciliary pattern of dorsolateral anterior region. Arrowheads mark brush rows. **p:** Ciliary pattern of dorsal side. Arrowheads mark brush rows. CV – contractile vacuoles, respectively, their excretory pores. Scale bars 30 µm (o), 100 µm (p).

Occurrence and ecology: To date found at type location, where it was rather numerous for some days, especially when nassulids were abundant. The occurrence at site (58) indicates that it might be a limnetic species.

Comparison with related species: The general appearance and the ciliary pattern highly resemble *Supraspathidium multistriatum* FOISSNER & DIDIER, 1981 (Fig. 60k, n, p)[7]. There is, however, a conspicuous, unexpected difference, viz., the location of the contractile

[7] Originally spelled *S. multistriata*. As *Supraspathidium* is neuter gender, we emendate the name to *S. multistriatum* nom. corr.

vacuoles: dorsolateral in *S. etoschense* (Fig. 60o) and in line with the dorsal brush in *S. multistriatum* (Fig. 60p). Furthermore, the extrusomes are slightly different (straight rods with a subterminal inflation vs. slightly curved rods[8]; Fig. 60c, d, l; 326g) and most morphometrics, especially the number of ciliary rows, do not or only slightly overlap because *S. etoschense* is considerably smaller than *S. multistriatum* (Table 52).

The only other species similar to *S. etoschense* is *S. vermiforme* (PENARD, 1922) FOISSNER & DIDIER, 1981, which, however, is flattened leaf-like and loosely ciliated, while *S. etoschense* is unflattened and comparatively densely ciliated. *Supraspathidium armatum*, described below, differs from *S. etoschense* by many features, such as body size and shape and arrangement of the contractile vacuoles.

Table 52. Morphometric data on *Supraspathidium etoschense* (SE), *S. armatum* (SA) from sites (65) and (54), and *S. multistriatum* (SM; from FOISSNER & DIDIER 1981).

Characteristics [a]	Species	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	SE	161.8	155.0	26.2	6.4	16.2	115.0	210.0	17
	SA 65	340.0	335.0	53.5	26.8	15.8	290.0	400.0	4
	SA 54	217.1	210.0	23.5	8.9	10.8	185.0	255.0	7
	SM	251.1	240.0	56.1	17.8	22.4	180.0	350.0	10
Body, width	SE	64.4	66.0	8.6	2.1	13.4	46.0	78.0	17
	SA 65	33.5	34.0	1.7	0.9	5.2	31.0	35.0	4
	SA 54	45.1	48.0	8.1	3.1	18.0	32.0	53.0	7
	SM	71.5	68.0	17.4	5.5	24.3	50.0	110.0	10
Oral bulge, length of chord	SE	27.5	28.0	1.6	0.4	5.9	25.0	30.0	17
	SA 65	47.3	47.0	6.5	3.2	13.7	41.0	55.0	4
	SA 54	38.6	35.0	6.7	2.5	17.4	32.0	52.0	7
	SM	38.8	39.0	8.8	2.8	22.6	25.0	50.0	10
Macronucleus, length (spread; approximations)	SE	267.1	270.0	58.1	14.1	21.7	160.0	390.0	17
	SA 65	335.0	305.0	121.2	60.6	36.2	230.0	500.0	4
	SA 54	245.7	250.0	36.0	13.6	14.7	180.0	300.0	7
Macronucleus, width	SE	8.7	8.0	1.5	0.4	16.8	7.0	11.0	17
	SA 65	9.5	9.0	1.7	0.9	18.2	8.0	12.0	4
	SA 54	8.7	8.0	1.0	0.4	10.9	8.0	10.0	7
	SM	8.9	9.0	1.4	0.4	15.7	7.0	11.0	10
Macronucleus, thickness	SE	about as width							
	SA 65	3.8	4.0	1.0	0.5	25.5	3.0	5.0	4
	SA 54	4.1	4.0	–	–	–	4.0	5.0	7
	SM	about as width							
Brush row 1, length	SE	38.0	38.0	9.4	2.3	24.7	25.0	55.0	16
	SA 65	105.0	105.0	–	–	–	95.0	115.0	2
	SA 54	58.7	58.0	10.3	4.2	17.6	47.0	75.0	6

(continued)

[8] Not studied in detail in *S. multistriatum*, according to FOISSNER's original notes. Thus, the extrusomes of *S. etoschense* and *S. multistriatum* could be more similar than supposed. Generally, extrusome features are highly important. We know of a freshwater species that also looks similar to *S. multistriatum*, but has conspicuous, clavate extrusomes.

Characteristics [a]	Species	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Brush row 2, length	SE	43.6	43.0	7.6	1.9	17.4	30.0	58.0	16
	SA 65	115.0	115.0	–	–	–	105.0	125.0	2
	SA 54	65.8	68.0	11.6	4.7	17.6	50.0	80.0	6
Brush row 3, length	SE	36.3	35.0	6.7	1.7	18.5	20.0	45.0	16
	SA 65	95.0	95.0	–	–	–	80.0	110.0	2
	SA 54	56.0	55.0	9.3	3.8	16.6	45.0	68.0	6
Brush rows, number	SE	3.0	3.0	0.0	0.0	0.0	3.0	3.0	17
	SA 65	3.0	3.0	0.0	0.0	0.0	3.0	3.0	4
	SA 54	3.0	3.0	0.0	0.0	0.0	3.0	3.0	6
Somatic kineties, number	SE	44.3	44.0	4.4	1.1	10.0	35.0	50.0	17
	SA 65	41.8	43.0	3.4	1.7	8.2	37.0	45.0	4
	SA 54	32.9	34.0	2.8	1.0	8.5	29.0	36.0	7
	SM	74.4	75.0	7.5	2.8	10.1	65.0	86.0	7
Kinetids in 10 µm, number	SE	11.7	12.0	1.7	0.4	14.9	10.0	15.0	17
	SA 65	8.3	9.0	1.7	0.9	20.7	6.0	10.0	4
	SA 54	8.0	8.0	2.2	0.9	28.0	4.0	10.0	7
	SM	16.4	16.0	2.1	0.7	12.6	14.0	22.0	10

[a] Data based on protargol-impregnated (FOISSNER's method), mounted specimens from non-flooded Petri dish cultures (*S. etoschense* and *S. armatum*) and field material (*S. multistriatum*). Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Supraspathidium armatum nov. spec. (Fig. 61a–j; Table 52)

Diagnosis: Size about 350 × 35 µm in vivo; elongate lanceolate with distinctly narrowed posterior region, unflattened. Oral bulge elliptical and oblique, longer by one third than broadest postoral region. Macronucleus tortuous, about as long as cell, conspicuously flattened band-like. A row of contractile vacuoles each in ventral and dorsal side. Extrusomes elongate clavate, about 9 µm long. On average 42 ciliary rows.

Type location: Highly saline soil from margin of Etosha Pan, Namibia, 18°55'S 16°25'E (site 65 in figures 2, 3 and chapter 2.1.2).

Etymology: The Latin adjective *armatum* (armed) refers to the conspicuous extrusomes.

Description: This species was very rare. We saw only about 10 individuals, of which four could be impregnated with protargol (mediocre quality). Accordingly, data are not very detailed, especially morphometry. However, it was carefully observed in vivo and better impregnated in the slides from site (54), where, however, the specimens were considerably smaller and stouter casting doubts on conspecificity (Table 52).

Size 300–400 × 30–40 µm, usually about 350 × 35 µm in vivo; length:width ratio 8.5–12:1, on average near 10:1. Lanceolate, that is, anteriorly obliquely truncate and gradually narrowed posteriorly, where it is usually slightly inflated in protargol preparations; laterally flattened in oral and tail area. Macronucleus in central body portion, highly tortuous and

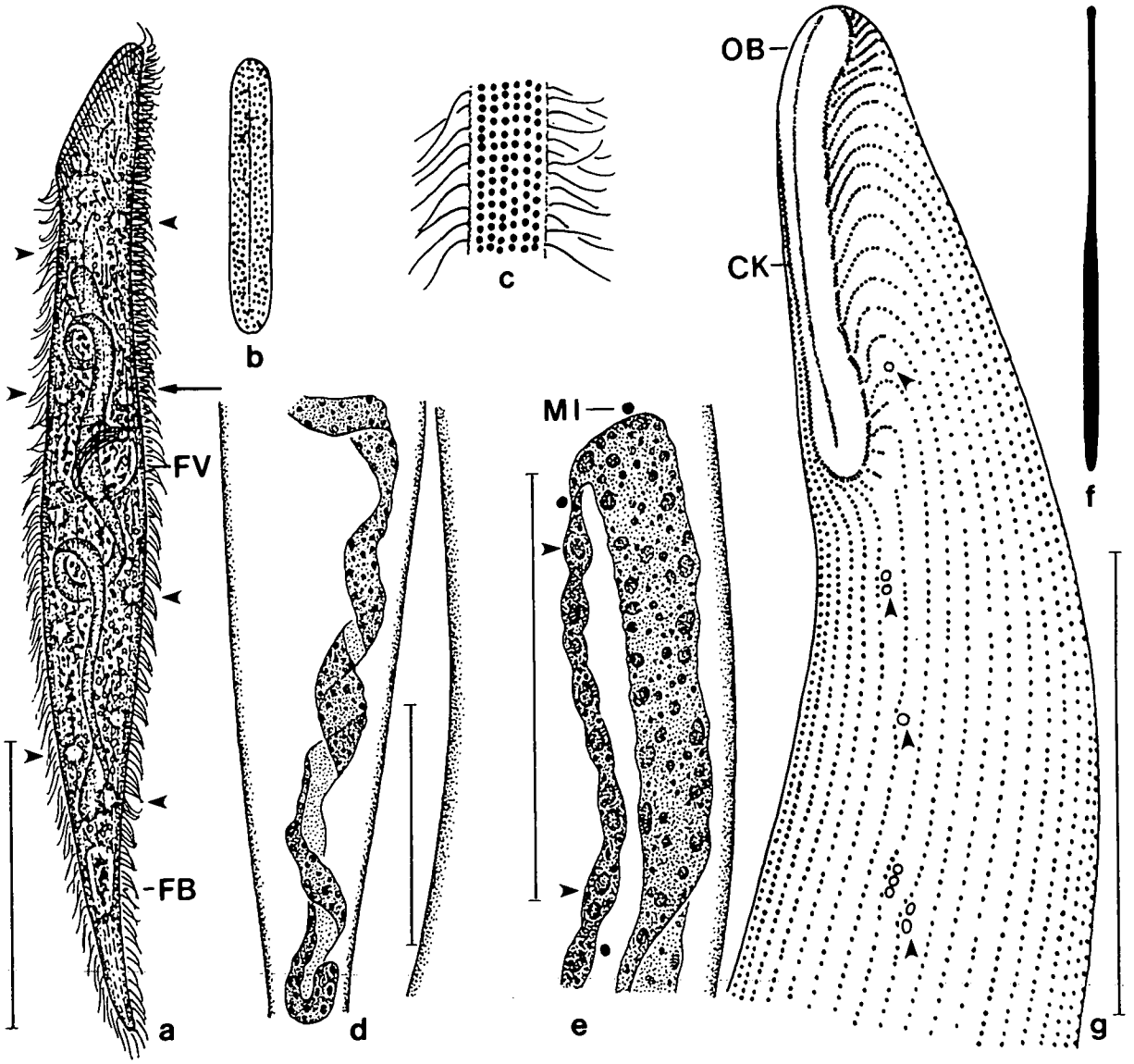

Fig. 61a–g. *Supraspathidium armatum* from life (a–c, f) and after protargol impregnation (d, e, g). **a:** Left side view of a representative specimen. Arrow marks end of dikinetidal portion of dorsal brush row 3. Arrowheads denote the two rows of contractile vacuoles. The food vacuole (FV) contains a *Nassula*, whose oral basket and extrusomes are still recognizable. **b:** Frontal view of oral bulge, which contains many extrusomes appearing as highly refractive dots. **c:** Surface view showing rows of yellowish, strongly refractive cortical granules (mucocysts?) between each two ciliary rows. **d, e:** The tortuous macronucleus (d, a posterior portion; e, a mid-portion) is flattened band-like, a unique feature of *S. armatum*. The nucleoli bulge the flat nuclear band (arrowheads). **f:** Oral bulge extrusomes are elongate clavate and 8–10 μm long. **g:** Ventrolateral view showing oral and somatic ciliary pattern in anterior body region. Arrowheads mark excretory pores of ventral row of contractile vacuoles. CK – circumoral kinety, FB – egestion vacuole, FV – food vacuole, MI – micronucleus, OB – oral bulge. Scale bars 40 μm (d, e, g) and 100 μm (a).

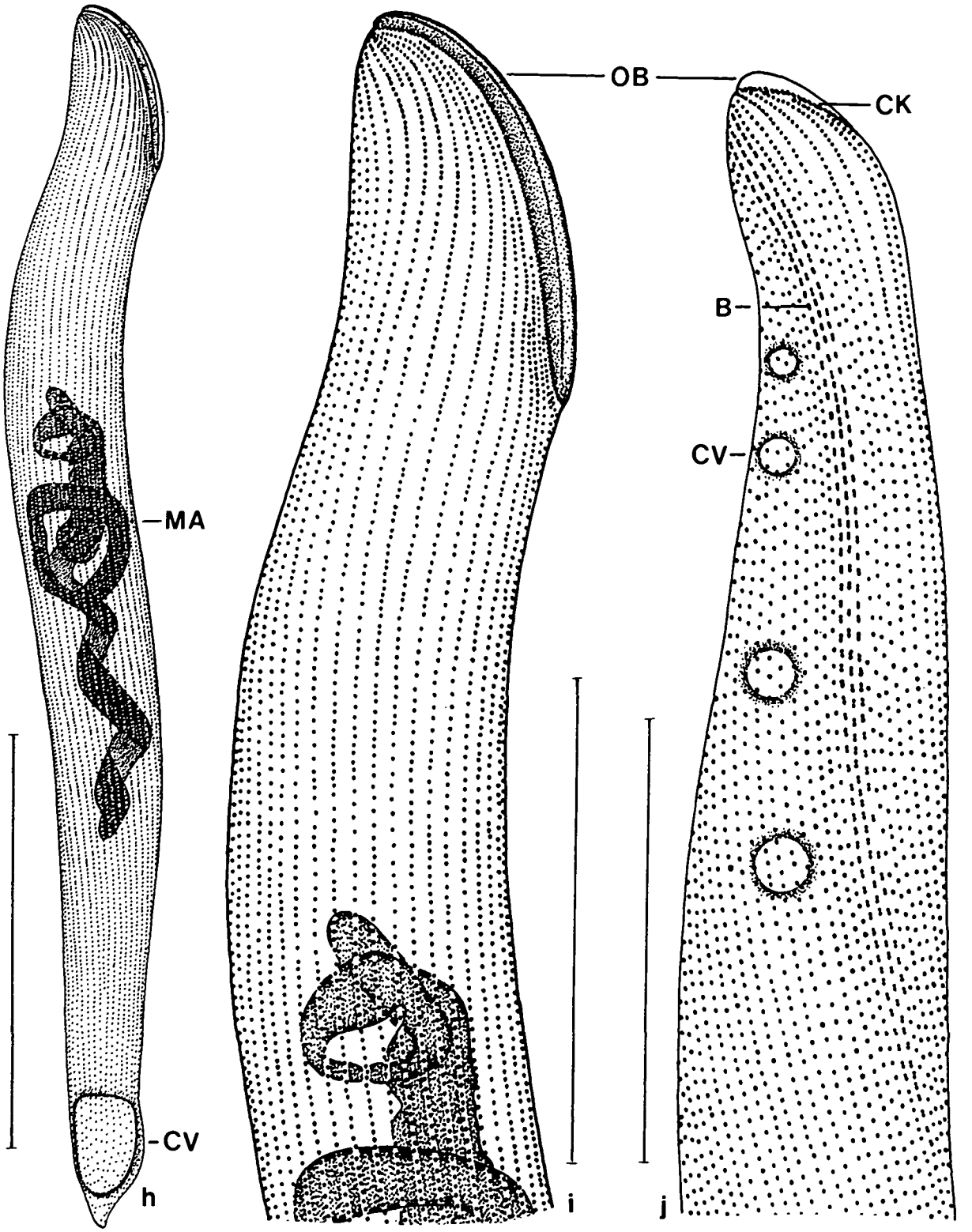

Fig. 61h–j. *Supraspathidium armatum*, ciliary pattern after protargol impregnation. **h**: Right side overview. **i**: Anterior portion of previous specimen. **j**: Dorsal view showing the three long brush rows. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuole, MA – macronucleus, OB – oral bulge. Scale bars 100 µm (h) and 50 µm (i, j).

flattened band-like (Fig. 61d, e, h; Table 52), a rare feature found also in → *Protospathidium namibicola*, albeit less pronounced; contains many minute and rather large nucleoli bulging nuclear band. Many globular micronuclei which, however, could not be counted because of similarly sized and impregnated cytoplasmic inclusions. Many contractile vacuoles in two rough rows: one row in ventral side slightly left of midline, the other right of dorsal brush between left and dorsal side; most vacuoles with two or more excretory pores (Fig. 61a, g, j). Extrusomes packed in oral bulge and scattered in cytoplasm, 8–10 µm long, elongate clavate, that is, posterior half thicker than anterior bearing minute globule on top (Fig. 61a, b, f); do not impregnate with protargol. Cortex very flexible, contains about six rows of yellowish, highly refractive granules (mucocysts ?) between each two ciliary rows (Fig. 61c). Cytoplasm colourless, usually packed with lipid droplets 1–3 µm across. Feeds on various ciliates, for instance, *Nassula*, whose oral basket and extrusomes can be recognized in the food vacuoles. Swims rapidly, in spite of the large size, showing great flexibility when touching obstacles and under the cover-glass.

Cilia about 12 µm long, closely spaced, arranged in meridional rows, whose densely ciliated anterior portion forms steep angles with the circumoral kinety on right side, while left side ends are curved ventrally; some rows slightly shortened anteriorly or posteriorly (Fig. 61g, i). Three dorsal ciliary rows anteriorly differentiated to an about 120 µm long dorsal brush composed of rod-shaped, 3–4 µm long, comparatively widely spaced bristle pairs; row 3 continues with monokinetidal, 2–3 µm long bristles to at least mid-body (Fig. 61a, j; Table 52).

Oral area flattened and usually set off from body proper by a slight constriction. Oral bulge obliquely (~ 45°) truncate, oblong and, although only 3–4 µm high, rather conspicuous due to the many refractive extrusomes contained. Circumoral kinety at base of oral bulge and thus also oblong, its composition of dikinetidal kinetofragments is occasionally well-recognizable (Fig. 61a, b, g–i).

Occurrence and ecology: To date found only at type location and sites nearby, all very saline habitats, where it was rare in the non-flooded Petri dish cultures.

Comparison with related species: *Supraspathidium armatum* has so many special features (body and extrusome shape, two rows of contractile vacuoles, band-like flattened macronucleus) that it cannot be confused with any other ciliate. However, most morphometrics are highly variable (Table 52).

Arcuospathidium namibiense nov. spec.

Diagnosis: Size about 160 × 10 µm in vivo. Very slenderly cylindroidal with inconspicuous, obliquely truncated, cuneate oral bulge occupying about 6% of body length. Approximately 20 scattered macronuclear nodules and 2 fusiform micronuclei. Extrusomes oblong or oblanceolate, about 1 µm long. Usually 4–6 ciliary rows, 2 or 3 anteriorly differentiated to short, but conspicuous dorsal brush having some 15–20 µm long bristles at anterior end of row 3; row 1 lacking or consisting of few bristles.

Remarks: We split this species into two subspecies, differing mainly in the shape of the

extrusomes (oblanceolate vs. oblong), but also in details of the brush (two vs. three rows) and the number of ciliary rows (four vs. five).

Generic classification: *Arcuospathidium namibiense* has so few ciliary rows that their arrangement in the oral area, which is crucial for generic assignment (FOISSNER 1984), is difficult to follow. However, if some obviously related species are taken into consideration, then it becomes likely that the African populations are extreme members of *Arcuospathidium*, as defined by FOISSNER (1984). It is possible to construct a series of transitions starting with *A. multinucleatum* FOISSNER, 1999b (15 ciliary rows) over *A. vermiforme* FOISSNER, 1984 (11 ciliary rows) to *A. namibiense* (4–6 ciliary rows).

Comparison with related species (see also → *Protospathidium vermiforme*): *Arcuospathidium namibiense* differs, inter alia, by the scattered macronuclear nodules from most described congeners, especially *A. vermiforme* FOISSNER, 1984 (two macronuclear nodules), *A. cooperi* FOISSNER, 1996b (single, reniform macronucleus), and *A. vlassaki* FOISSNER, 2000d (single, rod-shaped macronucleus). Only *A. multinucleatum* FOISSNER, 1999b has the same nuclear pattern as *A. namibiense*. However, both species are easily distinguished by body shape (14:1 vs. 7:1 in preparations) and number of ciliary rows (4–6 vs. 11–19).

At first glance, *Arcuospathidium namibiense* looks like *Spathidium bonneti* BUITKAMP (1977a). However, a more detailed comparison reveals significant differences, although the description of *S. bonneti* is brief and lacks detailed morphometrics and data about the extrusomes. The most important difference concerns the distinctly elongated (15–20 µm!) and thus highly characteristic bristles at top of brush row 3. These bristles and their basal bodies are so distinct in vivo and protargol preparations that one cannot assume that BUITKAMP (1977a) overlooked them. A further main difference is the body's length:width ratio, which is 30:1 in *S. bonneti*, according to BUITKAMP's description and illustration (Fig. 63o). In *A. namibiense namibiense* and *A. namibiense tristicha,* only two of 42 specimens analyzed have a ratio of 24:1, while the average values are much lower, viz., 13.7:1 and 15.1:1 (Table 53). The third main difference concerns the location of the single dikinetid composing brush row 1 (Fig. 63n, q): distinctly underneath the circumoral kinety in *S. bonneti*, while close to the circumoral kinety in *A. namibiense tristicha*. Finally, the location of the contractile vacuole (distinctly subterminal vs. terminal) and body shape (distinctly vs. slightly narrowed posteriorly) are slightly different.[9]

In vivo, *A. namibiense* is rather similar to *Spathidium procerum* KAHL, 1930a, as redescribed by FOISSNER (1984). However, this species is a "true" *Spathidium*, has up to 10 µm long, rod-shaped extrusomes, lacks elongated dorsal bristles, and possesses 10 ciliary rows. As concerns the elongated dorsal bristles, *A. namibiense* resembles *S. falciforme* PENARD, 1922, which, however, is only 40–60 µm long.

In vivo, *A. namibiense* is indistinguishable from → *Protospathidium vermiforme*. Thus,

[9] We discussed the problem with Dr. BUITKAMP, whose slides of *Spathidium bonneti* are, unfortunately, completely bleached. In his letter, BUITKAMP stated: (i) My prepared specimens have a similar size as yours, but I remember that they were distinctly narrower in vivo; (ii) With interference contrast, I could recognize in two specimens at least one 15 µm long dorsal bristle, which I obviously overlooked previously, but the whole dorsal brush pattern seems to be distinctly different in *S. bonneti* and *A. namibiense*; (iii) I believe that *S. bonneti* and *A. namibiense* are different species.

protargol impregnation is required to reveal the structure of the circumoral kinety (FOISSNER 1984): composed of a single line distinctly set off from the ciliary rows (Fig. 63j, p, q) vs. short fragments attached to the ciliary rows (Fig. 69f–j).

Arcuospathidium namibiense namibiense nov. sspec. (Fig. 62a–i; Table 53)

Diagnosis: Extrusomes oblong. 4–5 ciliary rows, 2 anteriorly modified to brush.

Type location: Soil from *Aloe dichotoma* forest near the Gariganus Guest Farm, Namibia, 26°30'S 18°25'E (site 5 in figure 2 and chapter 2.1.2).

Etymology: Named after the country discovered.

Description: Size highly variable, in vivo 110–210 × 8–15 µm, usually about 160 × 12 µm; length:width ratio also highly variable, that is, 9:1 – 24:1, on average 14:1 in preparations (Table 53). Cylindroidal to slightly fusiform, frequently strongly curved or sigmoidal and slightly twisted about main body axis, rather distinctly flattened laterally (Fig. 62a, h); acontractile and rather fragile, specimens thus sometimes distorted and/or inflated in protargol preparations. Nuclear apparatus in middle quarters of cell on average (Fig. 62a, h). Macronuclear nodules basically scattered with a tendency to form a cluster each in second and third quarter of cell; rarely in series or single accumulation near body centre; individual nodules globular to elongate ellipsoidal, on average ellipsoidal, usually contain one or two large nucleoli; unite to a globular mass in middle dividers. Usually two micronuclei, one each in anterior and posterior third of nuclear figure; individual micronuclei conspicuous because ellipsoidal, fusiform or slenderly ovate and about 4 × 2 µm in size, that is, almost as large as macronuclear nodules; micronuclei lacking or not clearly recognizable in about one third of specimens due to similarly sized and shaped cell inclusions. Contractile vacuole in rear body end, some subterminal excretory pores on ventral side. Extrusomes in oral bulge, oblong, extremely minute, that is, 1–1.2 µm long; do not impregnate with the protargol method used (Fig. 62a, c). Cortex very flexible, thin, contains inconspicuous rows of loosely spaced, colourless granules less than 0.5 µm across. Cytoplasm hyaline, contains some bright lipid droplets 1–2 µm across and about 5 µm-sized food vacuoles each containing only one or two bacterial rods. Slowly gliding and wriggling like an eel, showing great flexibility when creeping among soil particles.

Cilia about 7 µm long in vivo, invariably arranged in four or five, usually four slightly spiralling, equidistant rows; distances between individual cilia about 4 µm to up to 6 µm in longest specimens, ciliature thus loose; as is usual in haptorid gymnostomes, barren basal bodies may occur near ciliated ones. All ciliary rows abut on circumoral kinety, except for one or two (in specimens with five rows) anteriorly distinctly shortened right side rows. Brush conspicuous, although occupying only 10% of body length, because of its long bristles easily recognizable even at low magnification (≥ ×100)[10]. Dorsal brush row 2 composed of an

[10] Brush row 1 is lacking, compared with *A. namibiense tristicha*, where it is present but consists of only one or few kinetids. To make morphometrics comparable, we consider the first (right) brush row of *A. namibiense namibiense* as row 2.

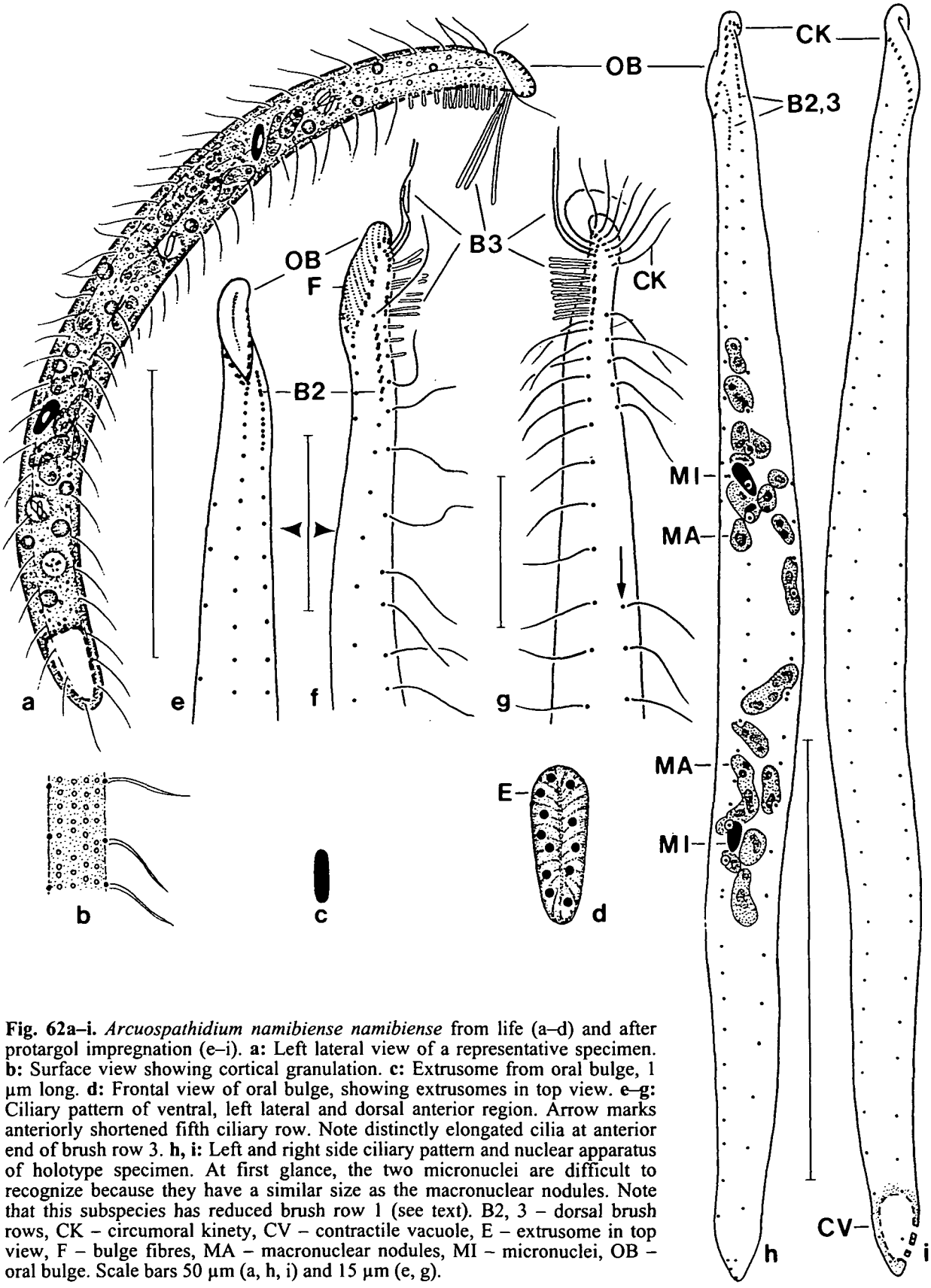

Fig. 62a–i. *Arcuospathidium namibiense namibiense* from life (a–d) and after protargol impregnation (e–i). **a:** Left lateral view of a representative specimen. **b:** Surface view showing cortical granulation. **c:** Extrusome from oral bulge, 1 µm long. **d:** Frontal view of oral bulge, showing extrusomes in top view. **e–g:** Ciliary pattern of ventral, left lateral and dorsal anterior region. Arrow marks anteriorly shortened fifth ciliary row. Note distinctly elongated cilia at anterior end of brush row 3. **h, i:** Left and right side ciliary pattern and nuclear apparatus of holotype specimen. At first glance, the two micronuclei are difficult to recognize because they have a similar size as the macronuclear nodules. Note that this subspecies has reduced brush row 1 (see text). B2, 3 – dorsal brush rows, CK – circumoral kinety, CV – contractile vacuole, E – extrusome in top view, F – bulge fibres, MA – macronuclear nodules, MI – micronuclei, OB – oral bulge. Scale bars 50 µm (a, h, i) and 15 µm (e, g).

average of seven dikinetids bearing about 5 µm long bristles, usually separated from circumoral kinety by a single monokinetid, continues as ordinary somatic ciliary row posteriorly. Brush row 3 anteriorly with two to four closely spaced, about 15 µm long and thus highly conspicuous, rod-shaped bristles obliquely spread posteriorly in gliding and swimming specimens; large bristles followed by an average of five dikinetids having about 5 µm long bristles; then likely continues with a few 2–3 µm long monokinetidal bristles before extending backwards as ordinary somatic kinety (Fig. 62a, e–i; Table 53).

Oral bulge about 3 µm high in vivo, minute because slightly narrower than widest postoral body region and occupying only about 6% of body length; slanted approximately 50° to main body axis, slenderly obovate or cuneate in frontal view, contains the minute extrusomes described above. Circumoral kinety composed of comparatively widely spaced dikinetids, each bearing a single cilium and a fibre extending into the oral bulge. Oral basket (rods) not recognizable in vivo or protargol preparations, not even in over-stained specimens (Fig. 62a, d, e–i; Table 53).

Occurrence and ecology: To date found only at type location, where it was rather abundant. This species is well-adapted to the sandy habitat by its slender body.

Table 53. Morphometric data on *Arcuospathidium namibiense namibiense* (upper line) and *A. namibiense tristicha* (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	147.7	143.0	27.4	6.0	18.5	100.0	190.0	21
	138.9	140.0	16.7	3.7	12.0	103.0	170.0	21
Body, width	10.8	10.0	1.9	0.4	17.6	7.0	15.0	21
	9.1	9.0	1.5	0.3	16.9	6.0	11.0	21
Body length:width, ratio	13.7	14.0	4.1	0.9	29.3	8.0	24.0	21
	15.2	15.0	3.6	0.8	23.0	11.0	24.0	21
Oral bulge (circumoral kinety), length	8.1	8.0	0.8	0.2	10.0	6.0	9.0	21
	8.6	8.0	1.1	0.2	13.0	7.0	12.0	21
Oral bulge, height	2.4	3.0	–	–	–	2.0	3.0	21
	1.9	2.0	–	–	–	1.0	3.0	21
Circumoral kinety to last dikinetid of brush row 1,				lacking				21
distance	2.2	2.0	0.5	0.1	24.1	2.0	4.0	21
Circumoral kinety to last dikinetid of brush row 2,	9.0	8.0	2.5	0.6	27.9	5.0	14.0	21
distance	14.7	15.0	2.0	0.4	13.5	11.0	18.0	21
Circumoral kinety to last dikinetid of brush row 3,	6.3	6.0	1.3	0.3	20.2	4.0	8.0	21
distance	8.2	8.0	1.4	0.3	17.1	6.0	11.0	21
Anterior body end to first macronuclear nodule,	35.4	37.0	10.0	2.2	28.2	11.0	50.0	21
distance	50.4	50.0	9.9	2.2	19.7	36.0	70.0	21
Nuclear figure, length	73.2	67.0	16.3	3.6	22.3	49.0	97.0	21
	61.2	62.0	12.4	2.7	20.2	36.0	84.0	21
Macronuclear nodules, length	6.2	6.0	1.9	0.4	30.4	3.0	12.0	21
	5.5	5.0	1.7	0.4	31.4	4.0	10.0	21
Macronuclear nodules, width	2.9	3.0	0.6	0.1	21.8	2.0	4.0	21
	3.0	3.0	0.9	0.2	30.7	1.0	5.0	21
Macronuclear nodules, number	19.2	20.0	6.8	1.5	35.6	6.0	34.0	21

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	25.3	22.0	7.0	1.5	27.7	16.0	42.0	21
Micronuclei, length	4.2	4.0	0.6	0.1	14.4	3.0	5.0	21
	5.1	5.0	0.8	0.2	15.4	4.0	7.0	21
Micronuclei, width	1.8	2.0	–	–	–	1.0	3.0	21
	1.8	2.0	–	–	–	1.0	2.0	21
Micronuclei, number	2.2	2.0	0.5	0.1	23.4	2.0	4.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Somatic kineties, number	4.1	4.0	–	–	–	4.0	5.0	21
	5.1	5.0	–	–	–	5.0	6.0	21
Ciliated kinetids in a right lateral kinety, number	35.8	35.0	7.5	1.6	21.0	23.0	54.0	21
	52.2	52.0	8.9	2.0	17.1	37.0	68.0	21
Dorsal brush rows, number [b]	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Dikinetids in brush row 1, number				lacking				21
	1.3	1.0	0.6	0.1	43.6	1.0	3.0	21
Dikinetids in brush row 2, number	7.0	7.0	1.6	0.4	23.0	2.0	9.0	21
	15.1	15.0	2.1	0.5	13.7	11.0	19.0	21
Dikinetids in brush row 3, number [c]	5.5	5.0	1.0	0.2	17.8	4.0	7.0	21
	7.3	7.0	1.1	0.2	14.5	4.0	9.0	21
Distinctly elongated brush bristles, number	3.3	4.0	0.9	0.2	25.8	2.0	4.0	17
	2.8	3.0	0.6	0.1	21.4	2.0	4.0	21
Circumoral kinetids, number	19.8	20.0	2.3	0.5	11.4	14.0	25.0	21
	30.9	30.0	4.2	0.9	13.4	25.0	40.0	21
Excretory pores, number	3.7	3.0	1.7	0.5	44.8	1.0	8.0	13
	5.8	6.0	2.2	0.7	37.1	3.0	10.0	10

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and selected (distinctly inflated or distorted specimens excluded in *A. namibiense namibiense*) or randomly selected (*A. namibiense tristicha*) specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max –maximum, Min – minimum, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] First row lacking in 1 out of 25 specimens of *A. namibiense tristicha.*

[c] Elongated bristles at anterior end not included because dikinetidal organization not clearly recognizable.

Arcuospathidium namibiense tristicha nov. sspec. (Fig. 63a–m, p–v; 327a–d, f–i; Table 53)

Diagnosis: Extrusomes oblanceolate. 5–6 ciliary rows, 3 anteriorly modified to brush rows.

Type location: Bark from a *Maytenus oleoides* tree (Celastraceae) in the botanical garden of Cape Town, Republic of South Africa, 33°53'S 18°25'E.

Etymology: Composite of the Greek words *tri* (three) and *sticha* (row), referring to the three dorsal brush rows.

Description: Size highly variable, that is, 110–190 × 6–12 μm in vivo, usually about 150 × 9 μm; length:width ratio also highly variable, that is, 11–24:1, on average 15.2:1 in preparations (Table 53). Cylindroidal to slightly fusiform or club-shaped, usually strongly curved or sigmoidal and distinctly twisted about main body axis, flattened only in anterior region; when gliding, anterior body half often straight, posterior more or less distinctly curved, providing cells with a characteristic L-shaped appearance; rarely, coiled specimens occur (Fig. 63a–c, r, t–v). Nuclear apparatus in middle and anterior half of last third of cell on average (Fig. 63a, l). Macronuclear nodules basically scattered with a tendency to form a cluster each in anterior and posterior end of nuclear figure; rarely in series or distinct clusters in anterior and posterior body half; individual nodules globular to elongate ellipsoidal, on average broadly ellipsoidal, usually contain some small nucleoli. Invariably two micronuclei, one each in anterior and posterior third of nuclear figure; individual micronuclei conspicuous because elongate ellipsoidal or fusiform and about 5 × 2 μm in size, that is, almost as long as macronuclear nodules. Contractile vacuole in rear end, some subterminal excretory pores on ventral side. Extrusomes in both sides of oral bulge, distinctly oblanceolate, extremely minute, that is, 1–1.2 × 0.5 μm; impregnate with the protargol method used and then resemble basal bodies (Fig. 63a, d, g, j, s; 327b–d). Cortex very flexible, thin, contains five to six rows of colourless, minute (< 0.5 μm) granules between each two ciliary rows. Cytoplasm hyaline, contains some bright lipid droplets 1–3 μm across and up to 12 μm-sized food vacuoles, once with an almost intact *Cyrtolophosis mucicola*. Glides rather rapidly on microscope slide, wriggling like an eel when creeping among soil particles.

Cilia about 7 μm long in vivo, invariably arranged in five to six, usually five distinctly spiralling, equidistant rows, distances between individual cilia 2–4 μm, ciliature thus moderately dense. All ciliary rows abut on circumoral kinety, except one or two (in specimens with six rows) anteriorly distinctly shortened right side rows (Fig. 63a, i–l, p, q; Table 53). Brush conspicuous, although occupying only 11% of body length, because of its long bristles, already recognizable at low magnification (≥ ×100). Brush row 1 consists of one to three, usually only one dikinetid separated from circumoral kinety by a single monokinetid; lacking in one out of 25 specimens investigated. Brush row 2 about 15 μm long in vivo, separated from circumoral kinety by a single monokinetid, continues as ordinary somatic kinety posteriorly, composed of an average of 15 closely spaced dikinetids having up to 10 μm long bristles gradually decreasing in length at row ends; anterior bristles of dikinetids longer than posterior and slightly inflated distally. Brush row 3 about 10 μm long in vivo, anteriorly with some very closely spaced, 15–20 μm long and thus highly conspicuous, rod-shaped bristles obliquely spread backwards in gliding and swimming specimens (Fig. 327a); composed of an average of seven dikinetids having up to 6 μm long bristles gradually decreasing in length at row ends; anterior bristles of dikinetids longer than posterior and slightly inflated distally; row then continues with some 2–3 μm long, monokinetidal bristles before extending as an ordinary somatic kinety backwards (Fig. 63a, i–l, m, q; Table 53).

Oral bulge up to 4 μm high in vivo and thus rather conspicuous, although slightly narrower than widest postoral region and occupying only about 6% of body length, slanted 40–60° to main body axis, slenderly obovate in frontal view, contains the minute extrusomes described above. Circumoral kinety composed of rather closely spaced dikinetids each bearing an about 7 μm long cilium. Oral basket (rods) not recognizable in vivo or protargol preparations, not even in over-stained specimens (Fig. 63a, d–f, i–l, p, q).

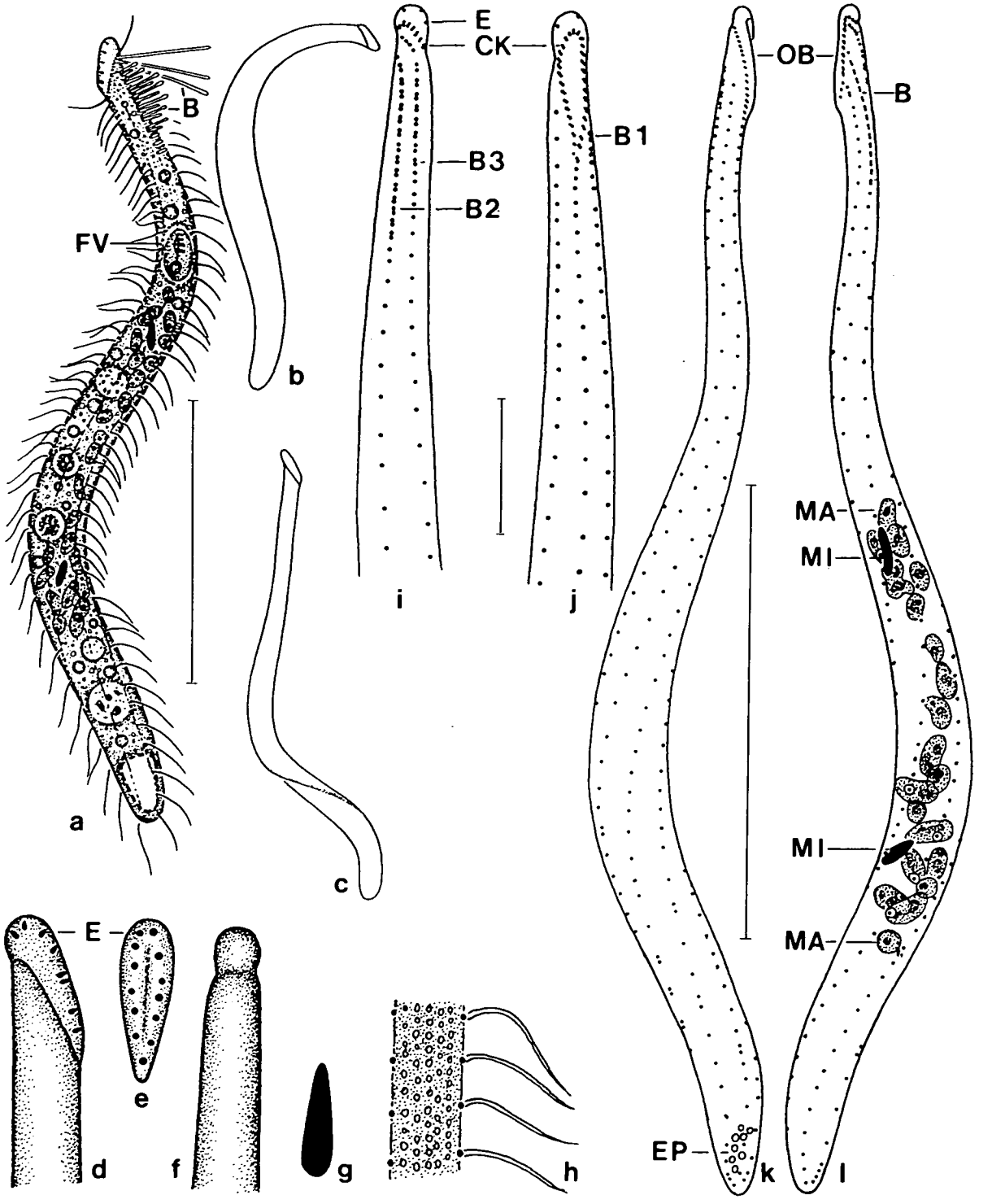

Fig. 63a–l. *Arcuospathidium namibiense tristicha*, Namibian site (5) specimens from life (a–h) and after protargol impregnation (i–l). **a:** Left side view of a representative specimen. **b, c:** Shape variants. **d–f:** Right lateral, frontal, and dorsal view of oral area. **g:** Extrusome, length 1 µm. **h:** Surface view showing cortical granulation. **i, j:** Ciliary pattern of anterior dorsal and ventral side. Brush details, see figures 63m, q. **k, l:** Right and left side ciliary pattern and nuclear apparatus of holotype specimen. B1-3 – dorsal brush rows, CK – circumoral kinety, E –extrusomes, EP – excretory pores, FV – food vacuole, MA – macronuclear nodules, MI – micronuclei, OB – oral bulge. Scale bars 50 µm (a, k, l) and 10 µm (i, j).

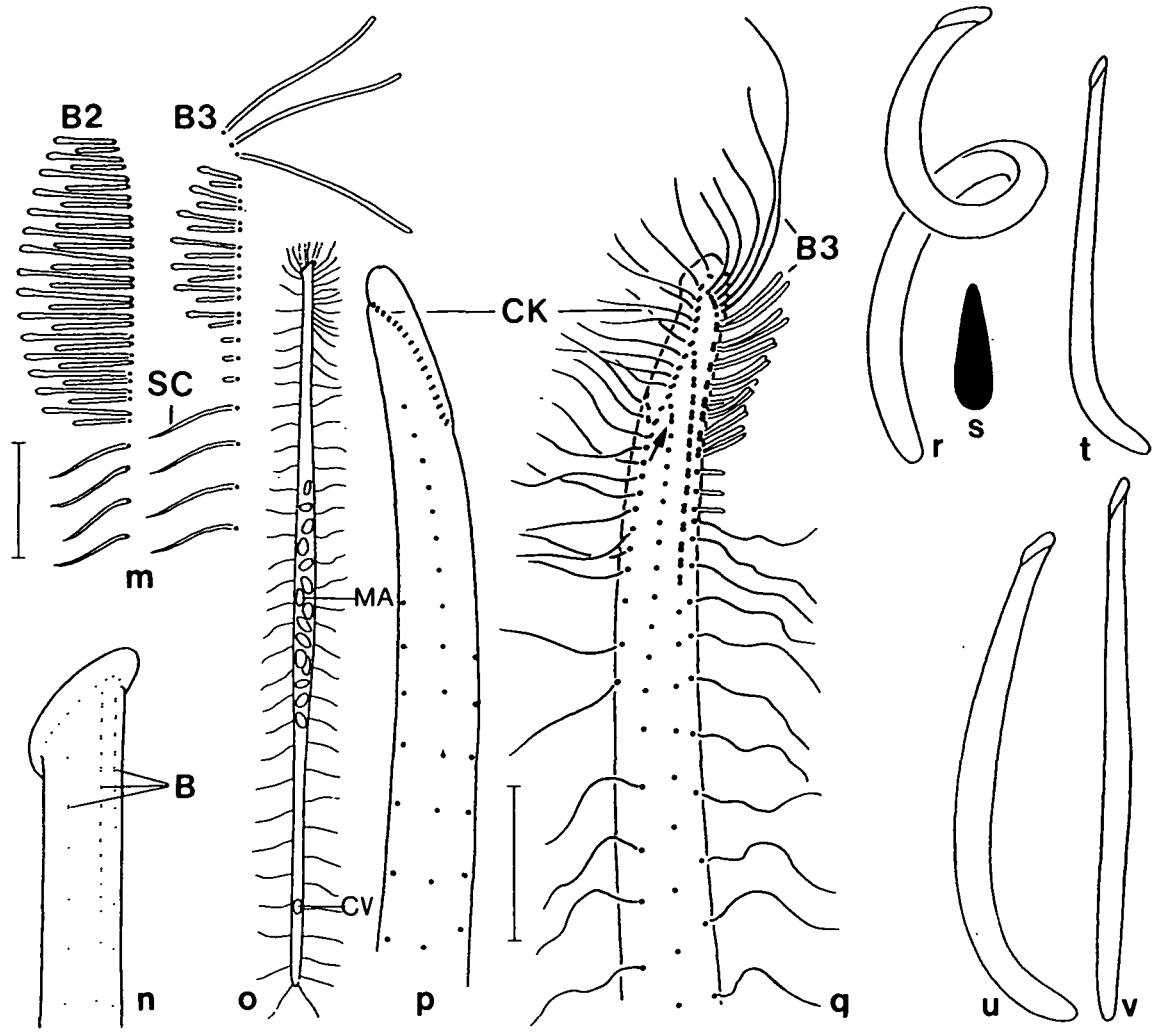

Fig. 63m–v. *Arcuospathidium namibiense tristicha* (m, p–v) and *Spathidium bonneti* (n, o; from BUITKAMP 1977a), Namibian site 5 (m, p, q), Ivory Coast (n, o), and Benin (r–v) specimens from life (m, o, r–v) and after protargol impregnation (n, p, q). **m:** Dorsal brush rows 2 and 3 of a very carefully studied specimen. Cilia drawn to scale. Note that the somatic cilia are shorter than most brush bristles. **n, o:** *Spathidium bonneti*, 150 × 5 µm, is considerably more slender than *A. namibiense* (30:1 vs. 14–16:1) and lacks elongated bristles at top of brush row 3. Furthermore, the single dikinetid composing brush row 1 is much farther underneath the circumoral kinety than in *A. namibiense* (q, arrow). **p, q:** Ciliary pattern of anterior right and left side. Arrow marks the single dikinetid composing brush row 1; it is much more close to the circumoral kinety than in *S. bonneti* (n). **r, t, u, v:** Shape variants, those shown in (t, u) are most typical. **s:** Extrusomes are oblanceolate and 1–1.5 × 0.5 µm in all populations of the subspecies *tristicha*. When exploded, they become drumstick-shaped and 3–5 µm long (Fig. 327h, i). B – dorsal brush, B2, 3 – dorsal brush rows, CK – circumoral-kinety, CV – contractile vacuole, MA – macronuclear nodules, SC – somatic cilium. Scale bars 10 µm (m, p, q).

Observations on other populations: This species is rather frequent in soils from Africa and possibly also South America (Fig. 327f–i). A rather weak population from Benin (soil sample from the farm of the Agricultural Faculty at the National University in the town of Abomey; kindly provided by Prof. Jean DRAGESCO) was studied in some detail (Fig. 63r–v). It matches the Namibian site (5) population well, especially in having long (about 13 µm as opposed to 7 µm long somatic cilia) bristles at anterior end of brush row 3 and minute, oblanceolate extrusomes which, however, do not impregnate with protargol. The macronucleus is more frequently indistinctly moniliform than in the Namibian specimens. Brush row 1 is lacking in about 20% of specimens and usually consists of three to six dikinetids in

the others, while rows 2 and 3 have only about half the number of dikinetids found in the Namibian specimens. Obviously, *A. namibiense tristicha* is rather variable in brush details, while the extrusomes are highly similar in the about 20 populations checked so far.

Occurrence and ecology: Found at various sites in Namibia (Table 4) and South Africa. Possibly also occurs in Venezuela. The species, which is well-adapted to soil life by its worm-like body, became abundant in the non-flooded Petri dish culture from the type location; usually, however, numbers are low.

Arcuospathidium etoschense nov. spec. (Fig. 64a–m; 332i; Table 54)

Diagnosis: Size about 190 × 15 µm in vivo. Very slenderly cylindroidal with comparatively conspicuous, strongly slanted oral bulge occupying about 16% of body length. On average 11 elongate ellipsoidal macronuclear nodules in series and 4 fusiform to elongate ovate micronuclei. Extrusomes slenderly cuneate, about 4 µm long. About 10 ciliary rows, 3 anteriorly differentiated to moderately distinct dorsal brush.

Type location: Highly saline swamp soil from around the Okerfontein water-hole in the Etosha National Park, Namibia, 18°45'S 16°45'E (site 69 in figures 2, 3 and chapter 2.1.2).

Etymology: Named after the region discovered.

Description: Unfortunately, this species did not impregnate well, and thus we cannot provide detailed data on the infraciliature. Usually, we do not describe such material, but this species has several distinct features making re-identification likely.

Size 140–250 × 10–25 µm in vivo, usually near 190 × 15 µm, length:width ratio also highly variable, that is, 7.4–22:1, on average 13.7:1 in vivo and protargol preparations. Body cylindroidal, rarely curved worm-like, oral and neck region flattened up to 2:1 laterally; acontractile and fairly robust (Fig. 64a, g, i, k, l; Table 54). Nuclear apparatus in middle quarters of cell (Fig. 64a, i, k, l). Macronucleus basically nodular; a long strand or a mixture of nodules and more or less long pieces occur, however, in early and late post-dividers (Fig. 64m), as explained in → *Spathidium turgitorum*. Individual macronuclear nodules in series with a tendency to form a cluster each anteriorly and posteriorly; globular to very elongate ellipsoidal, on average 11 × 4 µm in protargol preparations, contain many minute nucleoli. On average four fusiform, elongate ovate or reniform micronuclei near macronuclear nodules, difficult to recognize in vivo and only lightly impregnated with protargol. Contractile vacuole in posterior body end. Extrusomes in single, rough row in oral bulge and scattered in cytoplasm, difficult to recognize in vivo because of similar refractivity as cytoplasm; individual extrusomes slenderly cuneate and 3–4 µm long both in vivo and protargol preparations, where the posterior third impregnates heavily, while the anterior thirds impregnate lightly; exploded toxicysts obclavate and hyaline, up to 10 µm long (Fig. 64a, c–f, h–m; 332i). Cortex very flexible, contains closely spaced rows of minute (~ 0.2 mm) granules, which impregnate deeply and hide the ciliary pattern. Cytoplasm hyaline, contains some bright lipid droplets up to 2 µm across. Food not observed, likely small ciliates. Glides and swims rather rapidly showing great flexibility when creeping between soil particles.

Cilia about 10 µm long in vivo, arranged in about ten equidistant rows, distances between individual

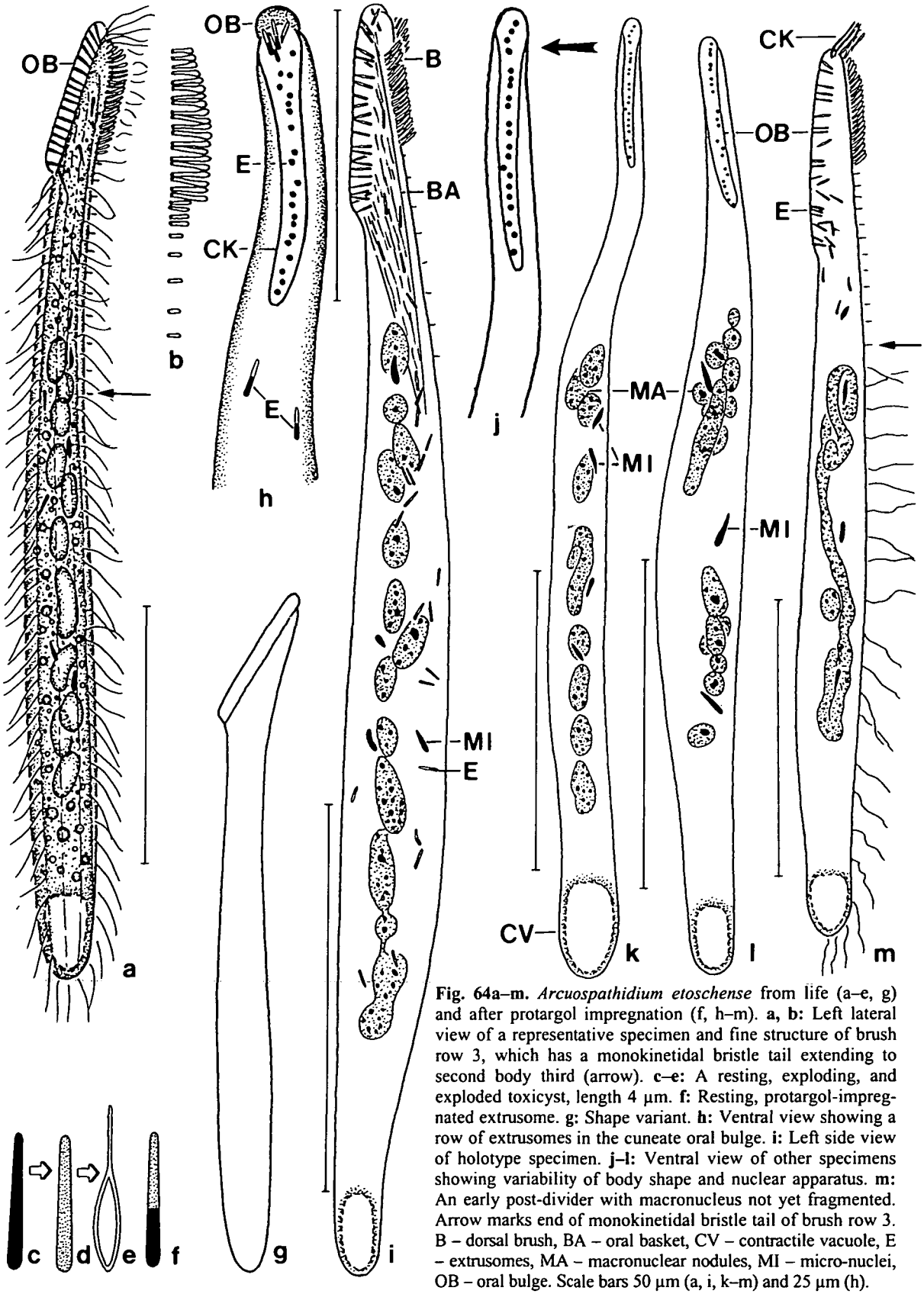

Fig. 64a–m. *Arcuospathidium etoschense* from life (a–e, g) and after protargol impregnation (f, h–m). **a, b:** Left lateral view of a representative specimen and fine structure of brush row 3, which has a monokinetidal bristle tail extending to second body third (arrow). **c–e:** A resting, exploding, and exploded toxicyst, length 4 µm. **f:** Resting, protargol-impregnated extrusome. **g:** Shape variant. **h:** Ventral view showing a row of extrusomes in the cuneate oral bulge. **i:** Left side view of holotype specimen. **j–l:** Ventral view of other specimens showing variability of body shape and nuclear apparatus. **m:** An early post-divider with macronucleus not yet fragmented. Arrow marks end of monokinetidal bristle tail of brush row 3. B – dorsal brush, BA – oral basket, CV – contractile vacuole, E – extrusomes, MA – macronuclear nodules, MI – micro-nuclei, OB – oral bulge. Scale bars 50 µm (a, i, k–m) and 25 µm (h).

Table 54. Morphometric data on *Arcuospathidium etoschense*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	175.5	171.0	28.3	6.0	16.1	130.0	233.0	22
Body, width	13.4	12.5	3.7	0.8	27.4	10.0	24.0	22
Body length:width, ratio	13.7	14.4	4.0	0.9	29.5	7.4	22.0	22
Oral bulge, length	28.1	26.5	5.0	1.1	17.6	18.0	40.0	22
Oral bulge (circumoral kinety), width	3.2	3.0	0.9	0.2	29.3	2.0	5.0	18
Body length:oral bulge length, ratio	6.3	6.2	1.0	0.2	15.4	4.7	8.8	22
Anterior body end to macronucleus	53.1	53.0	8.3	1.8	15.6	38.0	77.0	22
Macronuclear figure, length	83.6	83.0	19.0	4.1	22.7	54.0	115.0	22
Macronuclear nodules, length	11.3	10.0	3.7	0.8	32.4	6.0	20.0	22
Macronuclear nodules, width	4.1	4.0	0.7	0.2	17.2	3.0	5.0	22
Macronuclear nodules, number	10.9	11.5	2.8	0.5	25.7	4.0	15.0	30
Micronuclei, length	4.4	4.0	0.9	0.2	21.6	3.0	7.0	22
Micronuclei, width	1.3	1.2	–	–	–	1.0	2.0	22
Micronuclei, number	4.1	4.0	0.8	0.2	19.4	3.0	6.0	22
Somatic kineties, number [b]	9.5	10.0	–	–	–	8.0	11.0	13

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Approximations because of poor preparation.

cilia rather wide; three ciliary rows anteriorly differentiated to dorsal brush with longest row 2 slightly shorter than oral bulge, row 3 with a monokinetidal bristle tail extending to second third of body. Brush bristles about 4 µm long and distally slightly inflated in all rows (Fig. 64a, b, i, m; Table 54).

Oral bulge rather conspicuous because occupying 16% of body length on average, distinctly set off from body proper and so strongly slanted that it becomes orientated almost in parallel with main body axis; cuneate and about 4 µm wide in ventral view, 3–4 µm high in lateral view, contains a single, rough row of extrusomes producing a small bundle in broadened anterior end. Circumoral kinety continuous, associated with very fine nematodesmata forming long, faintly impregnated basket (Fig. 64a, g–m; Table 54).

Occurrence and ecology: To date found only in saline soil of the Etosha National Park (Table 4), indicating that it is a euryhaline species. *Arcuospathidium etoschense* is well adapted to soil life by its slender body.

Generic classification and comparison with related species: The generic classification remains somewhat doubtful because the ciliary pattern could not be seen clearly, except for the circumoral kinety, which is continuous. Thus, the population belongs either to *Spathidium* or *Arcuospathidium*. Fortunately, the species highly resembles *A. vlassaki* FOISSNER, 2000d and thus likely belongs to this genus. Actually, *A. etoschense* differs from *A. vlassaki* only by one main feature, viz., the macronucleus which is nodular in the former and a long strand in the latter. Minor differences occur in body shape (length:width ratio 13:1 vs. 10:1), the extrusomes (slenderly cuneate vs. obovate), and the oral bulge, which

is longer and more distinct than in *A. vlassaki*. Other *Arcuospathidium* species either also have a different macronuclear pattern or long dorsal bristles (→ *A. namibiense*). Several *Spathidium* species are also rather similar, especially → *Spathidium turgitorum* (extrusomes rod-shaped, more than 40 scattered macronuclear nodules); *S. procerum*, as redescribed by FOISSNER 1984 (extrusomes rod-shaped, single macronuclear strand); *S. metabolicum* POMP & WILBERT, 1988 (oral bulge much less slanted and with three rows of elongate oval extrusomes); and *S. anguilla*, as redescribed by FOISSNER 1984 (oral bulge with many scattered, fusiform extrusomes, 26 macronuclear nodules, micronuclei globular).

Arcuospathidium etoschense and *A. vlassaki*, both discovered in highly saline soils of the Etosha National Park, are only the tip of an iceberg because we discovered two further new species of this type in highly saline soils of the northern Namib Desert. A specific and highly characteristic feature of these spathidiids are the slender micronuclei.

Arcuospathidium lorjeae nov. spec. (Fig. 65a–m; 328a–c, f; Table 55)

Diagnosis: Size about 200 × 18 µm in vivo. Slenderly spatulate with distinctly oblique, slenderly dumb-bell-shaped oral bulge occupying approximately 1/3 of body length. Macronucleus vermiform, tortuous. Extrusomes about 6 × 0.5 µm, slightly fusiform. On average 17 ciliary rows, 3 anteriorly modified to conspicuous dorsal brush having up to 10 µm long bristles and occupying 31% of body length.

Type location: Mud and soil from road puddles in the Bambatsi Guest Farm, Namibia, 20°10'S 15°25'E (site 49 in figure 2 and chapter 2.1.2).

Dedication: Sabine AGATHA dedicates this species to her teacher and friend, Dr. Jeannette Cornelie RIEDEL-LORJÉ, Hamburg.

Description: Size 150–250 × 10–25 µm in vivo, usually near 200 × 18 µm; length:width ratio 8.4–16.1:1, on average about 11:1 in vivo and protargol preparations (Table 55). Slenderly spatulate to almost rod-shaped because of the steep, hardly projecting oral bulge and the cylindroidal postoral portion; oral area, that is, anterior body third more or less distinctly curved dorsally and laterally flattened up to 2:1 (Fig. 65a, b, h–k; 328a). Macronucleus in central body portion, vermiform and up to 2:1 flattened, more or less distinctly nodular and tortuous; nucleoli minute, numerous. On average 13 globular micronuclei attached and near macronucleus. Contractile vacuole in rear end, about six excretory pores in posterior pole area. Extrusomes in an indistinct row each right and left of oral bulge midline and scattered in cytoplasm, do not impregnate with the protargol method used, except for a certain cytoplasmic developmental stage; individual extrusomes slightly fusiform because of inconspicuously narrowed and rounded ends, about 6 × 0.5 µm in size (Fig. 65b, e; 328b). Cortex flexible, conspicuous because containing narrowly spaced rows of highly refractive granules about 1 × 0.5 µm in size (Fig. 65f, g). Cytoplasm colourless and hyaline, especially in oral area, contains few to many lipid droplets up to 10 µm across. Food not known, likely other ciliates. Swims and glides rather rapidly showing great flexibility.

Cilia about 8 µm long in vivo, widely spaced in oral area, arranged in an average of 17 equidistant rows anteriorly directed dorsally at both sides of circumoral kinety, as typical for the genus (FOISSNER 1984). Three dorsal ciliary rows anteriorly differentiated to conspicuous

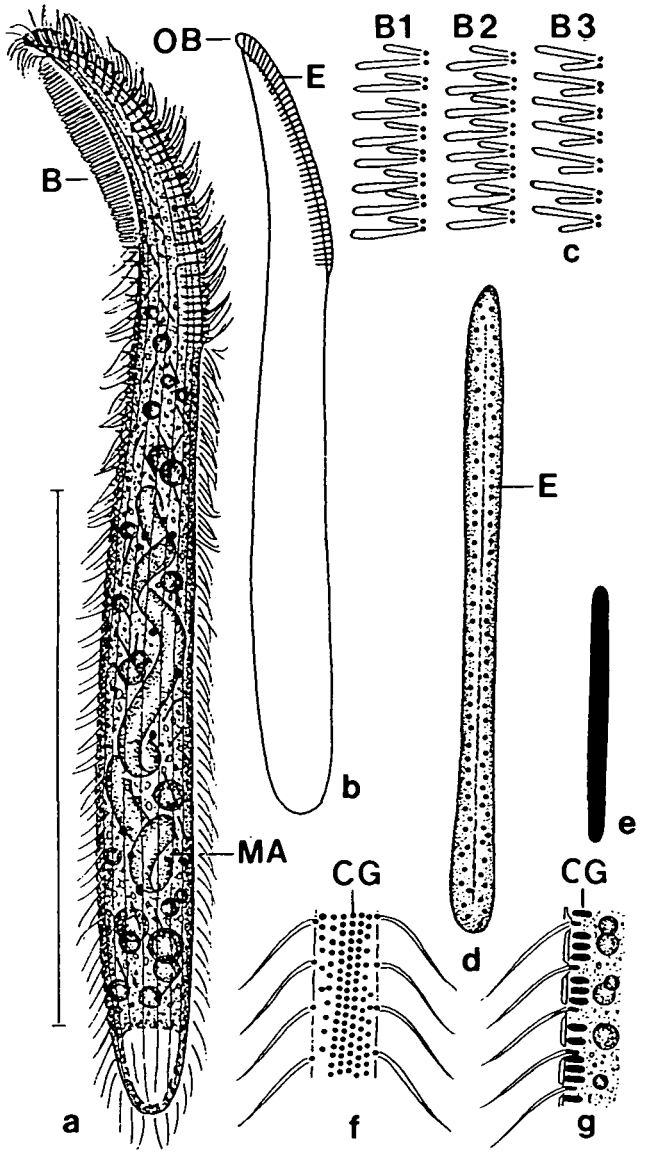

Fig. 65a–g. *Arcuospathidium lorjeae* from life. **a:** Right side view of a representative specimen. Note the conspicuous dorsal brush, whose bristles decrease in length anteriorly and posteriorly. Scale bar 100 µm. **b:** Shape variant. **c:** Mid-portion of dorsal brush according to life and SEM obser-vations. The anterior bristles are shorter than the posterior ones in rows 1 and 2, while vice versa in row 3. **d:** Frontal view of oral bulge containing a row of extrusomes right and left of midline. **e:** Oral bulge extrusome, about 6 × 0.5 µm. **f, g:** Surface view and optical section showing the densely spaced, highly refractive cortical granules. B(1-3) – dorsal brush (rows), CG – cortical granules, E – extrusomes, MA – macronucleus, OB – oral bulge.

dorsal brush occupying on average 31% of body length; brush bristles about 10 µm long in middle region becoming smaller anteriorly and posteriorly, up to twice as thick as ordinary somatic cilia and thus forming a jelly mass with details difficult to recognize both in vivo and the scanning electron microscope; distal bristle end becomes inflated on prolonged observation (Fig. 65a, c; 328c, f; Table 55). Brush row 1 slightly shorter than row 2, composed of an average of 34 moderately widely spaced dikinetids with anterior bristles only half as long as posterior; row 2 similar to row 1, but composed of an average of 53 very narrowly spaced dikinetids; dikinetidal portion of brush row 3 distinctly shorter than row 2, composed of an average of 24 comparatively widely spaced dikinetids with posterior bristles about half as long as anterior, has a long, monokinetidal tail made of 1 µm long bristles.

Oral area more or less distinctly curved dorsally and flattened up to 2:1. Oral bulge occupies one third of body length on average, inconspicuous because only about 3 µm wide and high and thus indistinctly set off from body proper, steep to very steep, that is, extends almost parallel to main body axis; in frontal view very elongate dumb-bell-shaped with tapered anterior and narrowly rounded posterior end both in vivo and preparations. Circumoral kinety of same shape as oral bulge, composed of ordinarily spaced dikinetids associated with fine nematodesmata extending posteriorly along oral bulge to form a narrow, straight funnel postorally; cilia of circumoral dikinetids of same length as somatic ones (Fig. 65a, b, d, h–l; 328a, b; Table 55).

Occurrence and ecology: To date found only at type location, where it was moderately abundant in the non-flooded Petri dish culture. The slender shape indicates that *Arcuospathidium lorjeae* is a terricolous species.

Comparison with related species: *Arcuospathidium lorjeae* likely belongs to the

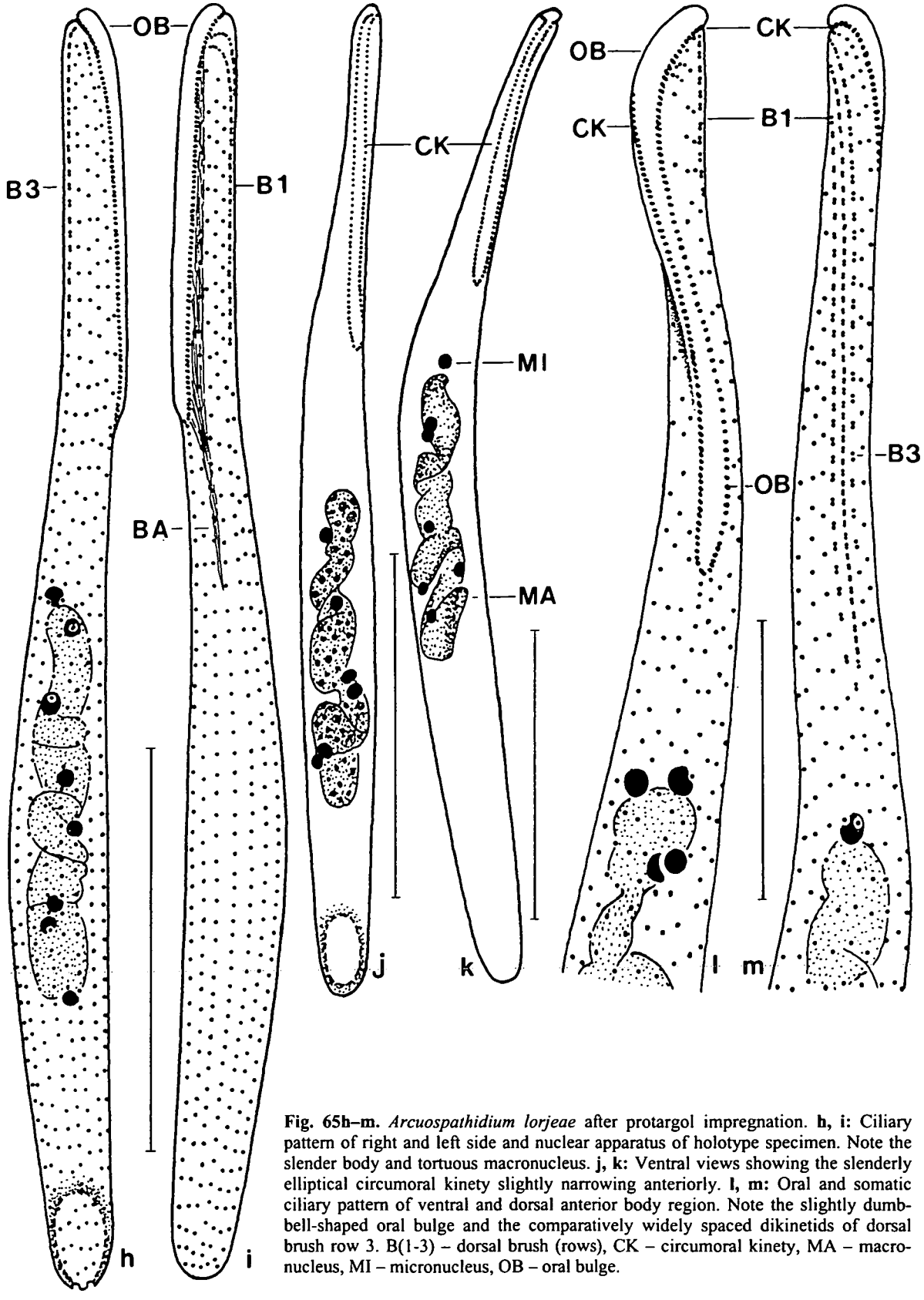

Fig. 65h–m. *Arcuospathidium lorjeae* after protargol impregnation. **h, i:** Ciliary pattern of right and left side and nuclear apparatus of holotype specimen. Note the slender body and tortuous macronucleus. **j, k:** Ventral views showing the slenderly elliptical circumoral kinety slightly narrowing anteriorly. **l, m:** Oral and somatic ciliary pattern of ventral and dorsal anterior body region. Note the slightly dumbbell-shaped oral bulge and the comparatively widely spaced dikinetids of dorsal brush row 3. B(1-3) – dorsal brush (rows), CK – circumoral kinety, MA – macronucleus, MI – micronucleus, OB – oral bulge.

Table 55. Morphometric data on *Arcuospathidium lorjeae* (upper line) and *Arcuospathidium cultriforme megastoma* (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	173.5	170.0	25.2	5.8	14.5	138.0	215.0	19
	219.8	210.0	39.8	12.6	18.1	165.0	280.0	10
Body, width	15.6	16.0	2.8	0.6	17.8	9.0	20.0	19
	29.3	27.5	7.3	2.3	24.8	20.0	44.0	10
Body length:width, ratio	11.4	11.3	2.1	0.5	18.5	8.4	16.1	19
	7.7	7.6	1.2	0.4	15.7	6.2	9.6	10
Oral bulge, length	59.0	58.0	11.5	2.6	19.5	38.0	80.0	19
	128.7	124.5	27.4	8.7	21.3	80.0	165.0	10
Body length:oral bulge length, ratio	3.0	2.9	0.5	0.1	15.6	2.3	3.9	19
	1.7	1.7	0.2	0.1	13.3	1.4	2.3	10
Circumoral kinety to last dikinetid of brush row 1, distance	47.4	50.0	9.0	2.1	19.1	25.0	60.0	19
	75.3	78.0	22.5	7.5	29.8	39.0	110.0	9
Dorsal brush row 1, number of dikinetids	33.8	33.0	6.7	1.5	19.7	23.0	44.0	19
	52.3	46.0	15.4	5.1	29.4	35.0	80.0	9
Circumoral kinety to last dikinetid of brush row 2, distance	53.4	53.0	8.0	1.8	15.0	37.0	68.0	19
	80.1	83.0	19.3	6.4	24.1	48.0	110.0	9
Dorsal brush row 2, number of dikinetids	53.2	53.0	11.1	2.6	20.9	36.0	75.0	19
	62.0	60.0	14.5	4.8	23.3	42.0	82.0	9
Circumoral kinety to last dikinetid of brush row 3, distance	42.8	44.0	7.3	1.7	17.1	27.0	52.0	19
	51.7	52.0	12.2	4.1	23.5	30.0	67.0	9
Dorsal brush row 3, number of dikinetids	24.4	25.0	4.4	1.0	17.9	18.0	33.0	19
	32.7	30.0	8.0	2.7	24.5	25.0	50.0	9
Anterior body end to macronucleus, distance	74.2	71.0	13.6	3.1	18.3	47.0	105.0	19
	87.8	89.5	22.3	7.1	25.4	46.0	120.0	10
Macronuclear figure, length	63.2	62.0	11.0	2.5	17.4	46.0	87.0	19
	93.4	79.5	30.2	9.5	32.3	55.0	150.0	10
Macronucleus, length (spread; approximate)	86.1	90.0	–	–	–	60.0	110.0	19
	121.0	100.0	–	–	–	80.0	200.0	10
Macronucleus, width	6.4	6.0	0.8	0.2	12.0	5.0	8.0	19
	7.7	7.5	1.0	0.3	12.3	7.0	10.0	10
Micronuclei, length	2.8	3.0	–	–	–	2.2	3.3	19
	2.5	2.6	–	–	–	2.0	3.0	10
Micronuclei, width	2.6	2.5	–	–	–	2.0	3.2	19
	2.5	2.5	–	–	–	2.0	3.0	10
Micronuclei, number	8.9	8.5	2.8	0.7	31.0	5.0	16.0	18
	13.1	15.0	4.4	1.7	33.6	8.0	19.0	7
Somatic kineties, number	17.1	17.0	1.4	0.3	8.0	14.0	20.0	19
	30.2	30.0	3.2	1.1	10.4	24.0	35.0	9
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
	3.0[b]	3.0	0.0	0.0	0.0	3.0	3.0	9
Ciliated kinetids in a lateral kinety, number	81.3	82.5	22.0	5.2	27.1	46.0	120.0	18
	99.6	100.0	24.8	9.4	24.9	70.0	150.0	7

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] A fourth, short row right of row 1 occurs in about half of the specimens (see text).

→ *Arcuospathidium cultriforme*-complex described below. Within this complex, it is most similar to *Arcuospathidium cultriforme cultriforme*, differing distinctly, however, in the length:width ratio (11.4:1 vs. 6.9:1), the number of ciliary rows (17 vs. 28) and, especially, the length of the dorsal bristles (up to 10 µm vs. up to 5 µm; Fig. 328d–f). It is the last feature, which makes the species so conspicuous.

Arcuospathidium cultriforme (PENARD, 1922) FOISSNER, 1984

Improved diagnosis: Size about 180–300 × 20–60 µm in vivo, usually near 230–280 × 30–40 µm. Spatulate to knife-shaped with distinctly oblique, slenderly cuneate to elliptical oral bulge occupying 1/3 to 2/3 of body length. Macronucleus vermiform, tortuous. Extrusomes 4–8 × 0.6–1 µm, rod-shaped to indistinctly fusiform or acicular. On average 28–32 ciliary rows, 3 anteriorly differentiated to dorsal brush occupying 27–36% of body length.

Remarks: We split this species into three subspecies mainly differing in the relative length of the mouth, which is an important morphometric feature causing a rather different overall appearance (Fig. 66a–f): *A. cultriforme cultriforme* (ACC; mouth one third of body length); *A. cultriforme lionotiforme* (ACL; mouth about half of body length); and *A. cultriforme megastoma* (ACM; mouth about two thirds of body length). There are also differences in some other features, such as details of body and extrusome shape, body size, and number of ciliary rows. However, all these differences are inconspicuous and likely within the range of the species' natural variability. Thus, we distinguish the subspecies only according to the relative mouth length at the present state of knowledge. This is also supported by the coefficients of divergence, reported in the next paragraph.

We calculated the "coefficient of divergence" for two main features of the three populations, according to the simple advice of MAYR (1975), using the redescriptions and original data of FOISSNER (1984). The coefficient of divergence is $D = (\bar{x}b - \bar{x}a)/(sa+sb)$, where (a) and (b) are the arithmetic means and (s) the standard deviations of the features to be compared. If the coefficient is < 1.28, subspecies are difficult to separate; if it is near 1.28, subspecies can be separated by 90% likelihood; and if it is ≥ 1.3, the populations are likely different species (MAYR 1975).

The following coefficients are obtained for the feature "ratio of body/mouth length": D (ACC + ACL) = 1.3; D (ACM + ACC) = 2.3; D (ACM + ACL) = 1.8. The feature "number of ciliary rows" provides the following coefficients: 1.8; 0.5; 0.5. Accordingly, *A. cultriforme* and *A. lionotiforme* are distinct subspecies, while *A. megastoma* seems to be a distinct species when the mouth length is considered. However, the number of ciliary rows does not separate *A. megastoma* from *A. cultriforme*, whereas *A. cultriforme* and *A. lionotiforme* are separated at subspecies level at least.

Arcuospathidium cultriforme cultriforme (PENARD, 1922) FOISSNER, 1984 **nov. stat.** (Fig. 66a, b)

Diagnosis: Mouth about one third of body length.

Locus classicus: Mosses in Switzerland (Chemin de la Montagne, sur un vieux mur).

Remarks: Detailed redescription by FOISSNER (1984).

Arcuospathidium cultriforme lionotiforme (KAHL, 1930) FOISSNER, 1984 nov. stat. (Fig. 66c, d; 328d, e)

Diagnosis: Mouth about half of body length.

Locus classicus: *Sphagnum* moss near Hamburg, Germany.

Remarks: Detailed redescription by FOISSNER (1984).

Arcuospathidium cultriforme megastoma **nov. subspec.** (Fig. 66e–m; 328h; Table 55)

Diagnosis: Mouth about two thirds of body length.

Type location: Mud and soil from road puddles in the Bambatsi Guest Farm, Namibia, 20°10'S 15°25'E (site 49 in figure 2 and chapter 2.1.2).

Etymology: Apposite noun of the Greek prefix *mega* (very large) and the Greek noun *stoma* (mouth), referring to the extraordinarily large mouth.

Description: Size 180–300 × 20–45 µm in vivo, usually near 250 × 30 µm; length:width ratio 6.2–9.6:1, on average 8.8:1 in protargol preparations, and thus slightly more slender than *A. cultriforme cultriforme* and *A. cultriforme lionotiforme* (both about 7:1, FOISSNER 1984). Knife-shaped to indistinctly spatulate with anterior body region more or less distinctly curved dorsally; flattened only in anterior half (Fig. 66e–g; Table 55). Macronucleus in posterior body half, vermiform and tortuous, about 90 µm long. Micronuclei attached and near macronucleus, about 3 µm across in vivo, that is, small as compared to body and macronucleus size (Fig. 66e, g). Contractile vacuole in rear end, several excretory pores in posterior pole area. Extrusomes in a row each right and left of midline of oral bulge, basically rod-shaped with slightly narrowed and rounded ends, making them indistinctly fusiform or acicular, 5–7 × 0.6–0.8 µm, that is, rather thick and highly refractive, impregnate occasionally with protargol (Fig. 66i, l, m; 328h); immature cytoplasmic extrusomes distinctly fusiform, impregnate black. Cytoplasm colourless, in some specimens packed with fat globules and food vacuoles up to 10 µm across and about 8 µm long pharyngeal baskets of prey ciliates; none of the 15 specimen seen, contained large prey. Creeps vividly on microscope slide curving mouth area to and fro.

Densely ciliated, except in anterior third. On average 30 ciliary rows most distinctly curved dorsally at both sides of oral bulge and abutting successively to the long circumoral kinety, as typical for the genus (FOISSNER 1984); three dorsal rows anteriorly differentiated to a long brush with up to 5 µm long bristles, a minute fourth row composed of only 3–5 dikinetids right of row 1 in about half of specimens, likely vestiges from patterning of rows 1–3, which frequently have some irregularities, such as a short overlapping or non-overlapping break (Fig. 66e, g, h, j, m; Table 55). Brush row 1 slightly shorter than row 2, composed of an

average of 52 dikinetids; brush row 2 longer than brush row 3 by about one third, composed of an average of 80 dikinetids slightly more narrowly spaced than those of row 1; brush row 3 composed of an average of 33 dikinetids more widely spaced than those of rows 1 and 2.

Oral bulge conspicuous because bright due to the thick extrusomes contained and its enormous length, that is, occupying almost 60% of body length on average, straight to distinctly curved, depending on the state of the anterior body third; only 5 µm wide and 2–3 µm high, and thus indistinctly set off from body proper. Circumoral kinety very narrowly elliptical, not widened anteriorly, composed of narrowly spaced dikinetids associated with very fine nematodesmata producing a narrow, somewhat branched bundle along oral bulge (Fig. 66e–m).

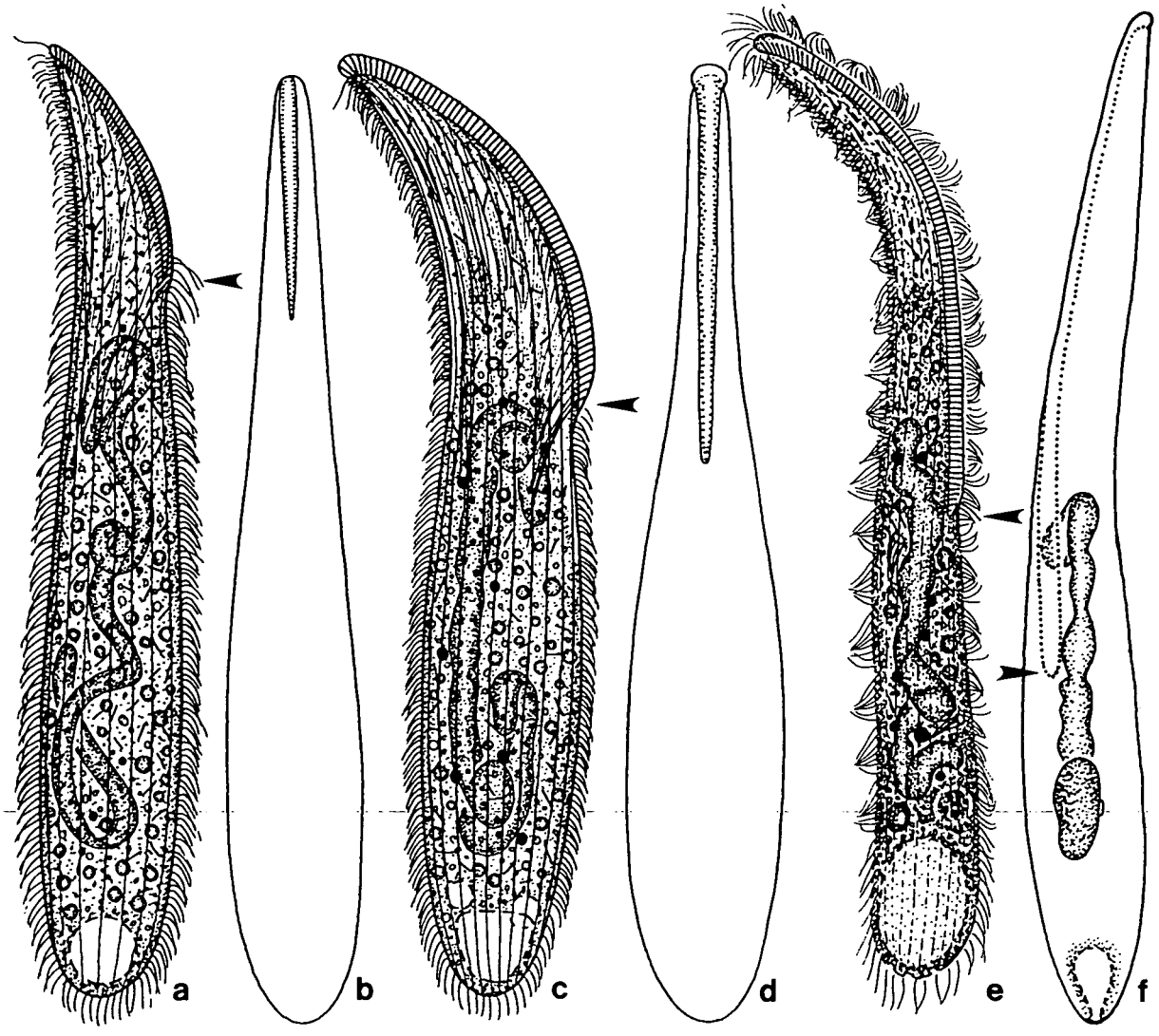

Fig. 66a–f. Comparison of the subspecies of *Arcuospathidium cultriforme* from life (a–e) and after protargol impregnation (f). Arrowheads mark posterior end of oral bulge. **a, b:** *Arcuospathidium cultriforme cultriforme*, right side and ventral view, length 250 µm (from FOISSNER 1984). **c, d:** *Arcuospathidium cultriforme lionotiforme*, right side and ventral view, length 270 µm (from FOISSNER 1984). **e, f:** *Arcuospathidium cultriforme megastoma*, right side and ventrolateral view, length 250 µm.

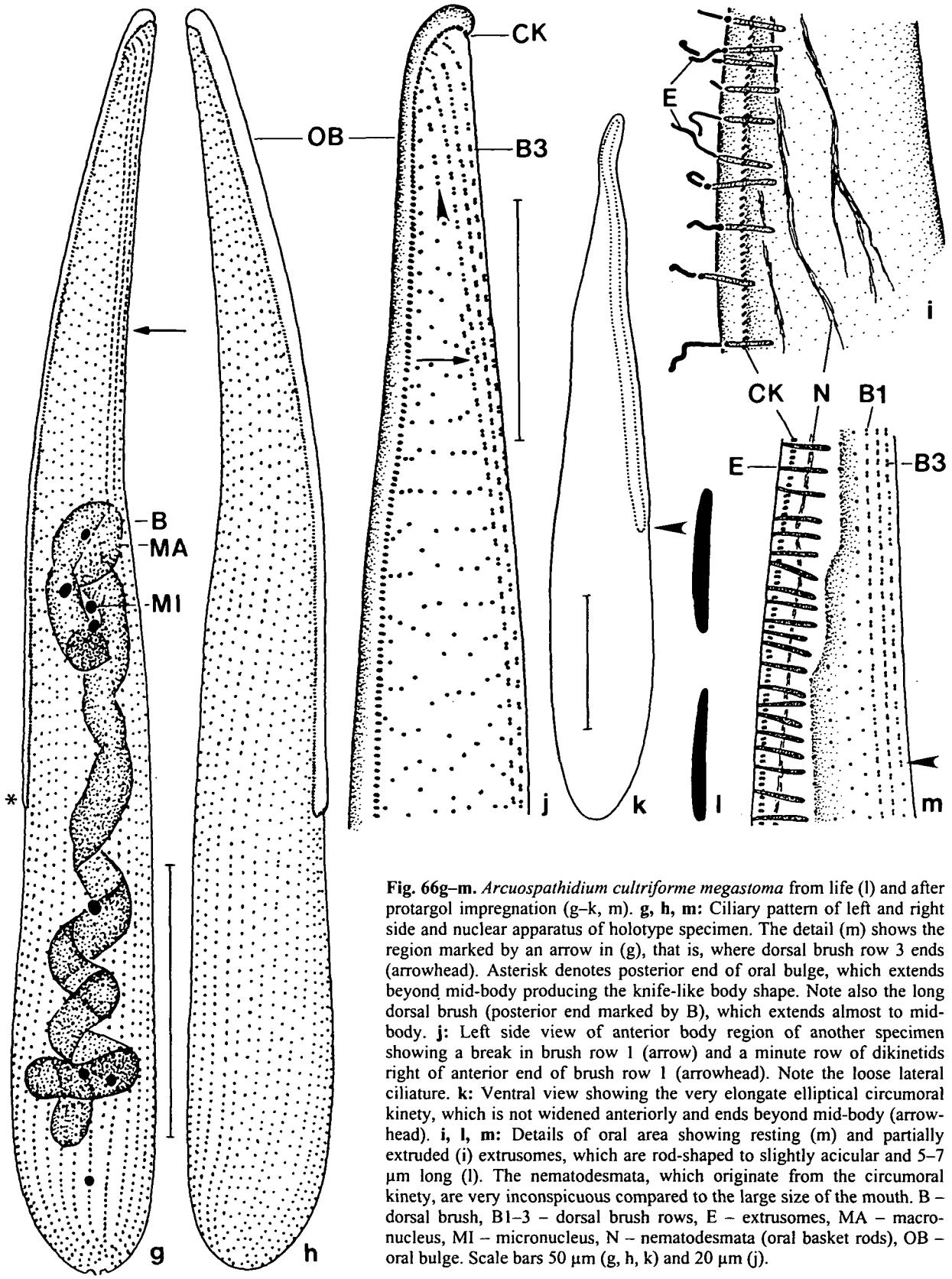

Fig. 66g–m. *Arcuospathidium cultriforme megastoma* from life (l) and after protargol impregnation (g–k, m). **g, h, m:** Ciliary pattern of left and right side and nuclear apparatus of holotype specimen. The detail (m) shows the region marked by an arrow in (g), that is, where dorsal brush row 3 ends (arrowhead). Asterisk denotes posterior end of oral bulge, which extends beyond mid-body producing the knife-like body shape. Note also the long dorsal brush (posterior end marked by B), which extends almost to mid-body. **j:** Left side view of anterior body region of another specimen showing a break in brush row 1 (arrow) and a minute row of dikinetids right of anterior end of brush row 1 (arrowhead). Note the loose lateral ciliature. **k:** Ventral view showing the very elongate elliptical circumoral kinety, which is not widened anteriorly and ends beyond mid-body (arrowhead). **i, l, m:** Details of oral area showing resting (m) and partially extruded (i) extrusomes, which are rod-shaped to slightly acicular and 5–7 µm long (l). The nematodesmata, which originate from the circumoral kinety, are very inconspicuous compared to the large size of the mouth. B – dorsal brush, B1–3 – dorsal brush rows, E – extrusomes, MA – macronucleus, MI – micronucleus, N – nematodesmata (oral basket rods), OB – oral bulge. Scale bars 50 µm (g, h, k) and 20 µm (j).

Occurrence and ecology: To date found only at type location. It was rare in the non-flooded Petri dish culture. The slender shape indicates that it prefers terrestrial habitats as do the other subspecies. All subspecies prefer, or are even confined to terrestrial habitats, especially mosses and leaf litter.

Arcuospathidium novaki nov. spec. (Fig. 67a–k; Table 56)

Diagnosis: Size about 270 × 55 µm in vivo. Spatulate with oblique, cuneate oral bulge about as long as widest trunk region. Macronucleus vermiform and tortuous. Oral bulge extrusomes acicular, about 7 × 0.8 µm; body extrusomes attached to entire somatic cortex, rod-shaped, approximately 4 × 0.3 µm. About 20 ciliary rows, 3 anteriorly modified to inconspicuous dorsal brush.

Type location: Mud and soil from road puddles in the Bambatsi Guest Farm, Namibia, 20°10'S 15°25'E (site 49 in figure 2 and chapter 2.1.2).

Dedication: We dedicate this species to Dr. Rudolf NOVAK, scientific manager of the Austrian Science Foundation.

Description: This large ciliate was rare and the few cells found in the protargol slides were poorly impregnated. Thus, data are incomplete. In spite of this, we describe and name the population because it has several outstanding features facilitating identification and contributing to the general morphology of the spathidiids.

Size conspicuous, that is, 200–350 × 40–70 µm in vivo, usually near 270 × 55 µm; length:width ratio about 5:1 in vivo, while 2.3–5.9:1, on average 3.8:1 in protargol preparations, indicating some inflation during preparation (Table 56). Shape inconspicuous, that is, spatulate with distinctly oblique oral bulge occupying 1/4–1/5 of body length; acontractile. Oral area hyaline because flattened approximately 3:1, oral and body extrusomes thus distinct; postoral region fusiform and dark at low magnification (≤ ×100) due to numerous cytoplasmic inclusions (Fig. 67a, b, i). Macronucleus in central quarters of cell, vermiform and highly tortuous, when spread about as long as body. Many micronuclei difficult to distinguish from similar-sized and impregnated cytoplasmic inclusions. Contractile vacuole in rear end; no second contractile vacuole. Extrusomes highly remarkable because a special type each in oral bulge and somatic cortex (Fig. 67a, d–g, h, j, k). Oral bulge extrusomes form a rough row each in right and left half of oral bulge, acicular, about 7 × 0.8 µm in vivo, compact and thus highly refractive, do not impregnate with protargol. Body extrusomes randomly attached to somatic cortex, lacking in oral bulge, rod-shaped, 3–4 × 0.3 µm in vivo, difficult to recognize, except in hyaline oral area; when extruded, occasionally impregnate with protargol showing a dark, thick posterior half and a brownish, thin anterior half with a minute globule at top. Cortex very flexible, contains about 15 rows of minute (~ 0.2 µm) granules between two kineties each and extrusomes, as described above, appearing as bright dots among the pale granules (Fig. 67k). Cytoplasm colourless, usually packed with globular and irregular, highly refractive fat inclusions up to 30 µm across. Feeds on ciliates, for instance, *Colpoda minima*, recognizable in a food vacuole 90 × 55 µm in size. Glides and swims slowly showing great flexibility.

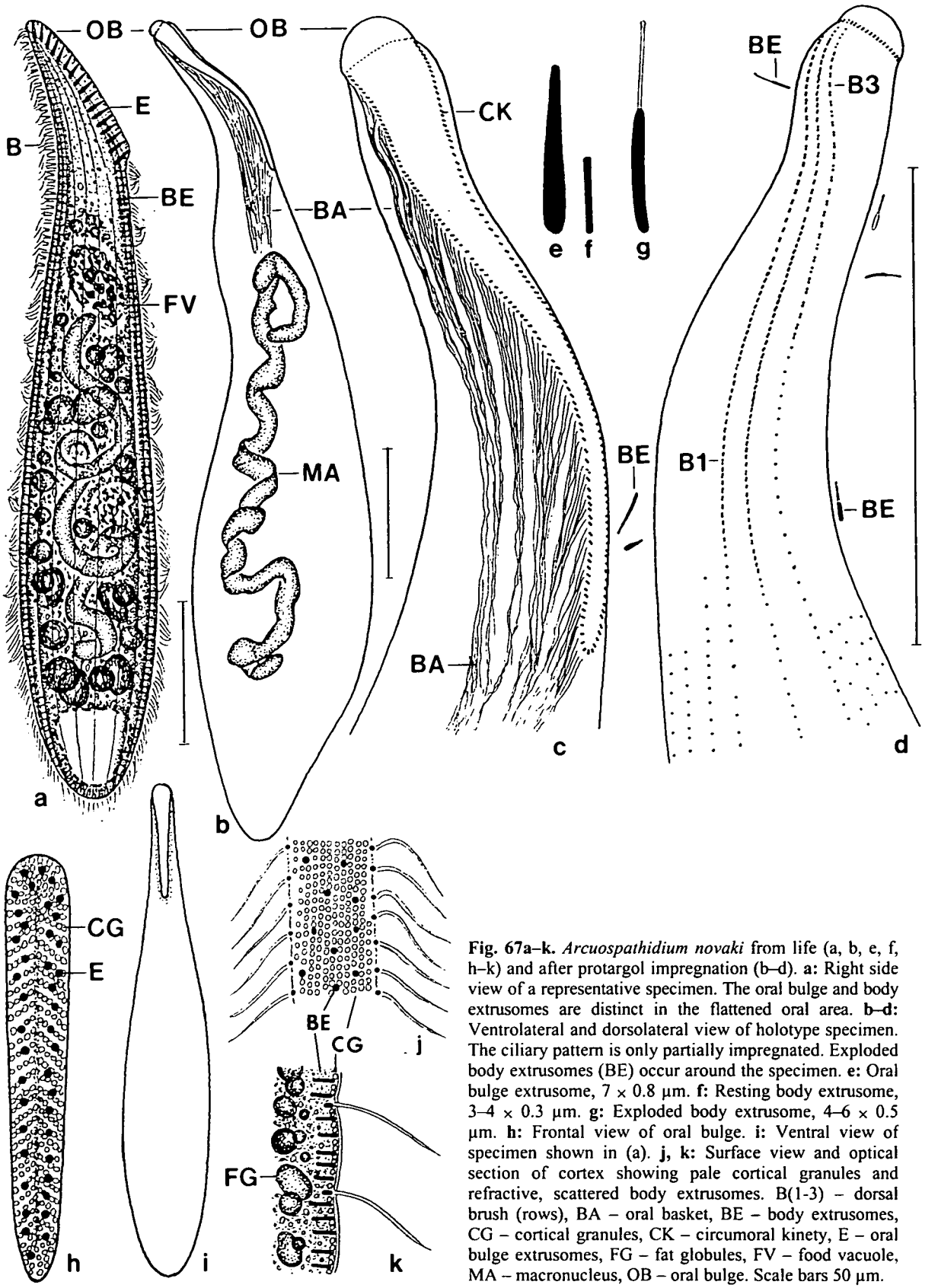

Fig. 67a–k. *Arcuospathidium novaki* from life (a, b, e, f, h–k) and after protargol impregnation (b–d). **a:** Right side view of a representative specimen. The oral bulge and body extrusomes are distinct in the flattened oral area. **b–d:** Ventrolateral and dorsolateral view of holotype specimen. The ciliary pattern is only partially impregnated. Exploded body extrusomes (BE) occur around the specimen. **e:** Oral bulge extrusome, 7 × 0.8 µm. **f:** Resting body extrusome, 3–4 × 0.3 µm. **g:** Exploded body extrusome, 4–6 × 0.5 µm. **h:** Frontal view of oral bulge. **i:** Ventral view of specimen shown in (a). **j, k:** Surface view and optical section of cortex showing pale cortical granules and refractive, scattered body extrusomes. B(1-3) – dorsal brush (rows), BA – oral basket, BE – body extrusomes, CG – cortical granules, CK – circumoral kinety, E – oral bulge extrusomes, FG – fat globules, FV – food vacuole, MA – macronucleus, OB – oral bulge. Scale bars 50 µm.

Cilia 10 µm long and ordinarily spaced in vivo, arranged in about 20 widely spaced rows, three anteriorly modified to an about 70 µm long, ordinary dorsal brush with up to 4 µm long, rod-shaped bristles. Brush dikinetids more closely spaced in rows 1 and 2 than in row 3, which is also distinctly shorter, but has a monokinetidal tail of 1 µm long bristles extending to second third of cell (Fig. 67a, d).

Oral bulge about 60 µm long in vivo and 5 µm high at dorsal end, distinctly oblique and slightly convex, cuneate to slenderly cuneate in frontal view, covered by oblique rows of cortical granules. Circumoral kinety conspicuously cuneate, composed of narrowly spaced dikinetids, distinctly separate from somatic ciliary rows. Oral basket voluminous.

Occurrence and ecology: To date found only at type location, where it was rare in the non-flooded Petri dish culture. The large size indicates that it is a limnetic species.

Comparison with related species: *Arcuospathidium novaki* has several outstanding features, viz., body (somatic) extrusomes (toxicysts) and, in spite of the huge size, only about 20 ciliary rows. Thus, it is easily distinguished from all other *Spathidium* s.l. species, except of → *Apospathidium* spp., which also have body extrusomes and few ciliary rows. However, → *Apospathidium terricola* and → *A. atypicum* are smaller (< 200 µm) and tail-like narrowed posteriorly, and have a short, rod-shaped macronucleus.

The generic classification of this population is somewhat uncertain because the ciliary pattern is poorly impregnated. However, the cuneate oral bulge and the continuous circumoral kinety exclude *Apospathidium* and suggest that it belongs to *Arcuospathidium*.

Table 56. Morphometric data on *Arcuospathidium novaki*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	242.5	245.0	60.6	24.7	25.0	175.0	325.0	6
Body, width	66.1	67.0	13.5	5.5	20.4	48.0	80.0	6
Body length:width, ratio	3.8	3.5	1.2	0.5	32.7	2.3	5.9	6
Oral bulge, length	52.0	49.0	8.9	4.5	17.1	45.0	65.0	4
Macronuclear figure, length	129.2	130.0	29.7	12.1	23.0	90.0	165.0	6
Macronucleus, length (spread; approximate)	248.0	250.0	–	–	–	150.0	320.0	6
Macronucleus, width	8.0	8.0	1.1	0.4	13.7	7.0	10.0	6

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Protospathidium namibicola nov. spec. (Fig. 68a–n; 330d–h; Table 57)

Diagnosis: Size about 210 × 20 µm in vivo. Elongate claviform with conspicuous, hemispherical oral bulge about half as wide as broadest body region. Macronucleus in middle and posterior body third, frequently flattened band-like and tortuous. Extrusomes rod-shaped,

about 5 µm long. On average 9 ciliary rows, 3 anteriorly differentiated to inconspicuous dorsal brush occupying 10% of body length.

Type location: Dune soil (sand) in the Central Namib Escarpment, north of the village of Solitaire, Namibia, 23°50'S 16°E (site 33 in figure 2 and chapter 2.1.2).

Etymology: The Latin *namibicola* (inhabiting the Namib Desert) refers to the habitat (Namib Desert) the species was discovered.

Description: Size 150–280 × 10–30 µm in vivo, usually about 210 × 20 µm, length:width ratio also highly variable, viz., 6.2–19.2:1, on average near 11:1 (Table 57); unflattened and acontractile. Shape basically elongate claviform gradually broadening posteriorly, widest region in or below mid-body, both ends narrowly rounded (Fig. 68a, d, i; 330d); slenderest specimens rod-shaped, broadest ordinarily claviform (Fig. 68f, g); more or less distinctly inflated immediately after ingesting large prey ciliates. Macronucleus invariably a long, tortuous strand usually commencing in second third of body and extending to near body end; flattened band-like and/or more or less distinctly spiralized in about 70% of specimens; nucleoli globular, small; condenses to a globular mass in middle dividers. Many ellipsoidal micronuclei along macronucleus, difficult to identify because of similarly sized and impregnated cytoplasmic inclusions. Contractile vacuole in rear body end, on average five excretory pores on left posterior pole area. Extrusomes packed in oral bulge and scattered in cytoplasm, posterior third occasionally impregnates with protargol; individual extrusomes rod-shaped with rounded ends, about 5 µm long (Fig. 68a, c, e). Cortex very flexible, contains about eight rows of minute (≤ 0.4 µm), colourless granules between each two ciliary rows (Fig. 68h). Cytoplasm colourless, contains few to many fat globules up to 5 µm across and remnants of prey ciliates, such as oral baskets and cytoplasmic crystals. Feeds on small (*Leptopharynx costatus*, *Pseudochilodonopsis mutabilis*) and medium-sized (*Gonostomum affine*) ciliates ingested whole because still identifiable in young food vacuoles; some specimens contained five to ten only partially digested prey ciliates, showing that *P. namibicola* is an effective predator. Glides and swims slowly, often appearing vermiform due to the strong flexibility and curved anterior body half (Fig. 68d).

Cilia about 10 µm long in vivo, arranged in an average of nine equidistant, mostly bipolar rows connected with the circumoral kinetofragments and rather loosely ciliated in cylindroidal neck region (Fig. 68a, i, j; Table 57). Dorsal brush three-rowed, inconspicuous because occupying only 10% of body length and bristles merely up to 4 µm long; brush region soft because occasionally slightly inflated in protargol preparations. All brush rows have a rather long anterior tail composed of closely spaced, ordinary cilia and continue as somatic kineties posteriorly; row 1 composed of thirteen, row 2 of seventeen, and row 3 of ten dikinetids on average, each having a distally inflated, 3–4 µm long anterior bristle and a 2–3 µm long posterior bristle (Fig. 68a, b, l, n; 330h; Table 57).

Oral bulge conspicuous in vivo, although only half as wide as broadest body region, because hemispherical and up to 6 µm high when cell is viewed ventrally, appears as a distinct button at low and middle magnifications (Fig. 68a, d, f; 330e, f); obovate in frontal view and bright due to the extrusomes contained (Fig. 68c, m; 330f, g). Circumoral kinety at base of oral bulge, composed of dikinetidal kinetofragments attached to the somatic ciliary rows and separated from each other by gaps one to three dikinetids wide; individual kinetofragments composed of six to twelve zigzagging basal bodies, dikinetidal organization clearly recognizable only in strongly impregnated cells. Each dikinetid associated with a rather thick fibre

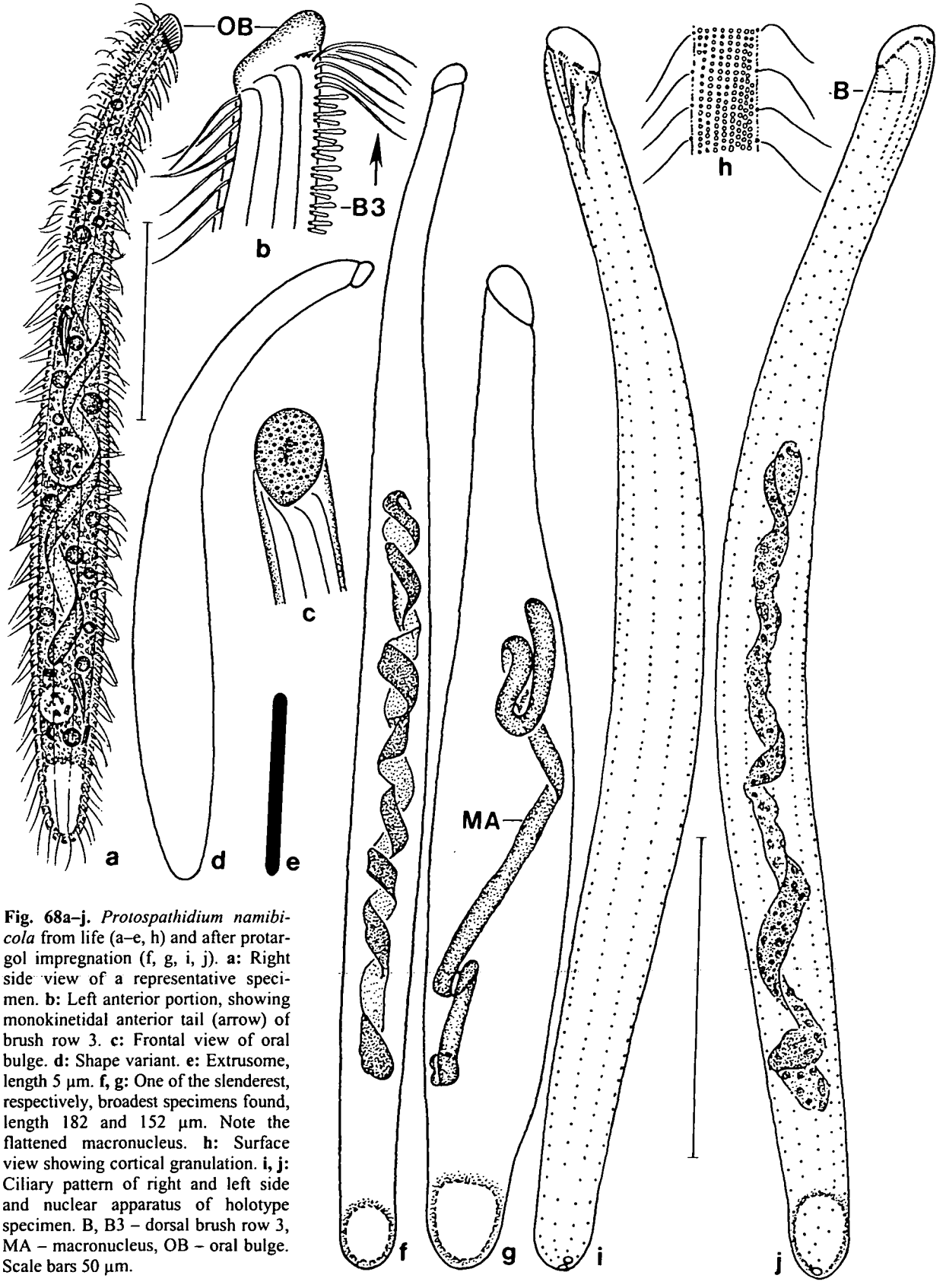

Fig. 68a–j. *Protospathidium namibicola* from life (a–e, h) and after protargol impregnation (f, g, i, j). **a:** Right side view of a representative specimen. **b:** Left anterior portion, showing monokinetidal anterior tail (arrow) of brush row 3. **c:** Frontal view of oral bulge. **d:** Shape variant. **e:** Extrusome, length 5 µm. **f, g:** One of the slenderest, respectively, broadest specimens found, length 182 and 152 µm. Note the flattened macronucleus. **h:** Surface view showing cortical granulation. **i, j:** Ciliary pattern of right and left side and nuclear apparatus of holotype specimen. B, B3 – dorsal brush row 3, MA – macronucleus, OB – oral bulge. Scale bars 50 µm.

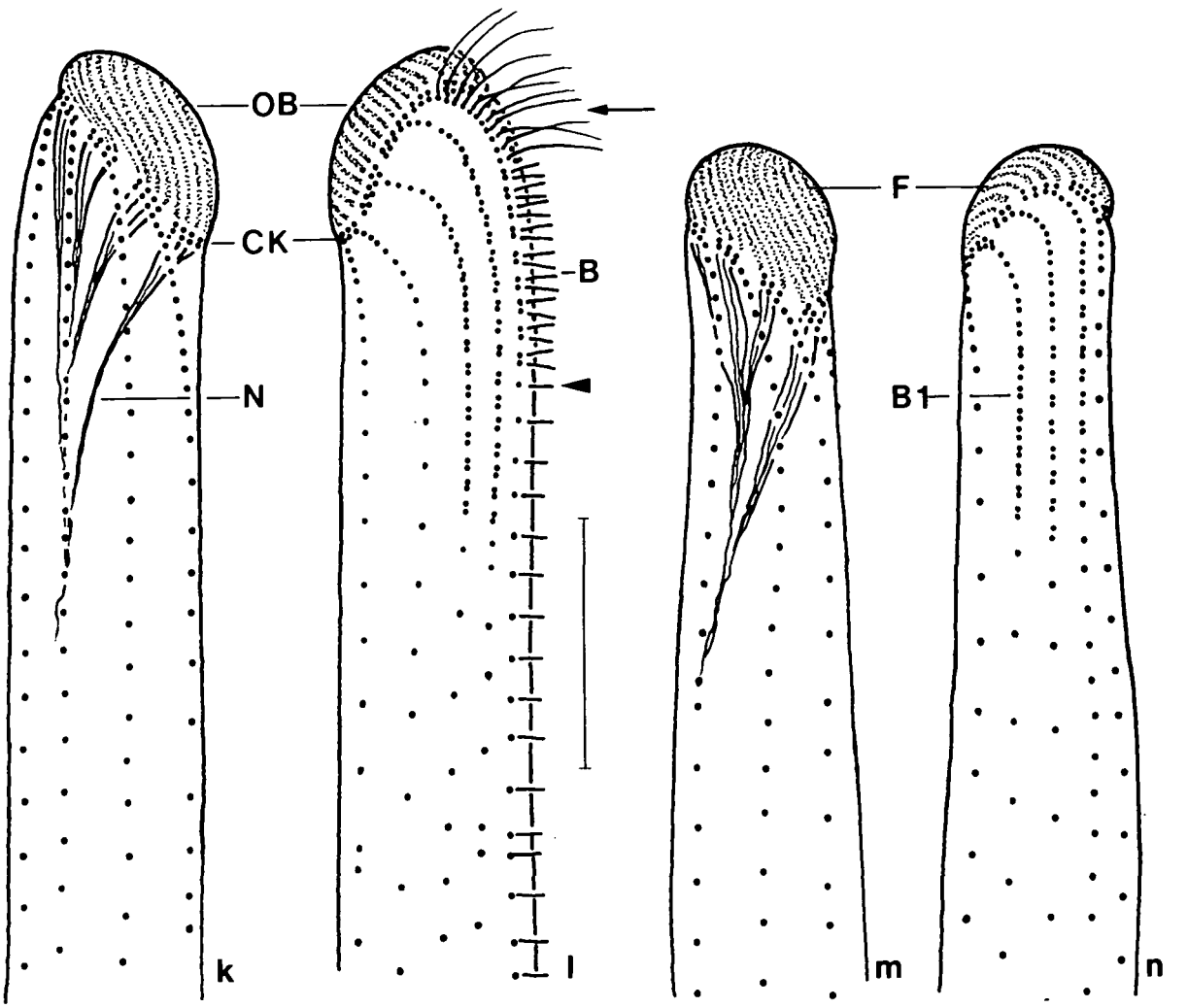

Fig. 68k–n. *Protospathidium namibicola*, somatic and oral infraciliature of right (k, m) and left (l, n) side of anterior body portion after protargol impregnation; figures (k, l) show the same cell as figures (i, j), that is, the holotype specimen. Arrow marks monokinetidal tail at anterior end of brush rows, while the arrowhead denotes the monokinetidal posterior bristle tail of brush row 3. Note the hemispherical oral bulge, which contains distinct fibres (F) extending spirally to the bulge centre. Nematodesmata (oral basket rods, N) originate only from circumoral kinety fragments (CK). B1, 3 – dorsal brush rows, CK – circumoral kinety (fragments), F – fibres, N – nematodesmata, OB – oral bulge. Scale bar 10 µm.

spiralling to bulge centre, and a short nematodesma contributing to the inconspicuous oral basket (Fig. 68a, i–n; 330e–g).

Occurrence and ecology: To date found only at type location, where it was abundant, indicating a high prey density not only in the non-flooded Petri dish culture, but also under natural conditions. *Protospathidium namibicola* is well adapted to the sandy habitat by its slender, flexible body.

Comparison with related species: *Protospathidium namibicola* has a clear identity and cannot be confused with *P. muscicola* (Fig. 50s, t) or → *P. vermiforme*, which

are smaller (< 150 µm on average) and have scattered macronuclear nodules and a distinctly reduced brush row 1; furthermore, → *P. vermiforme* is often narrowed tail-like posteriorly. Generally, however, care must be taken not to confuse *P. namibicola* with other slender spathidiids, for instance, → *Arcuospathidium namibiense* (brush with up to 15 µm long cilia, scattered macronuclear nodules) and *Spathidium bonneti* (scattered macronuclear nodules, brush row 1 reduced to a single dikinetid; Fig. 63n, o). Furthermore, there are some slender *Enchelyodon* species, for instance → *E. armatides*, which look fairly similar due to the button-shaped oral bulge.

Table 57. Morphometric data on *Protospathidium namibicola*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	188.3	192.0	26.8	5.9	14.3	136.0	250.0	21
Body, width	17.6	18.0	4.3	0.9	24.4	9.0	24.0	21
Body length:width, ratio	11.4	10.4	3.4	0.8	30.2	6.2	19.2	21
Oral bulge, width	9.3	10.0	1.0	0.2	10.4	7.0	11.0	21
Oral bulge, height	4.4	4.0	1.0	0.2	23.2	3.0	6.0	21
Body length:oral bulge width, ratio	20.4	19.5	2.8	0.6	13.8	16.0	25.9	21
Anterior body end to macronucleus, distance	60.7	60.0	13.3	2.9	22.0	44.0	95.0	21
Macronuclear figure, length	97.9	96.0	20.8	4.5	21.3	60.0	136.0	21
Macronucleus, length (spread; approximate)	134.5	140.0	–	–	–	90.0	180.0	21
Macronucleus, width	4.7	5.0	1.0	0.2	21.8	3.0	7.0	21
Circumoral kinety to end of brush row 1, distance	15.6	15.0	2.3	0.5	14.6	12.0	21.0	21
Circumoral kinety to end of brush row 2, distance	18.5	18.0	2.6	0.6	13.9	14.0	24.0	21
Circumoral kinety to end of brush row 3, distance	12.0	12.0	1.6	0.4	13.6	9.0	17.0	21
Somatic kineties, number	9.4	10.0	1.2	0.3	12.8	7.0	11.0	21
Ciliated kinetids in a ventral kinety, number	80.9	78.0	13.9	3.0	17.1	63.0	115.0	21
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Dikinetids in brush row 1, number	13.0	13.0	2.9	0.6	21.9	8.0	18.0	21
Dikinetids in brush row 2, number	15.9	17.0	2.7	0.6	17.2	11.0	21.0	21
Dikinetids in brush row 3, number	9.7	10.0	1.8	0.4	18.5	7.0	13.0	21
Excretory pores, number	5.3	5.0	1.8	0.4	33.2	3.0	8.0	21

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Protospathidium vermiforme nov. spec. (Fig. 69a–j)

1981 *Protospathidium bonneti* nov. comb. (BUITKAMP, 1977) — FOISSNER, Zool. Jb. Syst., 108: 271 (misidentification).

1986 *Protospathidium bonneti* (BUITKAMP, 1977) — DRAGESCO & DRAGESCO-KERNÉIS, Faune Tropicale, 26: 156 (revision).

Diagnosis: Size 80–160 × 5–13 µm in vivo. Rod-shaped with inconspicuous, obliquely truncated oral bulge. About 15 macronuclear nodules and 8 ciliary rows, 3 anteriorly differentiated to conspicuous dorsal brush having about 8 µm long bristles.

Type location: Grassland soil from the surroundings of the "Wallack-Haus" at the Grossglockner-Hochalpenstrasse, Carinthia, Austria, 47°N 12°50'E.

Etymology: The Latin adjective *vermiforme* (worm-like) refers to the worm-like shape.

Description and comparison with related species: For description, see FOISSNER (1981b) and figures 69a–j. The species needs redescription to obtain detailed information on extrusomes and morphometrics. In vivo, *P. vermiforme* is indistinguishable from → *Arcuospathidium namibiense* and *Spathidium bonneti* BUITKAMP, 1977a. Thus, protargol impregnation is required to reveal the structure of the circumoral kinety (FOISSNER 1984): composed of a single line of dikinetids in *Spathidium* and *Arcuospathidium* vs. short, dikinetidal fragments attached to the ciliary rows in *Protospathidium* (Fig. 69f–j). As concerns the congeners, only *P. serpens* is similar to *P. vermiforme*. However, *P. serpens* is distinctly stouter (< 6:1 vs. > 10:1) and has a tortuous, moniliform macronucleus (FOISSNER 1981b, 1996a).

Remarks: FOISSNER (1981b) redescribed *Spathidium bonneti* BUITKAMP, 1977a from soil of the Austrian Central Alps and transferred it to *Protospathidium*, assuming that BUITKAMP overlooked the protospathidiid circumoral kinety fragments in his population from the Ivory Coast (Fig. 63n, o). However, DRAGESCO & DRAGESCO-KERNÉIS doubted FOISSNER's identification and suggested that the Austrian population is a new species and BUITKAMP's species the representative of a new genus. As concerns the species, we fully agree with DRAGESCO & DRAGESCO-KERNÉIS because we learned that there are quite a lot of slender spathidiids in soil, some of which have, like BUITKAMP's species, a "closed" circumoral kinety, for instance, → *Arcuospathidium namibiense*. Comparing the figures of *Protospathidium vermiforme* (Fig. 69a–c) with that of *Spathidium bonneti* (Fig. 63o), FOISSNER's misidentification appears understandable. Such mistakes are simply caused by our great ignorance of ciliate diversity outside the holarctic region. Whether BUITKAMP's species belongs to *Spathidium* or *Arcuospathidium* needs further investigation (see also → *Arcuospathidium namibiense*).

There are now five well-defined *Protospathidium* species: *P. muscicola* DRAGESCO & DRAGESCO-KERNEIS, 1979; *P. serpens* (KAHL, 1930a) FOISSNER, 1981b; *P. terricola* FOISSNER, 1998a; → *P. namibicola* nov. spec., and → *P. vermiforme* nov. spec. Except of *P. terricola*, all are slender, indicating that the genus evolved in soil. Further, all have rod-shaped extrusomes. Likely, there are further species with differently shaped extrusomes, as in the other spathidiid genera.

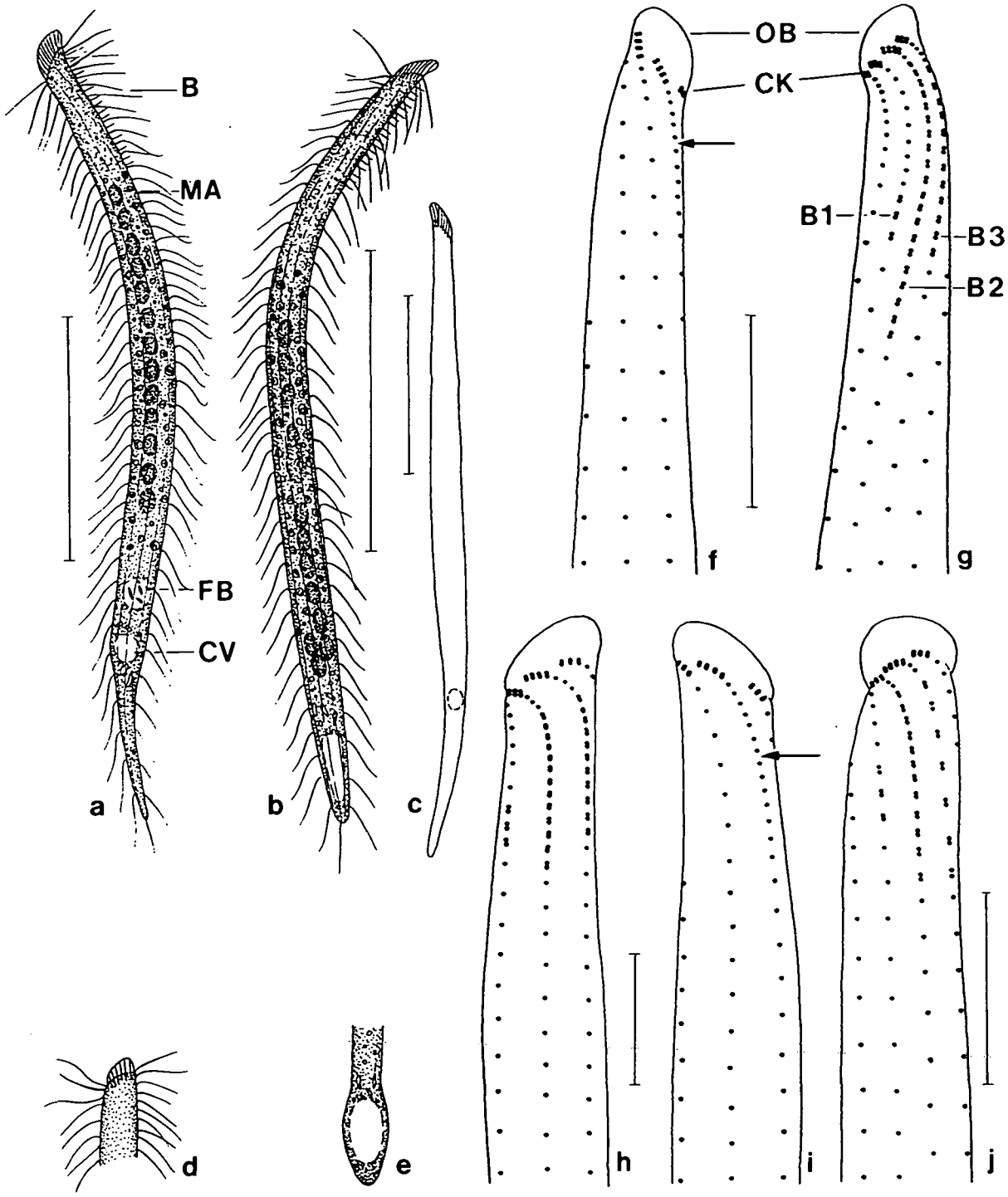

Fig. 69a–j. *Protospathidium vermiforme* (from FOISSNER 1981b) from life (a–e) and after protargol impregnation (f–j). **a, b:** Left side views of representative specimens. **c:** A very slender specimen. **d:** Dorsolateral view of anterior body region. **e:** Posterior body end when contractile vacuole is filled. **f–j:** Ciliary pattern in anterior right (f, i), left (h, h), and dorsal (j) body region; figure pairs (f, g) and (h, i) each show both sides of a specimen. Arrows mark condensation of cilia in anterior portion of a ventrolateral kinety. The protospathidiid circumoral kinety fragments are very distinct. Brush row 1 consists of three dikinetids far away from the circumoral kinety. B1-3 – dorsal brush rows, CK – circumoral kinety fragments, CV – contractile vacuole, FB – egestion vacuole, MA – macronucleus, OB – oral bulge. Scale bars 40 μm (a–c) and 20 μm (f–j).

Epispathidium polynucleatum nov. spec. (Fig. 70a–m; 329a–u; Table 58)

Diagnosis: Size about 190 × 30 µm in vivo. Indistinctly spatulate with elliptical, oblique, thick oral bulge about as long as widest postoral body region. On average 30 ellipsoidal, scattered macronuclear nodules and 22 ciliary rows. Extrusomes rod-shaped and distinctly curved, about 10 × 0.5 µm. Dorsal brush inconspicuous.

Type location: Soil and litter under an *Euphorbia* cushion at east margin of Namib desert, 26°40'S 16°50'E (site 13 in figure 2 and chapter 2.1.2).

Etymology: Composite of *poly* (many) and *nucleus*, referring to the main feature of the species, viz., the many macronuclear nodules.

Description: Two populations were studied in detail, viz., from Namibia (type) and Australia. They are indistinguishable, as also evident from the very similar morphometrics (Table 58). The description, however, is mainly based on the Namibian population, which was cultivated (in Eau de Volvic enriched with some crushed wheat grains to stimulate growth of small food ciliates) and investigated with the scanning electron microscope.

Size 130–230 × 25–40 µm, usually near 190 × 30 µm in vivo; length:width ratio 5–9.4:1, frequently 6–7:1 both in vivo and protargol preparations (Table 58). Shape fairly constant and conspicuous, that is, almost cylindroidal because oral bulge about as wide as broadest postoral body region and flattened only in oral area (Fig. 70a, c; 329a–c). Macronuclear pattern highly variable because nodules develop from a tortuous strand in post-dividers; thus, about 5% of specimens have a single or few long macronuclear pieces (see discussion). Ripe cells possess an average of 30 scattered, globular to elongate ellipsoidal, rather large (12 × 5 µm) nodules, each with a branched nucleolus or a few globular nucleoli. Many scattered micronuclei 1.5–2.5 µm across (Fig. 70a, c; 329s, t). Contractile vacuole in rear end, several excretory pores in posterior pole area. Extrusomes virtually identical in Namibian, Australian, and Venezuelan population (Fig. 70a, f, h–k; 329e–g, i, o–r): ripe organelles fine, distinctly curved rods with slightly narrowed ends, 8–10 ($\bar{x}$ = 9.3, n = 11) × 0.4–0.6 µm in size, studded in oral bulge, except for midline, do not impregnate with the protargol method used; many developing extrusomes scattered in cytoplasm, 6–8 µm long and with a conspicuous central or acentral inflation about 2 µm across, impregnate heavily with protargol. Cortex highly flexible, indistinctly furrowed by ciliary rows, contains innumerable, colourless granules about 0.4 µm across; granules around basal bodies of cilia and between kineties, form slightly oblique rows along or upon postciliary microtubule ribbons (Fig. 70g; 329n). Cytoplasm colourless and hyaline in oral area, while usually packed with macronuclear nodules and lipid droplets 1–8 µm across in postoral region. Feeds on small and medium-sized ciliates (*Protocyclidium terricola*, *Vorticella astyliformis*, *Colpoda maupasi*) ingested whole and thus recognizable in the predator's cytoplasm. Swims rather rapidly by rotation about main body axis and shows great flexibility when creeping on soil particles or organic debris. Specimens connected in oral area during conjugation; post-conjugates have 4–6 globular, rather large macronuclear nodules.

Somatic cilia about 10 µm long and rather closely spaced (2 µm on average; Table 58), especially in anterior portion of rows, where a conspicuous ciliary corona is produced; form an average of 22 straight, bipolar kineties with anterior end of left side rows slightly to distinctly curved ventrally. Dorsal brush of ordinary structure, inconspicuous because occupying

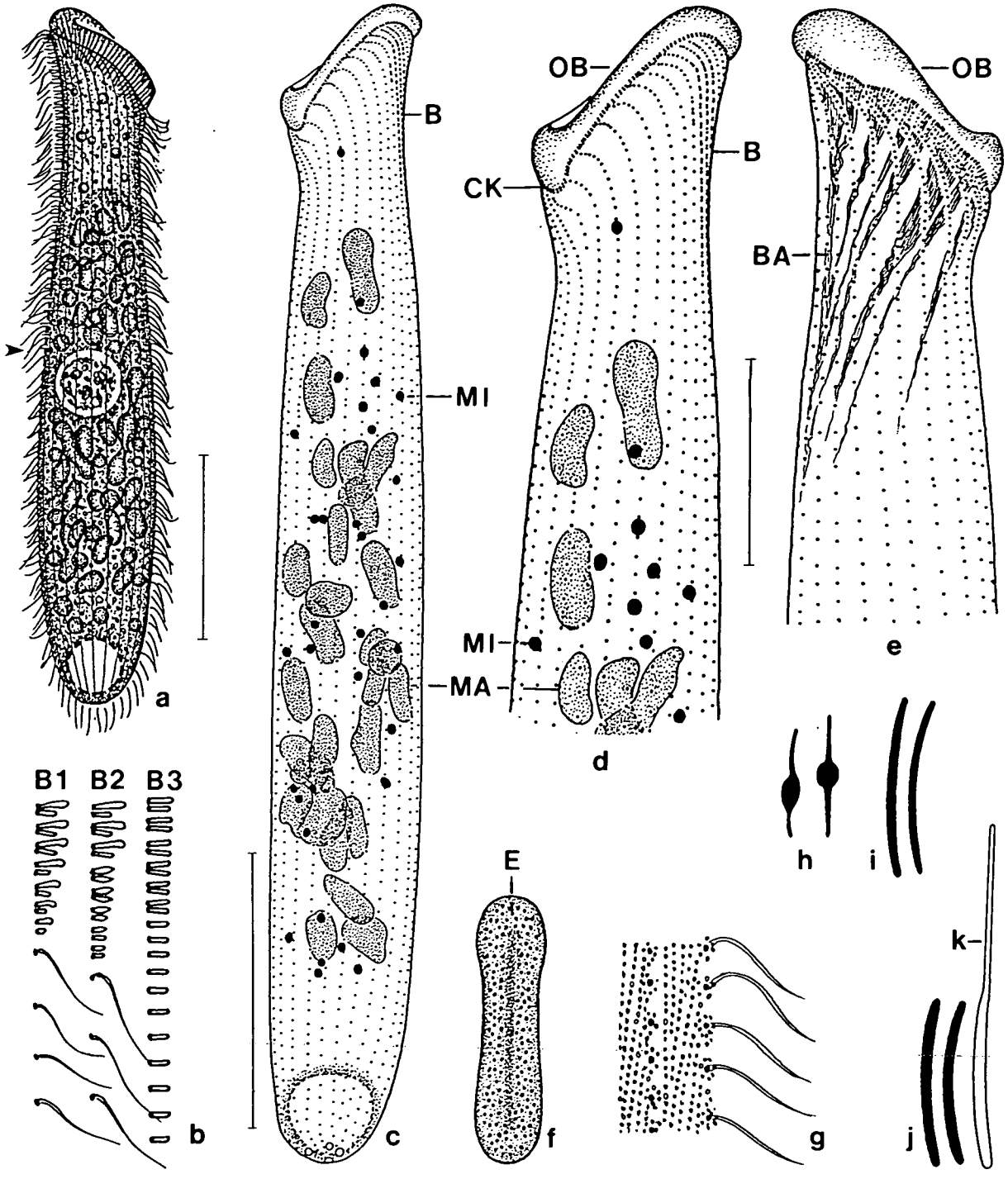

Fig. 70a–k. *Epispathidium polynucleatum* from life (a, b, f, g, i–k) and after protargol impregnation (c–e, h). **a:** Right side view of a representative specimen packed with macronuclear nodules and lipid droplets. Arrowhead marks end of brush row 3. **b:** Rear end of dorsal brush. Row 3 has a monokinetidal tail extending to mid-body (figure 70a). **c–e:** Ciliary pattern of left and right side and nuclear apparatus of holotype specimen. **f:** Frontal view of oral bulge studded with extrusomes. **g:** Surface view showing rows of minute cortical granules. **h:** Developing extrusomes in the cytoplasm. **i:** Extrusomes attached to oral bulge, length 10 µm. **j:** Extrusomes of Australian (left) and Venezuelan (right) specimens, length 10 µm. **k:** Exploded extrusome of an Australian specimen. B(1, 2, 3) – dorsal brush (rows), BA – oral basket, CK – circumoral kinety, E – extrusomes, MA – macronuclear nodules, MI – micronuclei, OB – oral bulge. Scale bars 50 µm (a, c) and 25 µm (d, e).

merely 20% of body length and composed of bristles only up to 3 µm long in vivo; middle brush row slightly longer than right and left; row 3 has a monokinetidal bristle tail extending to mid-body; frequently some dikinetids in first ordinary ciliary row right of brush kinety 1; further details, see figures 70a–e, l, m and figures 329c, j–m, and Table 58.

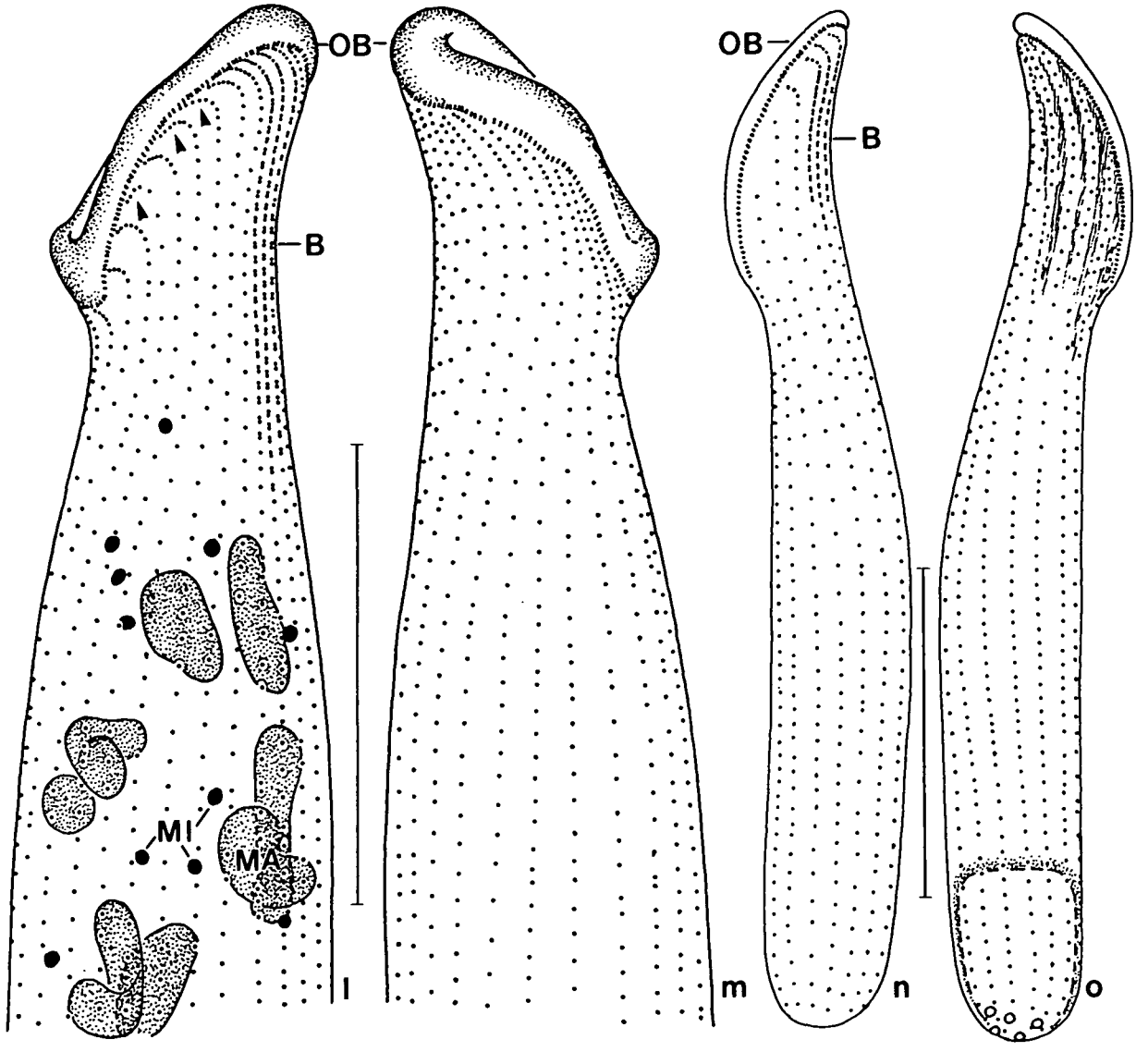

Fig. 70 l–o. *Epispathidium polynucleatum* (l, m) and *Arcuospathidium multinucleatum* (n, o; from FOISSNER 1999b), somatic and oral ciliary pattern after protargol impregnation. **l, m:** Left and right side view of anterior body region of an Australian specimen showing the typical *Epispathidium* pattern: the densely ciliated anterior end of the left side ciliary rows is curved ventrally to run in parallel with the circumoral kinety, which is thus seemingly doubled (arrowheads). However, this typical pattern is present in only few specimens, both in the Australian and Namibian population. **n, o:** *Arcuospathidium multinucleatum*, another multinucleate species, has a rather different (*Arcuospathidium*) ciliary pattern: the ventral left side ciliary rows become loosely ciliated anteriorly and curve more or less distinctly dorsally. Furthermore, the oral bulge is usually elongate cuneate, low, and steeper than in *Spathidium* and *Epispathidium*. B – dorsal brush, MA – macronuclear nodules, MI – micronuclei, OB – oral bulge. Scale bars 40 µm.

Oral bulge obliquely truncate by about 45°, conspicuous, although occupying only 15% of body length, because (i) thick and up to 5 µm high, (ii) ∞-shaped[11] in lateral and dumb-bell-shaped in frontal view, and (iii) glossy due to the many extrusomes contained. Circumoral kinety continuous and (sometimes indistinctly) separate from ciliary rows, composed of dikinetids each with an associated cilium and a rather long nematodesma; nematodesmata of neighbouring kinetids form more or less distinct bundles producing a rather conspicuous oral basket (Fig. 70a, d, e, l, m; 329a–e, h, i; Table 58).

Occurrence and ecology: *Epispathidium polynucleatum* occurs not only in Namibia (Table 4), but also in the Republic of South Africa (Cape Peninsula; mosses and soil from stones and Fynbos plants; pH 6.1), Australia (soil from rain forest near Cairns; pH 3.9; Fig. 70k–m), and South America (Venezuela; highly saline soil from a small pan in the Morrocoy National Park; pH 7.3; Fig. 70j). Obviously, *E. polynucleatum* has a wide ecological range, and thus it is surprising that Laurasian records are lacking; possibly it is substituted by *Spathidium bavariense*.

Generic classification: *Epispathidium polynucleatum* is in between *Spathidium* and *Epispathidium*, like its supposedly nearest relative, *E. ascendens*, because the left side kineties are usually only slightly curved ventrally; however, some specimens show a typical *Epispathidium* pattern (Fig. 70 l, m). Unfortunately, transitions between *Protospathidium*, *Spathidium*, *Epispathidium*, and *Arcuospathidium* exist and impair genus distinction. On the other hand, splitting the large genus *Spathidium* with the features discussed in FOISSNER (1984) is still highly appropriate because it greatly enhances species distinction and identification.

Comparison with related species: *Epispathidium polynucleatum* matches *E. ascendens* WENZEL, as redescribed by FOISSNER (1987b), except for the macronucleus, which is nodular in the former and a long, tortuous strand in the latter. However, in both species, specimens with a tortuous or nodular macronucleus occur, albeit rarely (see also WENZEL 1955). A careful analysis of the *E. polynucleatum* specimens with a tortuous macronucleus shows that these are usually post-dividers commencing macronuclear fragmentation, as evident from the moniliform appearance of the nuclear strand and the data from → *Spathidium turgitorum*. Thus, many macronuclear nodules are the ordinary state in *E. polynucleatum*, as evident from morphometry, where over 90% of the specimens have 20 or more nodules (Table 58). On the other hand, *Epispathidium ascendens* usually has a single, tortuous macronuclear strand. Thus, both are distinct, easy-to-separate species.

Epispathidium polynucleatum is also rather similar to → *Spathidium turgitorum*, but sufficiently different in the following features to be recognized as a distinct species: ciliary pattern (epispathidiid vs. spathidiid), body width (~ 30 vs. ~ 15 µm), length:width ratio (~ 6–7 vs. ~ 9–11), extrusome length (8–10 µm vs. 3–6 µm), shape of oral bulge (elongate elliptical vs. obovate or cuneate), number of macronuclear nodules (~ 30 vs. ~ 50), number of ciliary rows (~ 22 vs. 12–15), and number of dikinetids in brush row 2 (~ 30 vs. ~ 20). Certainly, some of these differences become inconspicuous in the extreme specimens, and if the cultivated → *S. turgitorum* is taken into account. This, however, should be avoided because cultivation obviously broadened the size range artificially.

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[11] This curious shape of the basically elongate elliptical bulge (Fig. 329i) is produced by a rather distinct twist of its main axis, making the bulge screwed like a propeller blade (Fig. 329d, e, h).

Epispathidium regium FOISSNER, 1984, which possesses, like *E. polynucleatum*, many macronuclear nodules, is distinctly stouter (3:1 vs. 6:1) and has considerably more ciliary rows ($\bar{x}$ = 41 vs. 22). There are several other spathidiids with a nodular macronucleus: *Spathidium multinucleatum* GELLÉRT, 1955, a poorly described species, is only 80 µm long and has "long trichites (extrusomes?)"; *Spathidium seppelti* PETZ & FOISSNER, 1997 and → *S. seppelti etoschense* are distinctly stouter (3–4:1 vs. 6:1) and have short (3–6 µm), straight extrusomes, which are distinctly different from the fine, curved extrusomes of *E. polynucleatum* (compare micrographs!); *Spathidium bavariense* KAHL, 1930a is also distinctly stouter than *E. polynucleatum* (3:1 vs. 6:1) and has short (4–5 µm), straight extrusomes and a more conspicuous oral bulge with an extrusome-bearing hump at either end; *Spathidium metabolicum* POMP & WILBERT, 1988 is much more slender than *E. polynucleatum* (11:1 vs. 6:1) and has only 12 ciliary rows; *Spathidium armatum* VUXANOVICI, 1959 is only 120 µm long and has numerous minute macronuclear nodules; *Spathidium nigrum* VUXANOVICI, 1959 is 280 µm long and has 24 µm long, straight extrusomes; *Arcuospathidium multinucleatum* FOISSNER, 1999b is smaller than *E. polynucleatum* (about 140 × 20 µm vs. 190 × 30 µm in vivo) and has a narrow, cuneate oral bulge, short (4–5 µm), straight extrusomes, and a different ciliary pattern (Fig. 70n, o).

There are also several → *Arcuospathidium* species with many macronuclear nodules, viz., *A. multinucleatum* FOISSNER, 1999b, → *A. namibiense*, and → *A. etoschense*. Of these, only *A. multinucleatum* resembles *E. polynucleatum*. However, *A. multinucleatum* has a more oblique, distinctly cuneate oral bulge and less ciliary rows (15–18 vs. 22–25 on average).

Table 58. Morphometric data on *Epispathidium polynucleatum* from Namibia (first line) and Australia (second line). The third line combines the Namibian and Australian specimens.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	173.7	169.0	19.8	5.7	11.4	140.0	217.0	12
	182.2	187.0	25.9	7.8	14.2	143.0	216.0	11
	176.0	174.0	21.6	4.6	12.3	140.0	217.0	23
Body, width	29.3	28.0	3.8	1.1	12.9	26.0	40.0	12
	27.5	27.0	2.3	0.7	8.5	23.0	32.0	11
	28.6	28.0	3.3	0.7	11.5	23.0	40.0	23
Body length:width, ratio	6.0	6.0	0.9	0.3	15.1	5.0	8.0	12
	6.7	7.0	1.3	0.4	19.7	5.0	9.4	11
	6.3	6.0	1.2	0.2	18.4	5.0	9.4	23
Oral bulge, length	27.3	28.0	2.4	0.7	8.9	22.0	31.0	12
	26.1	26.0	2.8	0.9	10.9	23.0	32.0	11
	26.6	27.0	2.5	0.5	9.6	22.0	32.0	23
Oral bulge, height	4.0	4.0	0.7	0.2	18.5	3.0	5.0	12
	2.8	3.0	–	–	–	2.0	3.0	11
	3.4	3.0	0.9	0.2	26.6	2.0	5.0	23
Anterior body end to first macronuclear nodule, distance	33.5	34.0	4.1	1.2	12.2	29.0	43.0	12
	32.9	34.0	7.0	2.1	21.4	19.0	46.0	11
	32.8	34.0	5.3	1.1	16.1	19.0	46.0	23
Macronuclear nodules, length	13.3	14.0	2.9	0.8	21.6	8.0	18.0	12
	9.7	10.0	3.6	1.1	37.5	5.0	16.0	11

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	11.4	12.0	3.6	0.8	31.9	5.0	18.0	23
Macronuclear nodules, width	4.8	5.0	0.8	0.2	15.9	4.0	6.0	12
	5.3	5.0	1.1	0.3	20.8	4.0	7.0	11
	5.0	5.0	1.0	0.2	19.2	4.0	7.0	23
Circumoral kinety to rear end of dorsal brush row 1, distance	28.2	28.0	3.9	1.1	13.5	22.0	34.0	12
	28.9	30.0	5.6	1.7	19.4	15.0	36.0	11
	28.3	29.0	4.5	1.0	15.8	15.0	36.0	23
Circumoral kinety to rear end of dorsal brush row 2, distance	33.6	35.0	3.1	0.9	4.4	28.0	38.0	12
	34.7	35.0	4.2	1.3	12.2	25.0	40.0	11
	34.3	35.0	3.7	0.8	10.8	25.0	40.0	23
Circumoral kinety to rear end of dikinetidal portion of dorsal brush row 3, distance	28.8	30.0	2.3	0.7	8.1	24.0	32.0	12
	32.1	33.0	5.6	1.7	17.4	21.0	40.0	11
	30.5	30.0	4.5	1.0	14.9	21.0	40.0	23
Dikinetids in dorsal brush row 1, number	22.4	23.0	1.9	0.6	8.6	20.0	27.0	12
	22.8	22.0	2.6	0.8	11.6	19.0	28.0	11
	22.6	23.0	2.3	0.5	10.2	19.0	28.0	23
Dikinetids in dorsal brush row 2, number	28.3	28.0	2.5	0.7	8.9	22.0	32.0	12
	28.8	30.0	3.3	1.0	11.6	23.0	32.0	11
	28.4	28.0	2.9	0.6	10.1	22.0	32.0	23
Dikinetids in dorsal brush row 3, number	20.8	21.0	1.5	0.4	7.4	18.0	23.0	12
	23.1	23.0	2.8	0.9	12.3	19.0	28.0	11
	21.8	22.0	2.6	0.6	11.7	18.0	28.0	23
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	12
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	23
Somatic ciliary rows, number	21.9	22.0	1.2	0.4	5.7	20.0	25.0	12
	24.6	25.0	2.2	0.7	8.8	21.0	28.0	11
	23.3	22.0	2.2	0.5	9.6	20.0	28.0	23
Ciliated kinetids in a right lateral kinety, number	92.4	87.0	13.7	4.0	14.8	80.0	120.0	12
	90.1	80.0	18.0	5.4	19.9	70.0	130.0	11
	90.8	84.0	15.7	3.4	17.3	70.0	130.0	23
Macronuclear nodules, number [b]	28.8	32.0	7.8	1.8	27.2	12.0	40.0	19
	32.6	35.0	10.3	2.4	31.7	10.0	50.0	19
	30.8	33.0	9.2	2.2	30.0	10.0	50.0	38
Micronuclei, number	28.7	28.0	5.6	1.6	19.5	20.0	40.0	12
	29.5	30.0	6.9	2.1	23.3	15.0	40.0	11
	28.9	30.0	6.2	1.3	21.3	15.0	40.0	23

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a pure culture (Namibia) and a non-flooded Petri dish culture (Australia). Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Specimens (likely post-dividers) with ≤ five macronuclear nodules were excluded, that is, four cells in Namibia and three in Australia.

Apertospathula nov. gen.

Diagnosis: Highly flexible Spathidiidae with continuous circumoral kinety shortened on left side of oral bulge and thus open ventrally. Oral bulge spatulate in frontal and cuneate in lateral view, rather distinctly set off from body proper and curved to ventral side. Dorsal brush rows of similar length.

Type species: *Apertospathula inermis* nov. spec.

Etymology: Composite of the Latin nouns *apertum* (open field) and *spatha* (spatula), and the diminutive suffix *ula*, referring to the ventrally opened oral bulge and the similarity to small species of the genus *Spathidium*. Feminine gender.

Comparison with related genera: *Apertospathula* differs from *Spathidium*, *Arcuospathidium*, *Epispathidium*, *Protospathidium*, and *Supraspathidium*, as defined by FOISSNER (1984), by the shortened and thus ventrally opened circumoral kinety. Likely, this is not caused by simple spatial constraints because several *Arcuospathidium* species with a similarly narrow oral bulge have a closed circumoral kinety (e.g. → *A. namibiense* and *A. vermiforme* FOISSNER, 1984); rather, this seems to be a distinct evolutionary branch. Certainly, the characteristics mentioned are not very different from those of the other spathidiid genera. However, as there are three well-defined species with the same features (see below) and the genus *Spathidium* already contains well over 150 species, it seems justified to separate this group at genus level. There are many more *Apertospathula* species because we found two further species in the Namibian preparations. Unfortunately, they were not studied in vivo and thus cannot be described properly.

The general organization of *Apertospathula* resembles that of *Arcuospathidium* FOISSNER, 1984 (somatic and oral ciliature distinctly separate) and *Spathidiodes* KAHL, 1926, a still poorly known genus differing from other spathidiids mainly by the bright, rigid cortex and the short, beak-like oral bulge (Fig. 71q). At present, the status of this genus cannot be reliably estimated, but the inflexible cortex indicates that it is considerably different from other spathidiids, all being very flexible. Likely, *Apertospathula* is most closely related to *Arcuospathidium*. This is indicated not only by the general organization mentioned above, but also by population II of *Arcuospathidium vermiforme* FOISSNER, 1984, which we now consider as a new species. We reinvestigated the slides of this species, which showed that is has a closed circumoral kinety and thus belongs to *Arcuospathidium*, although the general appearance highly resembles *Apertospathula*.

Apertospathula inermis nov. spec. (Fig. 71a–i; Table 59)

Diagnosis: Size about 55 × 12 µm in vivo. Indistinctly clavate to cylindroidal with oral bulge shorter than widest postoral body region. Macronucleus ellipsoidal. No extrusomes recognizable. On average 6 ciliary rows and 17 circumoral dikinetids. Dorsal brush three-rowed, each row composed of 3–4 dikinetids having about 1 µm long bristles.

Type location: Sand dune near the town of St. Anthony, Idaho, USA, 43°N 112°W.

Etymology: The Latin adjective *inermis* (unarmed) refers to the lacking extrusomes.

Description: Size 40–75 × 8–15 µm, usually near 55 × 12 µm in vivo; length:width ratio highly variable, that is, 2.7–7:1, on average near 5:1 in protargol preparations (Table 59). Shape usually slightly clavate because more or less distinctly inflated subapically and narrowing posteriorly; more rarely cylindroidal or somewhat fusiform (Fig. 71a, b, d, f, h); laterally flattened indistinctly. Macronucleus in widened anterior body half, usually elongate ellipsoidal, in five out of 30 specimens composed of two to five small globules, and in one cell even a tortuous strand; nucleoli globular and of ordinary size. Micronucleus attached to macronucleus, slightly ellipsoidal (Fig. 71a, b, d, f, h). Contractile vacuole in posterior body end. No extrusomes recognizable, even with interference contrast optics, in the three populations investigated. Cortex thin and flexible. Cytoplasm colourless, contains some lipid droplets. Food not known. Swims rather rapidly by rotation about main body axis.

Cilia 7–8 µm long in vivo, very loosely spaced, arranged in six to seven meridional, widely and equidistantly spaced rows anteriorly distinctly separated from circumoral kinety. Three dorsolateral rows anteriorly differentiated to short, very inconspicuous dorsal brush composed of paired basal bodies bearing only 1 µm long bristles difficult to recognize in vivo: rows 1 and 3 each composed of three dikinetids, row 2 with four bristle pairs on average; we did not check whether row 3 has a monokinetidal bristle tail; one or two ordinary cilia between anterior end of individual brush rows and circumoral kinety (Fig. 71a, d–i).

Oral bulge moderately distinct, surface slightly convex to concave and obliquely truncate with dorsal portion higher than ventral; about 8 µm long and up to 3 µm high in vivo; cuneate in lateral and spatulate in frontal view because gradually merging into ventral surface. Circumoral kinety at base of oral bulge, composed of an average of 17 comparatively widely spaced dikinetids each associated with a cilium and a short nematodesma contributing to the inconspicuous oral basket; open ventrally and longer by two to four dikinetids at right than left side of oral bulge, as also evident from fibres extending into the bulge (Fig. 71a–i).

Occurrence and ecology: The type population was discovered in sieved litter from a (likely volcanic) sand dune in Idaho, USA; pH 7.4. The Namibian population occurred in a different habitat, viz., at site (29), that is, the swampy margin of a pond. In Australia, *A. inermis* was found in a mud sample from a rock-pool at the entrance to the Sydney Harbour National Park. *Apertospathula inermis* was rare at all sites, at least in the non-flooded Petri dish cultures. The data indicate that it is a cosmopolitan species possibly occurring in both terrestrial and limnetic habitats.

Comparison with related species: *Apertospathula inermis* is a really inconspicuous ciliate because it is small and lacks distinct features, even extrusomes present in the other species described below. The lack of light microscopically recognizable extrusomes was carefully checked in the three populations and is thus a main feature of the species. Several *Spathidium* and *Spathidiodes* species also lack extrusomes (KAHL 1930a), and even some rather large *Arcuospathidium* species, viz., *A. vermiforme* FOISSNER, 1984 and *A. cooperi* FOISSNER, 1996b.

Apertospathula inermis resembles several *Spathidium* and *Spathidiodes* species, all rather superficially described and shown in figures 71j–q. The most similar species is probably *Spathidium microstomum* VUXANOVICI, 1962c, which, however, has an only 3 µm wide, button-shaped oral bulge (Fig. 71k–n). *Spathidium deforme* (Fig. 71p) is a true *Spathidium*,

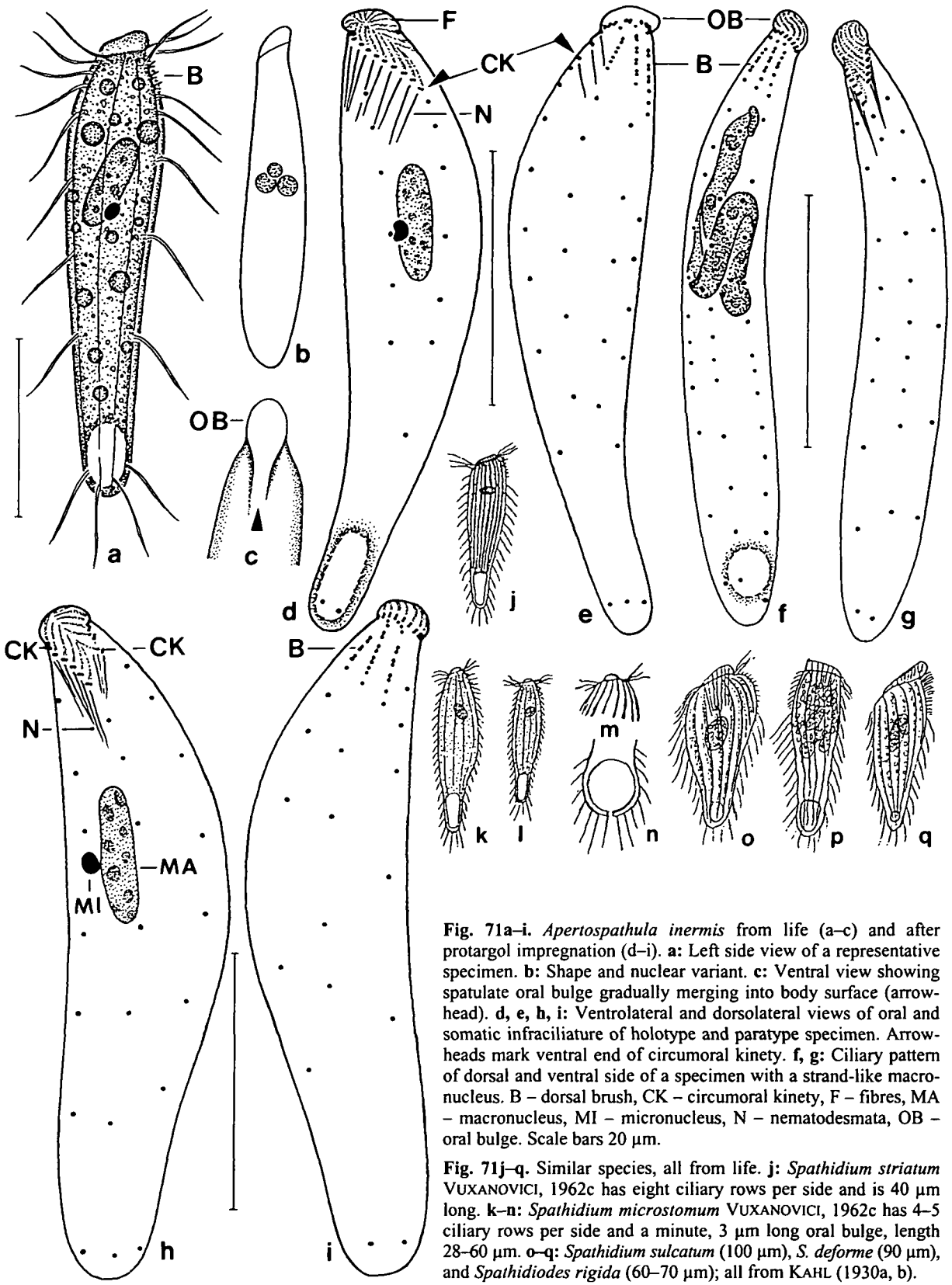

Fig. 71a–i. *Apertospathula inermis* from life (a–c) and after protargol impregnation (d–i). **a:** Left side view of a representative specimen. **b:** Shape and nuclear variant. **c:** Ventral view showing spatulate oral bulge gradually merging into body surface (arrowhead). **d, e, h, i:** Ventrolateral and dorsolateral views of oral and somatic infraciliature of holotype and paratype specimen. Arrowheads mark ventral end of circumoral kinety. **f, g:** Ciliary pattern of dorsal and ventral side of a specimen with a strand-like macronucleus. B – dorsal brush, CK – circumoral kinety, F – fibres, MA – macronucleus, MI – micronucleus, N – nematodesmata, OB – oral bulge. Scale bars 20 µm.

Fig. 71j–q. Similar species, all from life. **j:** *Spathidium striatum* VUXANOVICI, 1962c has eight ciliary rows per side and is 40 µm long. **k–n:** *Spathidium microstomum* VUXANOVICI, 1962c has 4–5 ciliary rows per side and a minute, 3 µm long oral bulge, length 28–60 µm. **o–q:** *Spathidium sulcatum* (100 µm), *S. deforme* (90 µm), and *Spathidiodes rigida* (60–70 µm); all from KAHL (1930a, b).

according to the redescription by LEITNER & FOISSNER (1997). All other similar species have extrusomes and/or a distinctly higher number of ciliary rows.

Table 59. Morphometric data on *Apertospathula inermis* (upper line) and *Apertospathula armata* (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	50.2	50.0	8.5	2.0	16.9	32.0	65.0	19
	51.0	52.0	7.6	2.2	14.9	38.0	66.0	12
Body, width	11.0	11.0	2.2	0.5	19.8	7.0	14.0	19
	15.4	15.0	2.4	0.7	15.8	12.0	20.0	12
Body length:width, ratio	4.8	4.6	1.2	0.3	24.4	2.7	7.0	19
	3.4	3.5	0.6	0.2	16.7	2.3	4.1	12
Anterior body end to macronucleus, distance	13.4	12.0	4.5	1.0	33.9	7.0	24.0	19
	13.6	13.0	4.4	1.3	32.3	8.0	21.0	12
Circumoral kinety to last dikinetid of brush row 1, distance	3.2	3.0	0.5	0.1	16.7	2.5	4.0	19
	4.7	5.0	0.7	0.2	14.0	4.0	6.0	12
Circumoral kinety to last dikinetid of brush row 2, distance	4.0	4.0	0.6	0.1	14.6	3.0	5.0	19
	5.0	5.0	0.7	0.2	14.8	4.0	6.0	12
Circumoral kinety to last dikinetid of brush row 3, distance	3.6	3.5	0.7	0.2	19.4	2.0	5.0	19
	4.8	5.0	0.8	0.2	15.9	4.0	6.0	12
Oral bulge (circumoral kinety), maximum length	8.0	8.0	0.9	0.2	11.8	6.0	10.0	19
	7.5	7.0	1.0	0.3	13.3	7.0	10.0	12
Macronucleus, length	11.8	11.0	2.9	0.7	24.9	7.0	18.0	16
	17.8	17.5	3.0	0.9	16.7	13.0	22.0	12
Macronucleus, width	3.2	3.0	0.6	0.1	17.9	2.0	4.0	16
	3.7	4.0	0.7	0.2	17.8	3.0	5.0	12
Micronucleus, length	2.4	2.0	–	–	–	2.0	3.0	13
	3.2	3.0	–	–	–	2.8	4.0	12
Micronucleus, width	1.8	2.0	–	–	–	1.5	2.0	13
	2.9	3.0	–	–	–	2.5	3.0	12
Somatic kineties, number	6.2	6.0	–	–	–	6.0	7.0	19
	6.3	6.0	–	–	–	6.0	7.0	12
Ciliated kinetids in a right side kinety, number	8.6	8.0	1.4	0.3	16.2	6.0	12.0	19
	11.0	11.0	2.5	0.7	22.9	7.0	15.0	12
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	12
Dikinetids in brush row 1, number	2.9	3.0	–	–	–	2.0	3.0	19
	3.8	4.0	0.6	0.2	15.1	3.0	5.0	12
Dikinetids in brush row 2, number	3.8	4.0	–	–	–	2.0	4.0	19
	4.8	5.0	0.9	0.3	18.2	4.0	7.0	12
Dikinetids in brush row 3, number	3.0	3.0	–	–	–	2.0	4.0	19
	3.9	4.0	0.7	0.2	17.1	3.0	5.0	12
Circumoral kinetids, number	17.0	17.0	1.2	0.3	7.1	15.0	20.0	19
	21.3	22.0	2.8	0.8	13.1	17.0	26.0	12

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Apertospathula armata nov. spec. (Fig. 72a–i; Table 59)

Diagnosis: Size about 60 × 15 µm in vivo. Indistinctly spatulate to cylindroidal with oral bulge shorter than widest body region. Macronucleus elongate ellipsoidal. Extrusomes ellipsoidal, 1.5 µm long. On average 6 ciliary rows and 22 circumoral dikinetids. Dorsal brush three-rowed, each row composed of 4–5 dikinetids having about 1 µm long bristles.

Type location: Loamy wheat field soil about 10 km south of Nazareth, Israel, 32°30'N 35°E.

Etymology: The Latin adjective *armatus* (armed) refers to the extrusomes.

Description: Size 45–75 × 10–20 µm, usually near 60 × 15 µm in vivo; length:width ratio moderately variable, on average 3.4:1 in protargol preparations (Table 59). Shape indistinctly spatulate, cylindroidal or fusiform, rather similar to that of → *A. inermis*, posterior third frequently wrinkled; oral area slightly flattened (Fig. 59a, b, d–f). Macronucleus in anterior body half, elongate ellipsoidal (3:1) to rod-shaped (up to 7:1); nucleoli globular to lobate. Micronucleus attached to macronucleus, 3–4 µm across and thus rather conspicuous, even in vivo (Fig. 59a, f, h). Contractile vacuole in posterior end. Extrusomes in oral bulge, ellipsoidal to indistinctly fusiform, only about 1.5 µm long in vivo. Cytoplasm colourless, packed with about 1µm-sized, bright globules and many, apparently empty vacuoles. Swims rather rapidly showing great flexibility when squeezed by soil particles.

Somatic and oral ciliary pattern as described in *A. inermis*, with slight morphometric differences shown in Table 59.

Occurrence and ecology: To date found only at type location.

Comparison with related species: See *A. inermis*, from which *A. armata* is distinguished mainly by the extrusomes. Morphometrics are almost identical or at least overlapping (Table 59).

Apertospathula dioplites nov. spec. (Fig. 73a–j; Table 60)

Diagnosis: Size about 95 × 20 µm in vivo. Oblong with ventral anterior third obliquely truncate. Oral bulge in dorsal half thick and curved laterally, distinctly longer than widest postoral body region. Macronucleus elongate reniform. Two types of extrusomes: type I obclavate and 5–6 × 0.8–1 µm; type II rod-shaped and about 2 µm long. On average 9 ciliary rows and 50 circumoral dikinetids. Dorsal brush three-rowed, rows 1 and 2 each composed of eight dikinetids, row 3 of four dikinetids on average.

Type location: Soil from margin of a small pond in the Aubschlucht, Namibia, 23°55'S 16°15'E (site 30 in figure 2 and chapter 2.1.2).

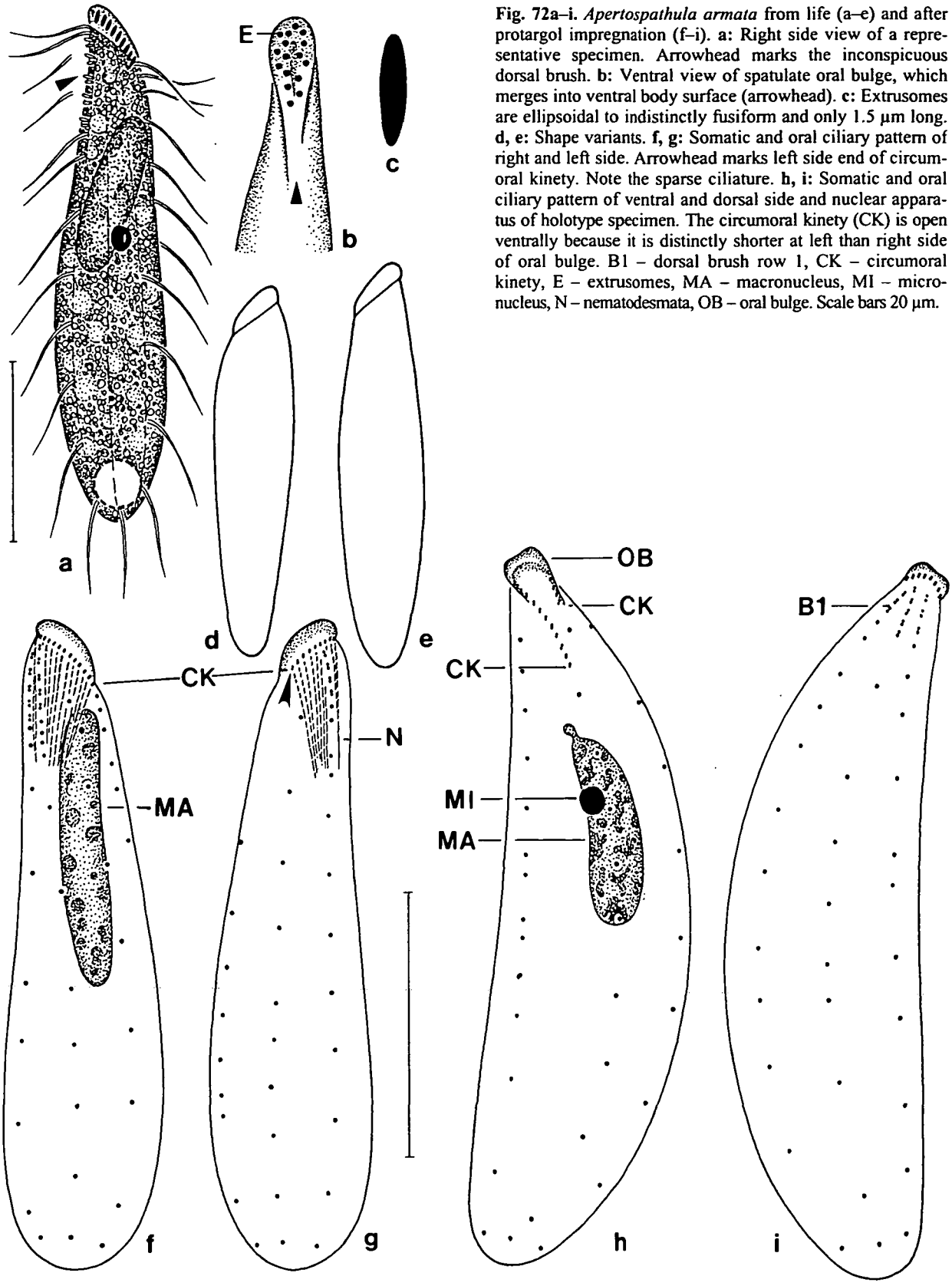

Fig. 72a–i. *Apertospathula armata* from life (a–e) and after protargol impregnation (f–i). **a:** Right side view of a representative specimen. Arrowhead marks the inconspicuous dorsal brush. **b:** Ventral view of spatulate oral bulge, which merges into ventral body surface (arrowhead). **c:** Extrusomes are ellipsoidal to indistinctly fusiform and only 1.5 µm long. **d, e:** Shape variants. **f, g:** Somatic and oral ciliary pattern of right and left side. Arrowhead marks left side end of circumoral kinety. Note the sparse ciliature. **h, i:** Somatic and oral ciliary pattern of ventral and dorsal side and nuclear apparatus of holotype specimen. The circumoral kinety (CK) is open ventrally because it is distinctly shorter at left than right side of oral bulge. B1 – dorsal brush row 1, CK – circumoral kinety, E – extrusomes, MA – macronucleus, MI – micronucleus, N – nematodesmata, OB – oral bulge. Scale bars 20 µm.

Etymology: Composite apposition of *di* (two) and *hoplites* (soldier ~ extrusome), referring to a main feature of the species, viz., the two types of extrusomes.

Description: Size 65–135 × 15–30 µm in vivo, usually about 95 × 20 µm; length:width ratio near 4–5:1; flattened up to 2:1 laterally, especially in oral region. Shape rather variable because posteriorly narrowed or widened, basically oblong with ventral anterior third, where the oral bulge extends, obliquely truncate (Fig. 73a, b, e; Table 60); very flexible but acontractile; postoral portion frequently wrinkled in protargol preparations. Macronucleus usually in anterior body half, elongate reniform with ends often slightly inflated; nucleoli small, globular and numerous. Micronucleus usually attached to concave side of macronucleus, broadly ellipsoidal, rather large and thus easy to recognize in vivo (Fig. 73a, f). Contractile vacuole in rear end, excretory pore(s) not impregnated. Cortex very flexible, thin, contains loosely spaced, pale granules about 0.2 µm across. Two shape and size types of extrusomes, which do not impregnate with the protargol method used, in oral bulge and cytoplasm (Fig. 73a, c, g): type I obclavate and 5–6 × 0.7–1 µm in size, less numerous than type II, a 4–5 µm long developmental stage impregnates in the cytoplasm; type II rod-shaped and about 2 µm long. Cytoplasm colourless, usually crammed with fat globules 0.2–10 µm across and large food vacuoles containing remnants of ciliates, especially *Metopus hasei*; in protargol preparations studded with minute, black granules having a similar size as basal bodies and thus disturbing the analysis of the infraciliature. Glides rather rapidly on soil particles and microscope slide.

Cilia about 12 µm long in vivo and protargol preparations, very loosely spaced, arranged in an average of nine widely and equidistantly spaced rows distinctly separate from circumoral kinety. Three dorsal rows anteriorly differentiated to short but rather conspicuous brush composed of paired basal bodies with up to 6 µm long bristles, some showing an unusual impregnation capability (Fig. 73a, e, f): row 1 composed of an average of eight dikinetids, of which the anterior bristle of the four posteriormost pairs impregnates rather intensely with protargol (Fig. 73e, h); row 2 also composed of an average of eight dikinetids with posterior bristles up to 6 µm long; row 3 consists of an average of four dikinetids with up to 5 µm long bristles and has a monokinetidal tail with 3 µm long bristles that impregnate intensely with the protargol method used (Fig. 73f, i; Table 60).

Oral apparatus occupies oblique anterior body third and is thus distinctly longer than widest postoral region. Oral bulge slightly convex and rather conspicuous because bright due to the extrusomes contained and 3–4 µm high with thick dorsal third curved laterally, exposing bulge front to the observer; ventral half flattened distinctly, bulge thus slenderly cuneate in frontal view (Fig. 73a, b, d). Circumoral kinety open ventrally, as is typical for the genus, left branch ends subapically, while right likely extends to near body end, as indicated by the kinetids of the first kinety, which are slightly enlarged and more intensely impregnated; however, nematodesmata and extrusomes are recognizable only in the anterior body third, but this does not disprove our suggestion because the former are very fine and faintly impregnated only in the holotype specimen (Fig. 73e, f). Circumoral kinetids widely spaced, except in dorsal region of kinety, each associated with an about 12 µm long cilium and a short, fine nematodesma contributing to the indistinct oral basket.

Occurrence and ecology: To date found only at type location, where it was very rare (about 30 specimens in 15 slides), but present for three weeks. Likely, we fixed the culture too early because some dividers were found, indicating onset of exponential growth phase.

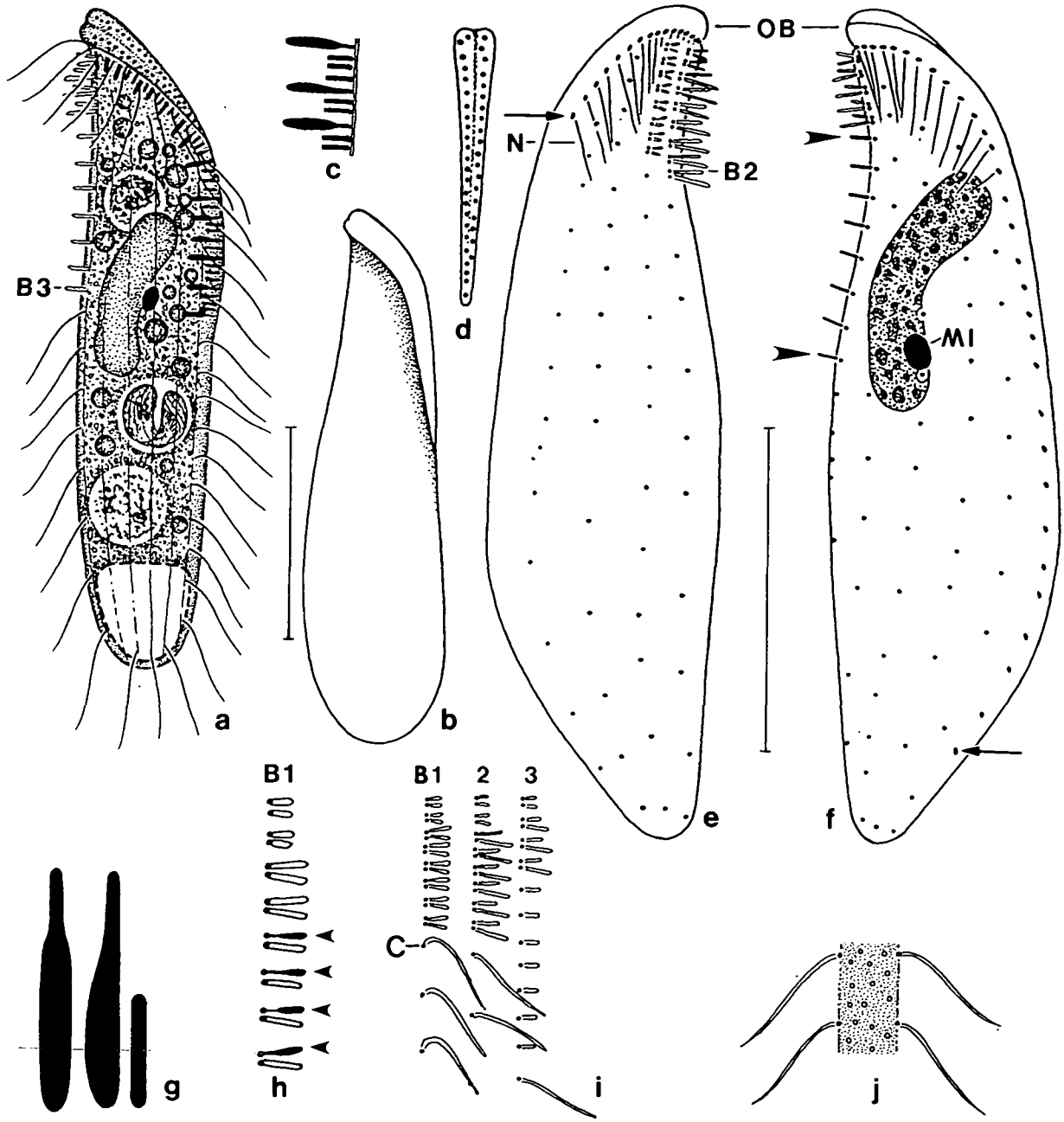

Fig. 73a–j. *Apertospathula dioplites* from life (a–d, g, i, j) and after protargol impregnation (e, f, h). **a:** Right side view of a representative specimen with the dorsal portion of the oral bulge curved laterally and thus exposing bulge front to the observer. **b:** Shape variant becoming wider posteriorly. **c:** Arrangement of type I (long) and type II (short) extrusomes in the oral bulge. **d:** Frontal view of oral bulge, containing a row of type I extrusomes each in right and left bulge half (schematic). **e, f:** Oral and somatic ciliary pattern and nuclear apparatus of holotype specimen. Arrows mark left and right end of circumoral kinety. Arrowheads denote the monokinetidal tail of brush row 3, whose bristles impregnate intensely with protargol. **g:** Type I (5–6 µm long and shown in two views) and type II (2–2.5 µm long) resting extrusomes at high magnification; drawn to scale. **h:** The anterior bristle of the four posterior bristle pairs of dorsal brush row 1 impregnates intensely with protargol. **i:** Structure of dorsal brush, drawn to scale, longest bristles 6 µm. **j:** Surface view showing inconspicuous cortical granulation. B1-3 – dorsal brush rows, C – ordinary somatic cilium, MI – micronucleus, N – nematodesmata, OB – oral bulge. Scale bars 30 µm.

Several of the specimens contained up to three only partially digested *Metopus hasei*, indicating that *A. dioplites* is a very effective predator that rapidly engulfs prey.

Generic classification and comparison with related species: If our interpretation is correct that the right branch of the circumoral kinety extends to almost posterior body end, *A. dioplites* is an extreme member of the genus because the length difference in the right and left branch of the circumoral kinety is much more pronounced than in → *A. inermis* and → *A. armata*. Likewise, the two extrusome types and the curious impregnation pattern of some brush bristles indicate that *A. dioplites* is the representative of a new genus. On the other hand, the general organization is quite similar to *Apertospathula*, especially the open circumoral kinety. Thus, we assign the species to that genus at the present state of knowledge.

Table 60. Morphometric data on *Apertospathula dioplites*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	89.0	90.0	20.0	6.0	22.5	60.0	125.0	11
Body, width	24.5	25.0	3.5	1.0	14.1	20.0	30.0	11
Body, thickness	19.6	21.0	3.2	1.2	16.1	14.0	23.0	7
Anterior body end to macronucleus, distance	27.7	24.0	15.8	4.8	56.9	11.0	58.0	11
Anterior body end to last left side circumoral kinetid, distance	9.5	10.0	3.1	0.9	32.2	5.0	16.0	11
Circumoral kinety to last dikinetid of brush row 1, distance	10.4	10.0	1.9	0.6	17.9	7.0	14.0	11
Circumoral kinety to last dikinetid of brush row 2, distance	11.7	11.0	2.1	0.7	17.7	10.0	16.0	9
Circumoral kinety to last dikinetid of brush row 3, distance	6.6	7.0	0.9	0.3	13.9	5.0	8.0	11
Circumoral kinety to last kinetid of monokinetidal tail of brush row 3, distance	30.3	30.0	7.9	2.4	26.1	18.0	42.0	11
Macronucleus, length	22.5	23.0	4.1	1.2	18.3	17.0	30.0	11
Macronucleus, width in mid	6.1	6.0	0.7	0.2	11.5	5.0	7.0	11
Micronucleus, length	3.5	3.5	–	–	–	2.7	4.0	11
Micronucleus, width	3.1	3.0	–	–	–	2.0	3.0	11
Somatic kineties, number	8.8	9.0	1.0	0.3	11.1	7.0	10.0	11
Kinetids in a right side kinety, number	15.7	16.0	2.2	0.7	14.2	11.0	18.0	11
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
Dikinetids in brush row 1, number	7.6	8.0	–	–	–	7.0	8.0	11
Dikinetids in brush row 2, number	8.1	8.0	0.8	0.3	9.6	7.0	9.0	9
Dikinetids in brush row 3, number	4.5	4.0	–	–	–	4.0	5.0	11
Bristles in monokinetidal tail of brush row 3, number	7.2	7.0	0.9	0.3	12.2	6.0	8.0	11
Circumoral kinetids, number	50.1	50.0	5.6	1.9	11.3	42.0	60.0	9

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

As concerns the species, *A. dioplites* is distinctly different from the congeners described above and from all *Spathidium* sensu lato species by the two types of extrusomes and the main genus feature, viz., the open circumoral kinety. As the cortex is flexible, it also cannot be identical to any of the *Spathidiodes* species mentioned in the discussion of the genus.

Semispathidium nov. gen.

Diagnosis: Spathidiidae with discoidal oral bulge and *Spathidium*-like oral and somatic infraciliature.

Type species: *Semispathidium enchelyodontides* nov. gen.

Etymology: Composite of the Latin prefix *semi* (partially) and the Latin noun *spatha* (spatula), referring to the lack of a *Spathidium*-like appearance. Neuter gender.

Comparison with related genera: The best justification for classifying *Semispathidium enchelyodontides* into a new genus is the fact that, based on the general appearance, nobody would assign it to *Spathidium* s. l., but likely classify it into → *Enchelyodon*, as we did in our notebook. However, silver impregnation reveals a basically spathidiid infraciliature, that is, somatic kineties with curved anterior end and a slightly twisted circumoral kinety. → *Enchelyodon*, in contrast, has meridional kineties and a flat circumoral kinety. Actually, it is only the small, discoidal oral bulge which produces the deviating appearance. In this respect, *Semispathidium* resembles → *Protospathidium* which, however, has the circumoral kinety fragments distinctly separated. → *Apospathidium* has oralized somatic monokinetids.

We do not expect that this new spathidiid genus is "sharper" than those defined by FOISSNER (1984), that is, species with transitions to *Spathidium* and/or *Protospathidium* likely will be found. In spite of this, it is evident that *Semispathidium enchelyodontides* is far from ordinary *Spathidium* species, representing a divergent evolutionary line needing generic separation. This is also evident from the second species, → *Semispathidium armatum*.

Species assignable: *Spathidium lagyniforme* KAHL, 1930a has the same infraciliature as *Semispathidium enchelyodontides*, according to the redescription by FOISSNER (1984). Interestingly, already KAHL (1930a) mentioned that "it is not a typical *Spathidium*". Thus, it is transferred to the new genus: *Semispathidium lagyniforme* (KAHL, 1930a) nov. comb. Likely, several other → *Spathidium* and *Enchelyodon* species reviewed in KAHL (1930a) or described later, also belong to *Semispathidium*, e.g., *Spathidium cylindricum* and *Enchelyodon mucicola*. However, detailed data are necessary before any new combinations are established.

Semispathidium enchelyodontides nov. spec. (Fig. 74a–l; 328i; Table 61)

Diagnosis: Size about 160 × 23 µm in vivo; cylindroidal to indistinctly obclavate. On average 21 macronuclear nodules. Two size-types of rod-shaped extrusomes: type I about 30 µm long, forms conspicuous bundle attached to centre of oral bulge; type II about 3 µm long,

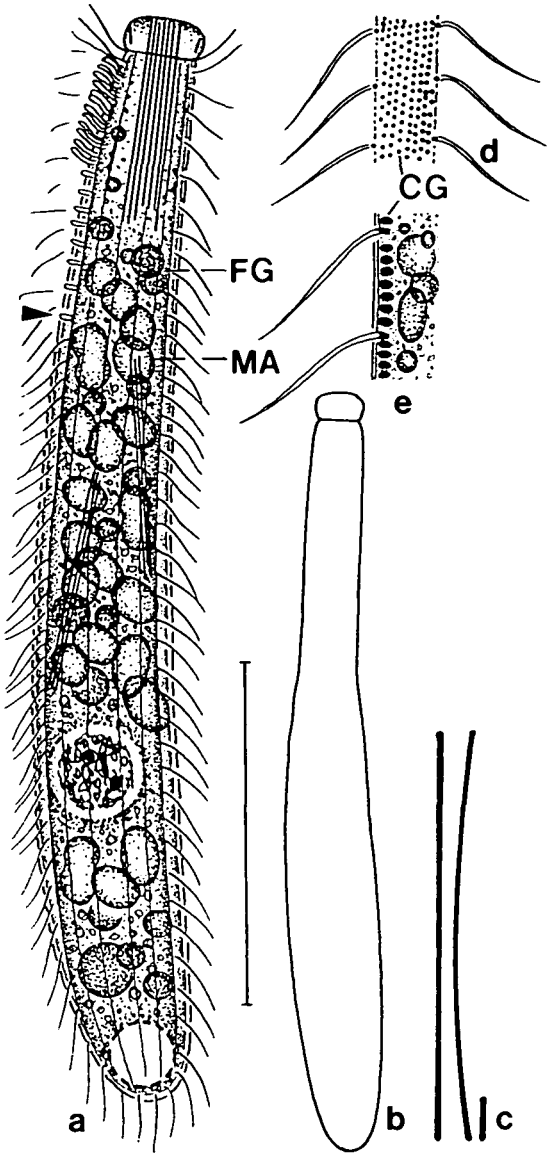

Fig. 74a–e. *Semispathidium enchelyodontides* from life. **a:** Right side view of a representative specimen packed with macronuclear nodules and fat globules. Arrowhead marks end of monokinetidal bristle tail of brush row 3. **b:** Slender, obclavate shape variant. **c:** Extrusomes, 30 µm and 3 µm; drawn to scale. **d, e:** Surface view and optical section showing cortical granules about 0.8 × 0.4 µm in size. CG – cortical granules, FG – fat globules, MA – macronuclear nodules. Scale bar 50 µm.

forms a ring in margin of oral bulge. On average 15 ciliary rows, 3 anteriorly differentiated to moderately distinct dorsal brush.

Type location: Mud and soil from road puddles in the Bambatsi Guest Farm, Namibia, 20°10'S 15°25'E (site 49 in figure 2 and chapter 2.1.2).

Etymology: Composite of *Enchelyodon* and the Greek suffix *ides* (look like), referring to the similarity with species of the genus → *Enchelyodon*.

Description: Size 120–210 × 20–35 µm in vivo, usually near 160 × 23 µm; length:width ratio highly variable, viz., 3.5–9.6:1, on average about 7:1 in protargol preparations. Shape inconspicuous, that is, cylindroidal to slightly obclavate or fusiform, anterior end somewhat inclined ventrally, posterior rounded; usually slightly curved when swimming; unflattened and acontractile (Fig. 74a, b, f; 328i; Table 61). Nuclear apparatus in central quarters of cell, consists of an average of 21 scattered macronuclear nodules and 7 globular micronuclei. Individual nodules globular to ellipsoidal, frequently more or less distinctly dumb-bell-shaped, about 8 × 6 µm in vivo and protargol preparations, usually contain a large, lobate nucleolus; rarely, several nodules form a somewhat moniliform pattern. Contractile vacuole in rear end, several excretory pores in posterior pole area. Two size-types of rod-shaped extrusomes (Fig. 74a, c, h–j; 328i): type I in vivo approximately 30 µm long, fine and flexible, forms conspicuous bundle attached to central area of oral bulge and several smaller cytoplasmic bundles, posterior 3–5 µm impregnate heavily with protargol; type II extrusomes about 3 µm long, rod-like to indistinctly flask-shaped, form a ring in margin of oral bulge, numerous and scattered in cytoplasm, posterior half occasionally heavily impregnates with protargol. Cortex very flexible, contains dense rows of refractive granules about 0.8 × 0.4 µm in size. Cytoplasm colourless, in well-fed specimens packed with globular and irregular fat inclusions 1–10 µm across. Feeds on heterotrophic flagellates and middle-sized ciliates, such as *Gonostomum strenuum*, which are ingested whole producing up to 50 × 25 µm-sized food vacuoles. Swims rather rapidly by rotation about main body axis.

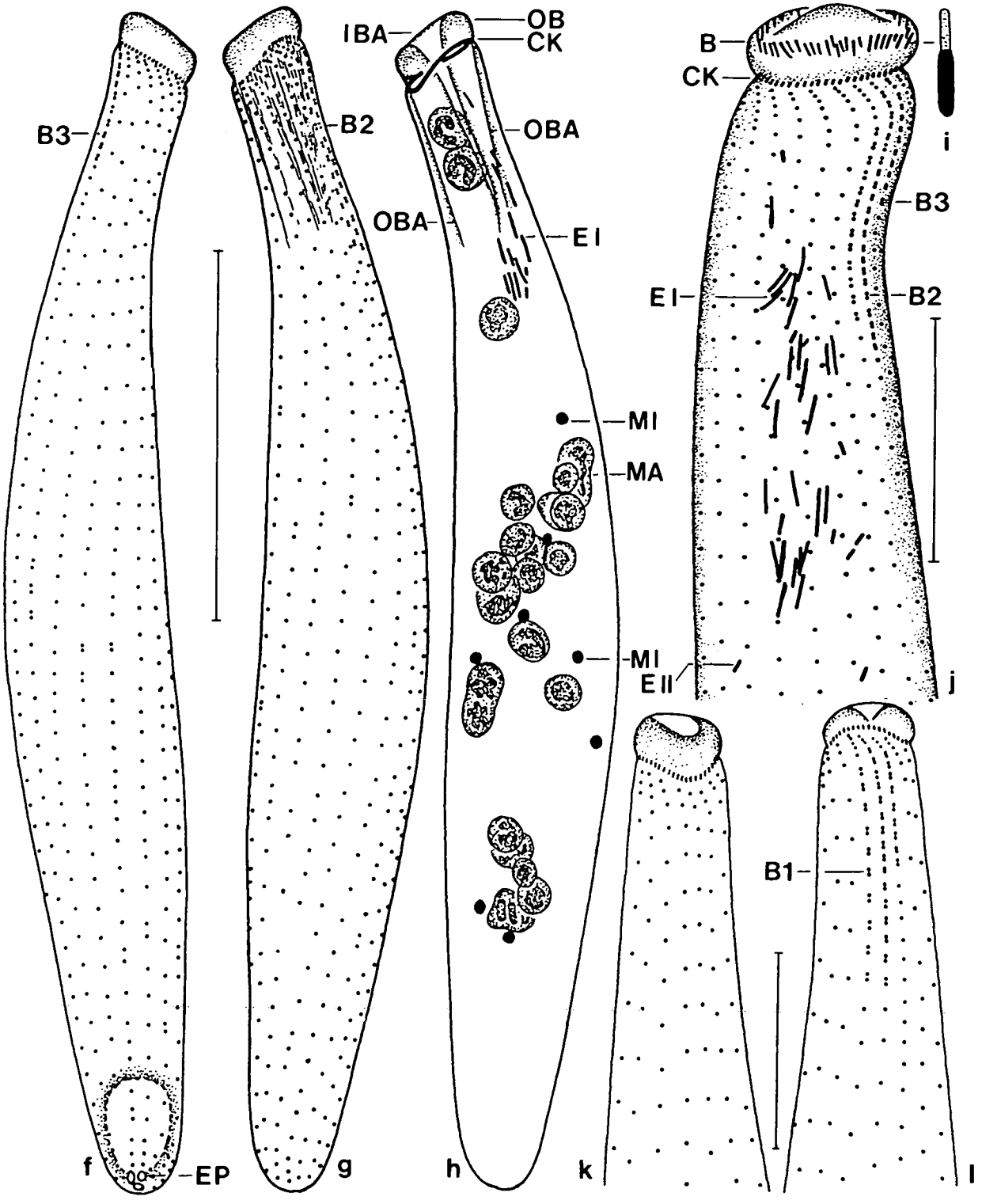

Fig. 74f–l. *Semispathidium enchelyodontides* after protargol impregnation. **f–h:** Ciliary pattern of right and left side and nuclear apparatus of holotype specimen. **i, j:** Oral bulge extrusome and dorsolateral view of ciliary pattern. **k, l:** Ciliary pattern of anterior ventral and dorsal side. B1-3 – dorsal brush rows, CK – circumoral kinety, E I, II – type I and II extrusomes, EP – excretory pores, IBA – inner oral basket, MA – macronuclear nodules, MI – micronuclei, OB – oral bulge, OBA – outer oral basket. Scale bars 50 µm (f–h) and 20 µm (j–l).

Cilia about 8 µm long in vivo, widely spaced (4 µm), especially in neck region, arranged in an average of 15 equidistant, bipolar rows anteriorly densely ciliated and curved dorsally on right side of cell, while ventrally on left, as in → *Spathidium* (FOISSNER 1984). Three dorsal rows anteriorly differentiated to moderately conspicuous dorsal brush with up to 4 µm long, distally slightly inflated bristles. Brush rows 1 and 2 of almost same length, but composed of 11, respectively, 17 dikinetids; row 3 shorter than rows 1 and 2, composed of an average of 9 dikinetids and an about 40 µm long, monokinetidal tail of 1–1.5 µm long bristles (Fig. 74a, f, g, j–l; 328i; Table 61).

Oral bulge discoidal, conspicuous because occupying anterior end of cell and about 13 × 5 µm in size, surface slightly convex; margin contains type II extrusomes, as described above, producing a nice, crown-like pattern when impregnated with protargol (Fig. 74j); bulge centre slightly to distinctly opened, forming a long, obconical inner oral basket lined by fibres originating from circumoral dikinetids (Fig. 74h). Circumoral kinety at base of oral bulge, ∞-shaped, that is, slightly twisted relative to transverse axis of cell (Fig. 74h), composed of comparatively widely spaced dikinetids associated with fibres extending anteriorly, as described above, and fine nematodesmata forming an about 30 µm long, outer oral basket only occasionally impregnated with the protargol method used (Fig. 74a, b, h, j, k; 328i; Table 61).

Occurrence and ecology: To date found only at type location. The slender shape indicates that *S. enchelyodontides* is a true soil inhabitant. It was moderately abundant in the non-flooded Petri dish culture.

Comparison with related species: This is a conspicuous ciliate with several distinct features, such as the long, slender body; the nodular macronucleus; and the 30 µm long extrusomes. Thus, it is easily identified and distinguished from → *S. armatum* and *S. lagyniforme*, which have an ellipsoidal macronucleus. On the other hand, similar features are found in several *Enchelyodon* and *Enchelys* species, for instance, *Enchelyodon terrenus* FOISSNER, 1984 (200–300 µm long, extrusomes acicular and only 14 µm long, 100–300 macronuclear nodules) and *Enchelys terricola* FOISSNER, 1987b (slenderly bursiform, extrusomes only 5 µm long). Thus, reliable identification requires protargol impregnation to reveal the ∞-shaped circumoral kinety and the curved anterior end of the ciliary rows.

Table 61. Morphometric data on *Semispathidium enchelyodontides* (upper line) and *Semispathidium armatum* (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	142.3	140.0	19.0	4.2	13.4	108.0	185.0	21
	224.1	248.5	50.8	18.0	22.7	153.0	280.0	8
Body, width	22.1	21.0	4.7	1.0	21.3	16.0	33.0	21
	40.8	38.5	7.8	2.7	19.0	33.0	53.0	8
Body length:width, ratio	6.7	7.4	1.6	0.4	23.8	3.5	9.6	21
	5.6	5.0	1.3	0.5	23.1	4.4	8.0	8
Oral bulge, width	11.0	11.0	1.2	0.3	11.1	9.0	13.0	21
	13.3	13.5	1.9	0.7	14.4	10.0	16.0	8
Oral bulge, height	4.1	4.0	0.7	0.2	17.6	3.0	6.0	21

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	3.5	3.5	0.5	0.2	15.3	3.0	4.0	8
Circumoral kinety to last dikinetid of brush row 1,	25.3	25.0	3.4	0.8	12.5	20.0	32.0	21
distance	49.0	52.5	18.1	6.4	36.9	22.0	77.0	8
Dikinetids in brush row 1, number	11.4	11.0	1.7	0.4	14.8	9.0	15.0	21
	25.5	24.5	4.3	1.5	17.0	20.0	31.0	8
Circumoral kinety to last dikinetid of brush row 2,	26.2	26.0	3.7	0.8	14.0	20.0	35.0	21
distance	58.5	65.0	17.2	6.1	29.4	28.0	75.0	8
Dikinetids in brush row 2, number	16.8	17.0	2.0	0.5	12.1	14.0	21.0	21
	39.8	40.5	6.5	2.3	16.4	31.0	48.0	8
Circumoral kinety to last dikinetid of brush row 3,	13.7	14.0	2.3	0.5	16.7	10.0	18.0	21
distance	20.0	19.5	4.0	1.4	20.0	15.0	25.0	8
Dikinetids in brush row 3, number	8.8	9.0	1.2	0.3	13.7	7.0	12.0	21
	14.3	14.5	1.7	0.6	11.7	12.0	17.0	8
Anterior body end to first macronuclear nodule,	41.7	43.0	13.3	2.9	31.8	13.0	63.0	21
distance	103.1	116.0	35.1	12.4	34.1	56.0	145.0	8
Macronuclear figure, length	72.0	62.0	18.0	3.9	25.1	50.0	110.0	21
	–	–	–	–	–	–	–	–
Macronuclear nodules, length	7.1	7.0	2.0	0.4	28.5	4.0	12.0	21
	44.3	46.0	10.4	3.7	23.6	25.0	58.0	8
Macronuclear nodules, width	5.2	5.0	0.8	0.2	15.9	4.0	7.0	21
	13.3	12.5	3.1	1.1	23.1	10.0	18.0	8
Macronuclear nodules, number	20.7	21.0	3.4	0.8	16.6	15.0	29.0	21
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	8
Micronuclei, length	2.1	2.0	–	–	–	2.0	2.5	21
	4.2	4.0	–	–	–	3.5	6.0	7
Micronuclei, width	2.0	2.0	–	–	–	1.5	2.5	21
	4.1	4.0	–	–	–	3.0	6.0	7
Micronuclei, number	7.0	7.0	1.6	0.4	23.5	4.0	10.0	21
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	7
Somatic kineties, number	15.4	15.0	0.7	0.2	4.8	14.0	17.0	21
	21.3	21.0	1.1	0.4	5.2	20.0	23.0	7
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	8
Ciliated kinetids in a ventral kinety, number	44.8	44.0	11.1	2.4	24.8	27.0	70.0	21
	91.4	90.0	17.8	6.7	19.5	73.0	120.0	7

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Semispathidium armatum nov. spec. (Fig. 75a–j; Table 61)

Diagnosis: Size about 270 × 40 µm in vivo; cylindroidal to indistinctly fusiform. Macronucleus ellipsoidal to elongate ellipsoidal. Oral extrusomes obclavate with rod-shaped

anterior process, total size about 10 × 1 µm. On average 21 ciliary rows, 3 anteriorly differentiated to moderately distinct dorsal brush with row 2 about twice as long as conspicuously shortened row 3.

Type location: Mud and soil from road puddles in the Bambatsi Guest Farm, Namibia, 20°10'S 15°25'E (site 49 in figure 2 and chapter 2.1.2).

Etymology: The Latin adjective *armatus* (armed) refers to a main feature of the species, viz., the conspicuous extrusomes.

Description: Size conspicuous, that is, 180–320 × 30–50 µm in vivo, usually near 270 × 40 µm; length:width ratio 4.4–8.1, on average 5.6:1 in protargol preparations. Shape inconspicuous, that is, slightly fusiform in vivo and distinctly so in preparations, anterior end slanted ventrally, posterior rounded; unflattened and acontractile (Fig. 75a, e; Table 61). Macronucleus in or near mid-body, rod-shaped to slightly reniform, ellipsoidal (2:1) to distinctly oblong (5:1); nucleolus reticulate. Micronucleus attached to macronucleus at varying position, about 5 µm across in vivo. Contractile vacuole in rear end, an average of six excretory pores in posterior pole area. Extrusomes scattered in cytoplasm and attached to oral bulge forming a ring-like array; conspicuous because 8–12 × 0.8–1 µm in size and obclavate with an about 5 µm long rod projecting anteriorly; mature organelles occasionally impregnate brownish with protargol, while a certain cytoplasmic developmental stage stains black (Fig. 75a–d). Cortex very flexible, contains rather dense rows of colourless granules. Cytoplasm packed with fat globules up to 5 µm across in well-nourished specimens; likely feeds on protists. Swims moderately fast by rotation about main body axis.

Cilia about 12 µm long in vivo, rather loosely spaced in neck region, arranged in an average of 21 equidistant, bipolar rows anteriorly densely ciliated and curved dorsally on right side of cell, while ventrally on left, as in → *Spathidium* (FOISSNER 1984). Three dorsal rows anteriorly differentiated to rather conspicuous dorsal brush with up to 6 µm long bristles, anterior bristle of pairs shortened. Brush row 1 slightly shorter than row 2, composed of an average of 25 dikinetids; row 2 twice as long as row 3, composed of 40 dikinetids on average; row 3 distinctly shortened consisting of only 14 dikinetids on average, but has a monokinetidal tail of 3 µm long bristles extending to at least mid-body (Fig. 75a, e–g, i, j; Table 61).

Oral bulge discoidal, moderately conspicuous occupying most of anterior end of cell, about 15 µm across and 4–5 µm high. Bulge centre slightly depressed and lined by an χ-shaped fibrillar core (inner oral basket) extending up to 10 µm into the cell. Circumoral kinety at base of oral bulge, flat as in → *Enchelyodon*, composed of narrowly spaced dikinetids associated with fine nematodesmata forming small bundles, which produce a rather inconspicuous, cylindroidal to conical, about 25 µm long oral basket impregnating with protargol (Fig. 75a, f–h; Table 61).

Occurrence and ecology: To date found only at type location, where it was very rare in the non-flooded Petri dish culture. The slender shape indicates that *S. armatum* is a true soil inhabitant. Interestingly, *S. armatum* occurred at the same site and habitat as → *S. enchelyodontides*.

Comparison with related species: This conspicuous ciliate is easily identified and distinguished from the two congeners, viz., → *S. enchelyodontides* and *S. lagyniforme*, by the large size, the reniform macronucleus, and the obclavate extrusomes. On the other hand,

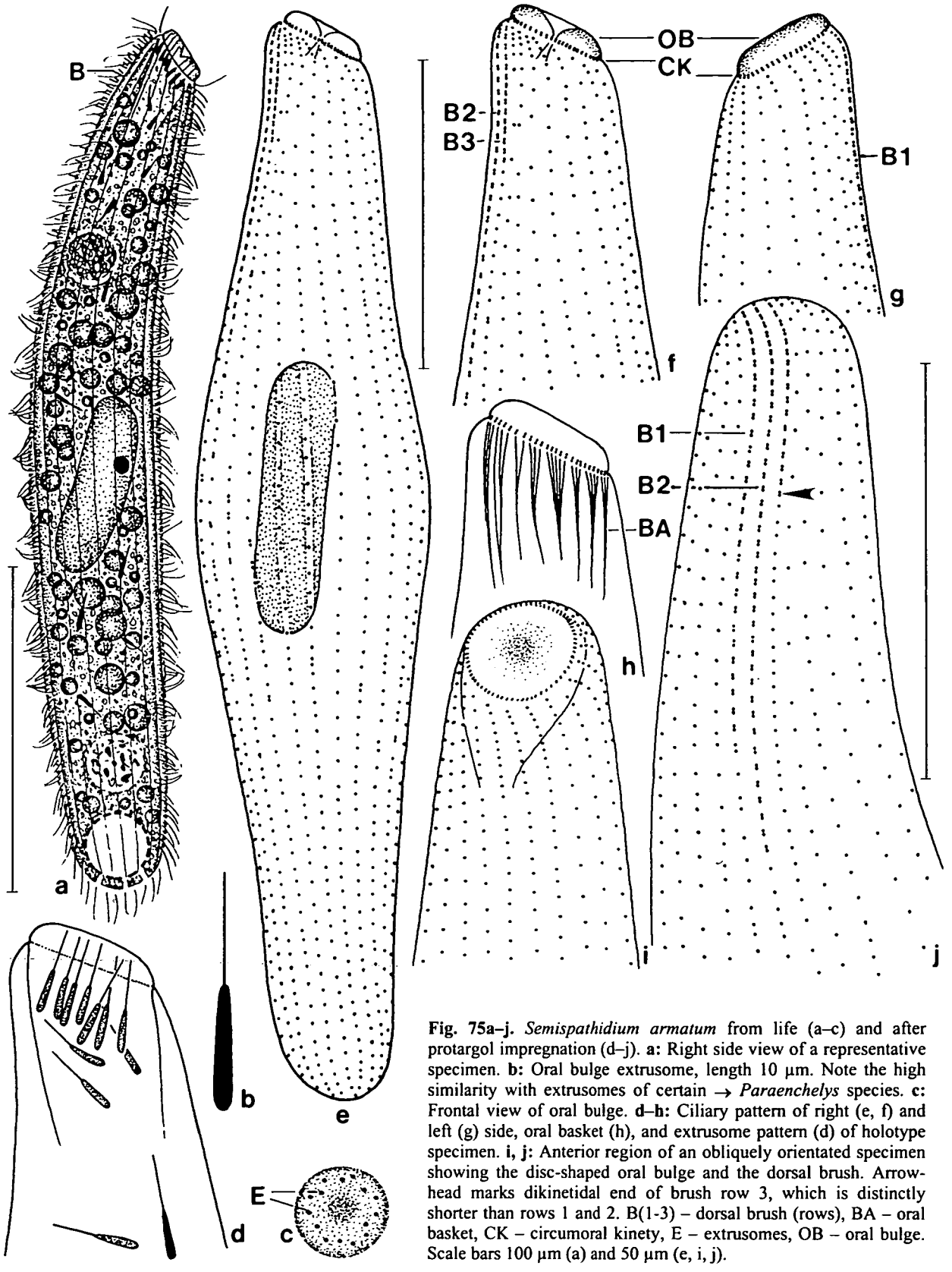

Fig. 75a–j. *Semispathidium armatum* from life (a–c) and after protargol impregnation (d–j). **a:** Right side view of a representative specimen. **b:** Oral bulge extrusome, length 10 µm. Note the high similarity with extrusomes of certain → *Paraenchelys* species. **c:** Frontal view of oral bulge. **d–h:** Ciliary pattern of right (e, f) and left (g) side, oral basket (h), and extrusome pattern (d) of holotype specimen. **i, j:** Anterior region of an obliquely orientated specimen showing the disc-shaped oral bulge and the dorsal brush. Arrowhead marks dikinetidal end of brush row 3, which is distinctly shorter than rows 1 and 2. B(1-3) – dorsal brush (rows), BA – oral basket, CK – circumoral kinety, E – extrusomes, OB – oral bulge. Scale bars 100 µm (a) and 50 µm (e, i, j).

similar features are found in several *Enchelyodon* and *Enchelys* species, for instance, *Enchelyodon terrenus* FOISSNER, 1984 (many macronuclear nodules). Thus, reliable identification requires protargol impregnation to reveal the curved anterior end of the ciliary rows.

Enchelyodon vermiforme, discovered by DRAGESCO (1970) in an ephemeral puddle in Cameroun, likely belongs to *Semispathidium* and is very similar to *S. armatum*, differing mainly by the 50 µm long, rod-shaped extrusomes. Unfortunately, the ciliary pattern is not known, and thus it cannot be combined with *Semispathidium.*

Apospathidium nov. gen.

Diagnosis: Amphoriform Spathidiidae (?) with oblique oral bulge. Oral basket rods (nematodesmata) originate from stepped dikinetidal kinetofragments and oralized monokinetids in the anterior region of the somatic kineties.

Type species: *Apospathidium terricola* nov. spec.

Etymology: Composite of the Greek prefix *apo* (derived from) and the Greek generic name *Spathidium* (spatulate animal), referring to the presumed nearest relative. Neuter gender.

Comparison with related genera and species assignable: This ciliate was a real surprise because it looked like an ordinary *Spathidium.* However, protargol impregnation revealed a unique feature as yet known mainly from the Enchelyina, viz., oralized somatic monokinetids (Fig. 76n; 330a, b). Thus, we cannot exclude that the spathidiid features evolved convergently and *Apospathidium* belongs to the Enchelyina FOISSNER & FOISSNER (1988). This is emphasized by the rows of body extrusomes present in *Apospathidium* and some Enchelyina (e.g. → *Diplites*), but lacking in spathidiids s. str. However, more distantly related spathidiids, such as → *Apobryophyllum*, also have rows of body extrusomes. In any case, the general appearance and some specific features, such as the location and structure of the oral kinetofragments, of *A. terricola* and → *A. atypicum* are so near to *Spathidium* that an enchelyine relationship is difficult to believe.

A reinvestigation of → *Apospathidium atypicum* showed that it has the same features as *Apospathidium terricola.* Thus, it will be transferred to that genus (see below). Both, BUITKAMP & WILBERT (1974) and FOISSNER (1981b), who redescribed this species, could not find the oral basket in their preparations and thus missed its special structure.

Apospathidium terricola nov. spec. (Fig. 76a–j; 330a–c; Table 62)

Diagnosis: Size about 150 × 35 µm in vivo. Slenderly amphoriform with short tail and oblique oral bulge about two thirds as long as widest trunk region. Macronucleus rod-shaped. Single micronucleus about 5 µm across. Contractile vacuole distinctly subterminal. Oral bulge and body extrusomes rod-shaped, about 5 µm long, the latter in 2 to 3 rows between each two kineties. On average 11 ciliary rows, 4 anteriorly differentiated to inconspicuous dorsal brush occupying about 10% of body length.

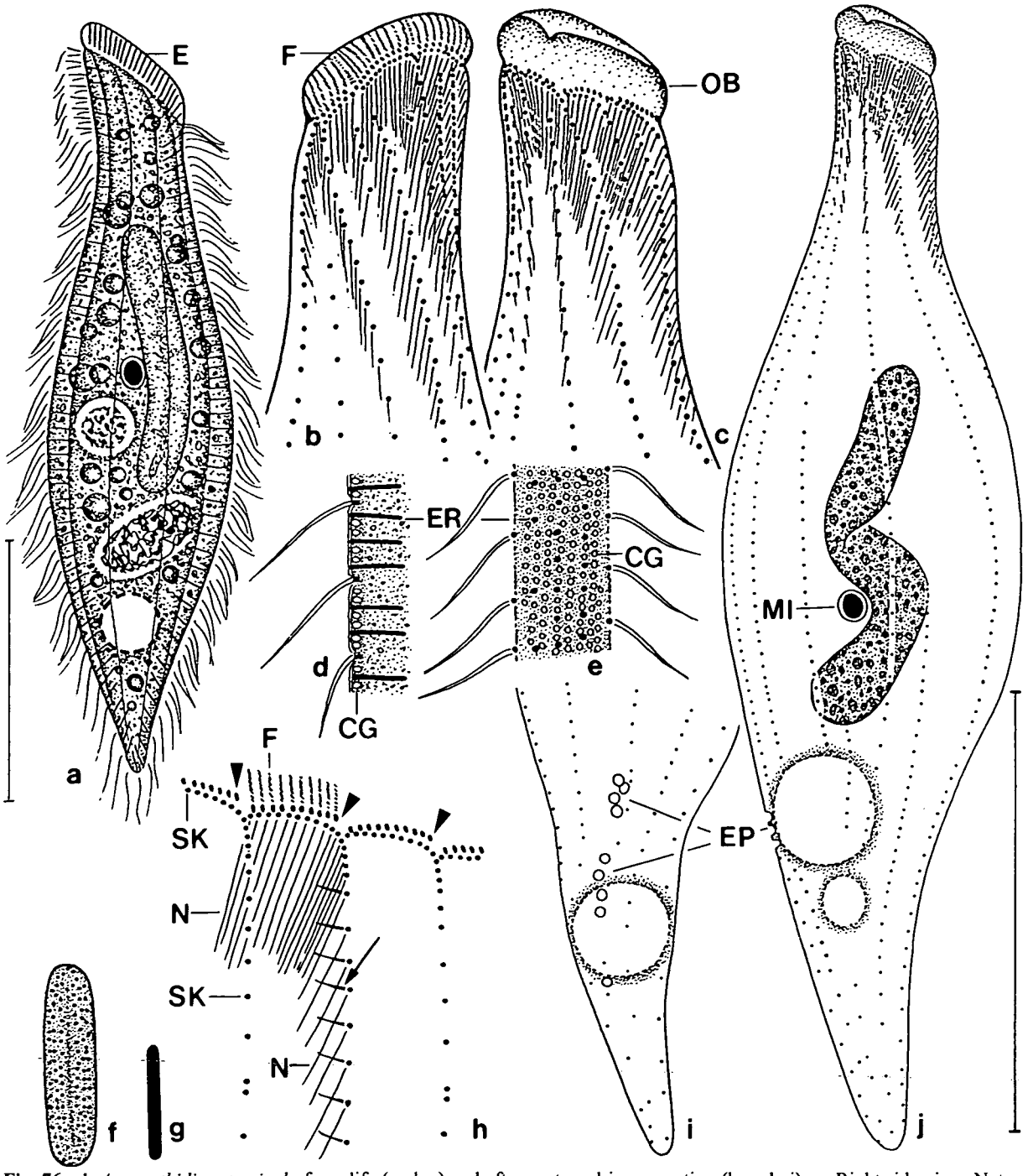

Fig. 76a–j. *Apospathidium terricola* from life (a, d–g) and after protargol impregnation (b, c, h–j). **a:** Right side view. Note the subterminal contractile vacuole and the fine body extrusomes anchored to the pellicle. **b, c, h–j:** Infraciliature of right and left side and nuclear apparatus of holotype specimen (b, c, j), and posterior dorsolateral portion of an individual from site (5). Details of the oral infraciliature are shown in figure (h): arrowheads mark stepped dikinetidal oral kinetofragments attached to the anterior end of the somatic kineties having oralized (with nematodesmata) monokinetids in the anterior region. Arrow denotes a short fibre (?) at right side of basal body. **d, e:** Optical section and surface view showing rows of body extrusomes and cortical granules. **f:** Frontal view of oral bulge packed with extrusomes. **g:** Oral bulge and body extrusome, about 5 × 0.5 µm. CG – cortical granules, E – oral extrusomes, EP – excretory pores, ER – rows of body extrusomes, F – fibres in oral bulge, MI – micronucleus, N – nematodesmata, OB – oral bulge, SK – somatic kinety. Scale bars 50 µm.

Type location: Mud and soil from granitic rock-pools on the Spitzkoppe, an Inselberg in the Namib Escarpment, Namibia, 21°45'S 15°8'E (site 41 in figure 2 and chapter 2.1.2).

Etymology: The Latin adjective *terricola* (living in soil) refers to the habitat the species was discovered.

Description: The species was rare at both sites (5, 41), and only one specimen from site 41 (type location) was observed in vivo, but two of the five specimens contained in the protargol slides were excellently impregnated. Morphometry was supplemented with three specimens from site (5). Altogether, data are sufficient for a reliable description, but should be refined from a more abundant population.

Size 130–170 × 25–50 µm in vivo, usually near 150 × 35 µm, length:width ratio 2.8–5.6:1, on average near 4:1 both in vivo and protargol preparations, where specimens are slightly inflated in mid-body. Slenderly amphoriform with oblique oral bulge about two thirds as long as widest trunk region, narrowed neck, and bluntly pointed posterior end (Fig. 76a, j; Table 62); flattened laterally, acontractile. Macronucleus in middle third of cell, rod-shaped and more or less distinctly tortuous, about 50 × 7 µm; nucleoli globular or lobate. Micronucleus attached to mid-region of macronucleus, about 5 µm across and surrounded by a distinct membrane. Contractile vacuole and about 10 dorsolateral excretory pores in rather long row far subterminal (Fig. 76a, i, j). Oral bulge and body extrusomes rod-shaped, about 5 µm long, in several indistinct rows in oral bulge and between somatic kineties; posterior half usually impregnates with protargol (Fig. 76a, d, f, g). Cortex flexible, contains closely spaced rows of granules about 1 µm across, between which the strongly refractive extrusomes are located (Fig. 76d, e). Cytoplasm colourless, contains many lipid droplets up to 10 µm across and large food vacuoles with remnants of protozoa. Glides rather rapidly on microscope slide.

Cilia arranged in an average of 11 widely spaced, bipolar, moderately densely ciliated rows distinctly curved at base of oral bulge, where conspicuous dikinetidal kinetofragments form a stepped circumoral kinety. Dorsal brush four-rowed (three-rowed in one out of eight specimens), inconspicuous because occupying only 10% of body length and bristles merely up to 4 µm long; all rows continue as somatic kineties posteriorly; row 1 composed of an average of eight dikinetids, row 2 of nine, row 3 of thirteen, and row 4 of four bristle pairs (Fig. 76a–c, j; 330a–c; Table 62).

Oral bulge about two thirds as long as widest trunk region and about 5 µm high in vivo, obliquely truncate, slightly convex and elongate elliptical in frontal view; contains faintly impregnated fibres originating from the anterior basal bodies of the dikinetidal circumoral fragments and extending obliquely to the slightly acentric bulge opening. Circumoral kinety elongate elliptical, composed of conspicuous, dikinetidal kinetofragments attached to the somatic kineties; individual fragments composed of 7–14 dikinetids, which show the different (angular) orientation of the basal bodies very clearly (Fig. 76h); fragments stepped because slightly curved and distance between basal bodies of individual dikinetids becomes gradually wider from distal to proximal, a curious feature shown in figure 76h. Oral basket inconspicuous because not sharply defined and basket rods (nematodesmata) do not form bundles. Nematodesmata originate from dikinetidal kinetofragments (possibly even from both bodies of a pair) and up to 20 oralized somatic monokinetids in the anterior region of the ciliary rows (Fig. 76a–c, f, h, j; 330a–c).

Table 62. Morphometric data on *Apospathidium terricola* (upper line) and *A. atypicum* (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	131.6	132.5	11.4	4.0	8.6	115.0	150.0	8
	111.3	110.0	15.5	3.6	13.9	82.0	152.0	19
Body, width	33.3	32.0	8.1	3.1	24.7	24.0	47.0	8
	18.0	17.0	3.5	0.8	19.3	13.0	28.0	19
Body length:width, ratio	4.2	3.8	1.0	0.7	24.4	2.8	5.6	7
	6.3	6.3	1.1	0.3	16.9	4.3	8.4	19
Oral bulge, length	17.6	17.0	2.8	1.1	16.0	15.0	22.0	7
	13.5	14.0	1.9	0.4	14.0	9.0	16.0	19
Oral bulge, height	3.6	4.0	–	–	–	3.0	4.0	7
	2.4	2.0	–	–	–	2.0	3.0	19
Anterior body end to macronucleus, distance	39.8	47.0	15.0	5.3	37.6	19.0	53.0	8
	46.1	45.0	6.0	1.4	13.0	34.0	56.0	19
Macronucleus, length (extended when curved;	47.1	45.0	–	–	–	35.0	85.0	8
values thus approximate)	30.9	30.0	–	–	–	18.0	40.0	19
Macronucleus, width	6.8	7.0	0.7	0.3	10.4	6.0	8.0	8
	4.8	5.0	0.5	0.1	10.4	4.0	6.0	19
Micronucleus, length	5.1	5.0	–	–	–	5.0	6.0	8
	2.9	3.0	–	–	–	2.0	4.5	19
Micronucleus, width	4.6	5.0	–	–	–	3.5	5.0	8
	2.7	3.0	–	–	–	2.0	4.0	19
Circumoral kinety to end of brush row 1, distance	7.4	7.0	2.5	1.1	33.9	5.0	10.0	5
	6.0	6.0	1.4	0.3	22.8	4.0	9.0	19
Circumoral kinety to end of brush row 2, distance	10.8	9.0	5.2	2.6	48.0	7.0	18.0	4
	11.1	11.0	1.5	0.3	13.3	8.0	13.0	19
Circumoral kinety to end of brush row 3, distance	11.4	11.0	3.0	1.3	26.0	7.0	15.0	5
	4.2	4.0	0.6	0.1	14.5	3.0	5.0	19
Circumoral kinety to end of brush row 4, distance	5.5	5.0	1.7	0.9	31.5	4.0	8.0	4
	–	–	–	–	–	–	–	–
Somatic kineties, number	11.3	11.0	1.3	0.5	11.1	10.0	13.0	7
	9.4	9.0	1.2	0.3	12.9	8.0	13.0	19
Ciliated kinetids in a lateral kinety, number	64.3	55.0	17.2	6.5	26.8	48.0	95.0	7
	45.1	45.0	6.5	1.5	14.5	35.0	60.0	19
Dorsal brush rows, number	3.9 [b]	4.0	–	–	–	3.0	4.0	8
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
Dikinetids in brush row 1, number	7.4	8.0	3.3	1.5	44.4	4.0	11.0	5
	6.4	6.0	1.5	0.3	22.9	4.0	9.0	19
Dikinetids in brush row 2, number	11.3	9.0	7.1	3.5	62.7	6.0	21.0	4
	12.1	12.0	2.2	0.5	17.8	8.0	16.0	19
Dikinetids in brush row 3, number	11.8	13.0	2.9	1.3	25.0	7.0	14.0	5
	4.5	4.0	0.7	0.2	15.6	3.0	6.0	19
Dikinetids in brush row 4, number	4.8	4.5	2.5	1.3	52.1	2.0	8.0	4

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Three-rowed in 1 out of 8 specimens.

Comparison with related species: *Apospathidium terricola* has, like the single congener, → *A. atypicum*, a highly characteristic, slenderly amphoriform shape and thus cannot be confused with any other member of the family. Both are easily distinguished in vivo and protargol preparations by the length:width ratio (near 4:1 vs. 9:1), the number of extrusome rows between the kineties (several vs. one), the number of ciliary rows (10–13 vs. 7–8), and the number of dorsal brush rows (4 vs. 3).

Apospathidium atypicum (BUITKAMP & WILBERT, 1974) **nov. comb.** (Fig. 77a–j; Table 62)

1974 *Spathidium atypicum* n. sp. BUITKAMP & WILBERT, Acta Protozool., 13: 202.
1977 *Spathidium longicaudatum* n. nom. BUITKAMP, Decheniana, 130: 117 (replacement name because of preoccupation).
1981 *Spathidium longicaudatum* BUITKAMP 1977 – FOISSNER, Zool. Jb. Syst., 108: 275 (redescription).

Nomenclature: The original name of the species (*atypicum*) becomes valid because *atypicum* is not occupied in the genus *Apospathidium* (articles 59, 60 of the ICZN 1999).

Type material: BUITKAMP's protargol slides are completely bleached, suggesting neotypification. However, our material is from a different biogeographic region and the identity of the species not threatened at present. Thus, neotypification can await redescription of a Canadian or, at least, North American population. Of course, we deposit voucher material of the Kenyan specimens (Table 1).

Improved diagnosis (including literature data): Size about 125 × 20 µm in vivo. Very slenderly amphoriform with fairly distinct tail and oblique oral bulge about two thirds as long as widest trunk region. Macronucleus rod-shaped. Single micronucleus approximately 4 µm across. Contractile vacuole 22% subterminal on average. Oral and body extrusomes rod-shaped, 3–4 µm long. On average 9 ciliary rows, 3 anteriorly differentiated to inconspicuous dorsal brush occupying about 10% of body length.

Observations: Our data basically match those of BUITKAMP & WILBERT (1974) and FOISSNER (1981b), except of the oral basket, as discussed above. Thus and because most important features can be seen in the figures and morphometrics, we emphasize only the following details: (i) Shape invariably very slenderly amphoriform and highly characteristic due to the tail-like posterior third (Fig. 77a–c, h); (ii) Macronucleus invariable of the shape of a short, more or less tortuous rod (Fig. 77a, c, h); (iii) Contractile vacuole conspicuously subterminal, on average 22% of body length ($\overline{x}$ = 24.4 µm, SD = 7.5 µm, CV = 30.8%, Min = 13 µm, Max = 40 µm, n = 19), that is, underneath base of tail. Several scattered excretory pores on dorsal side of cell (Fig. 77b, c, h); (iv) Extrusomes in oral bulge and attached to somatic cortex likely somewhat different because only the somatic ones lightly impregnate with protargol (Fig. 77g, j). The following shapes and sizes were observed: rod-shaped, 2.8–3.5 × ~ 0.4 µm (Namibian site 1); rod-shaped, oral extrusomes 4 µm long, body extrusomes about 2.5 × 0.2 µm (Namibian site 2); slightly fusiform and 3 µm long (Namibian sites 16, 17); rod-shaped and fine, about 4 × 0.2 µm (Venezuelan population); (v) Somatic and oral

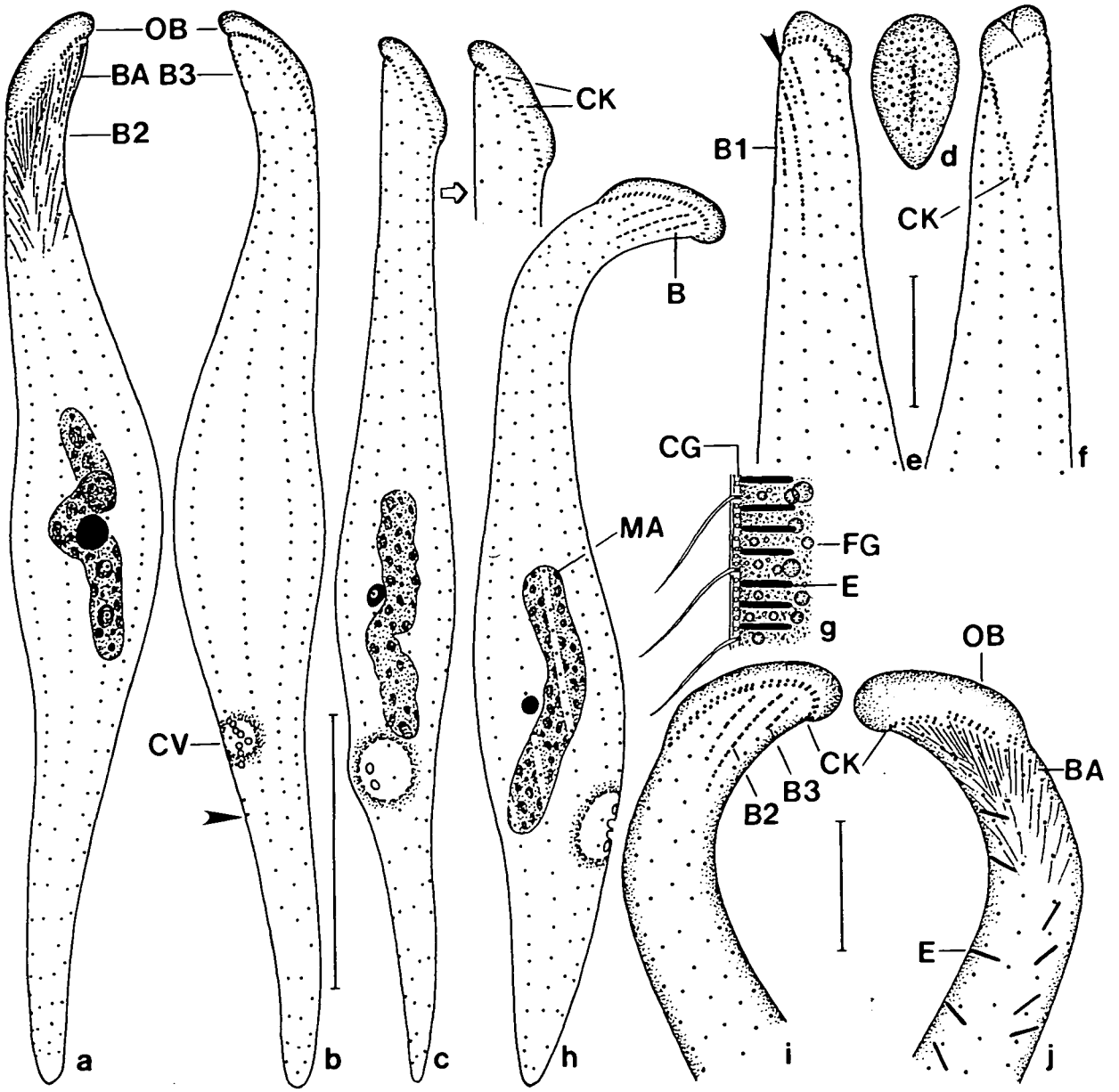

Fig. 77a–j. *Apospathidium atypicum*, Kenyan specimens from life (d, g) and after protargol impregnation (a–c, e, f, h–j). **a, b:** Ciliary pattern of left and right side of a representative specimen. Note the contractile vacuole, which is far subterminal and has many excretory pores on the dorsal side of the cell. Arrowhead marks end of a shortened ciliary row. As concerns the oral basket, see explanation to figures (i, j). **c:** Right side ciliary pattern and nuclear apparatus of another specimen, where the kinetofragments composing the circumoral kinety are incompletely aligned, producing a protospathidiid pattern. **d:** The oral bulge is obovate, while the circumoral kinety is cuneate (f). **e, f:** Ciliary pattern of anterior dorsal and ventral side showing the cuneate circumoral kinety and a short brush fragment (arrowhead) between rows 2 and 3. **g:** Optical section of somatic cortex studded with 3.5 µm long extrusomes, a main feature of the species. **h–j:** Oral and somatic ciliary pattern of left and right side and nuclear apparatus of another specimen. The inconspicuous oral basket (j) is fundamentally different from that of *Spathidium* because it is made of fine nematodesmata originating from the circumoral dikinetids and fine, short nematodesmata originating from the basal bodies at the anterior end of the somatic ciliary rows (oralized somatic monokinetids). Note the short, inconspicuous dorsal brush. B – dorsal brush, B1-3 – dorsal brush rows, BA – oral basket, CG – cortical granules, CK – circumoral kinety, CV – contractile vacuole, E – extrusomes, FG – fat globule, MA – macronucleus, OB – oral bulge. Scale bars 30 µm (a, b, c, h) and 10 µm (e, f, i, j).

ciliary pattern as described in → *A. terricola*. Dorsal brush inconspicuous because occupying only 10% of body length and longest bristles only 3–4 µm high; row 3 with a short monokinetidal bristle tail. (vi) Oral bulge obovate, while circumoral kinety distinctly cuneate, a remarkable difference observed in several specimens (Fig. 77d, f). Kinetofragments of right half of circumoral kinety often incompletely aligned, producing the stepped (protospathidiid) pattern typical for the genus (Fig. 77a–c, h, e, f, i, j).

Occurrence and ecology: *Apospathidium atypicum* has been reported from all main biogeographic regions, except of Antarctica (FOISSNER 1998a). Interestingly, the species is frequent, but never develops high abundances in the non-flooded Petri dish cultures. With its slender, flexible body, *A. typicum* is perfectly adapted to terrestrial habitats and to exploit even narrow soil pores.

Comparison with literature data and related species: Our observations basically match the original description and the redescription by FOISSNER (1981b). The Austrian specimens supposedly lack body extrusomes and has an elliptical circumoral kinety. However, FOISSNER's data are not very detailed, and thus the differences might be caused by incomplete observations.

Apospathidium atypicum differs from → *A. terricola* by the cuneate (vs. elliptical) oral bulge, the number of dorsal brush rows (three vs. four), and most morphometrics. Basically, *A. terricola* is larger and massiver than *A. atypicum*, which makes both easily distinguishable even in vivo.

Bryophyllum paucistriatum **nov. spec.** (Fig. 78a–w; 331a–d; Table 63)

Diagnosis: Body size (usually between 100–150 × 40–45 µm) and shape (narrowly to broadly lanceolate) and macronucleus (elongate reniform to a 120 µm long strand composed of up to 8 nodules) highly variable. Two types of extrusomes: type I rod-shaped to indistinctly acicular, moderately thick, about 8 µm long; type II rod-shaped, fine, about 2 µm long. On average 10–14 ciliary rows, 4–6 anteriorly differentiated to dorsal brush.

Type location: Savannah soil of the Masei Mara National Reserve, Kenya, 01°30'S 34°55'E.

Etymology: Composite of the Latin adjectives *pauci* (few) and *striatus* (striated ~ ciliary rows), referring to the low number of ciliary rows, a main species feature.

Description: Several populations were observed (see occurrence and ecology section). The diagnosis refers to those from Kenya and Namibian site (56), which were studied in detail. Size and shape of the body and macronucleus are extremely variable, both within and among populations (Table 63). As the extremes are connected by many transitions, we exclude having mixed up two cryptic species; however, we cannot exclude the occurrence of distinct races, possibly distinguishable at subspecies level; this is also indicated by the rather different extrusomes which, however, lack a biogeographic pattern.

Size 90–200 × 25–60 µm in vivo, usually 100–150 × 40–45 µm; length:width ratio also highly variable, viz., 1.5–7.8:1, especially in Namibian population (Table 63); slightly

contractile, under moderate cover-glass pressure up to 30%. Shape as is typical for genus, but highly variable, that is, broadly to slenderly lanceolate with ventral margin more or less distinctly convex and dorsal straight, slightly convex or concave (Fig. 78a, g, h, m–q); anterior ventral portion curved to left side in swimming specimens and frequently slightly set off, forming a spathidiid pattern; laterally flattened 2–3:1, depending on nutrition (Fig. 78g, k–m, o, p, r, v). Nuclear apparatus usually in middle third of cell. Macronucleus of Kenyan type population rod-shaped to elongate reniform, that of Namibian site (56) specimens rod-shaped, elongate reniform, or an up to 120 µm long, tortuous strand showing up to eight, usually four nodules (Fig. 78a, g, m–q, s, w). Micronucleus discoidal, about 6 × 3 µm in vivo, attached to macronucleus. Contractile vacuole near posterior dorsal margin of cell, about six to ten excretory pores on right side, viz., left of rear end of oral bulge (Fig. 78a, s, w). Two types of oral extrusomes, studied in five populations (Fig. 78a–g, i; 331a–d): type I forms short, oblique, bright rows and is, depending on population, rod-shaped to indistinctly acicular or fusiform, straight or slightly curved, moderately thick, and 5–10 µm long; type II very inconspicuous, rod-shaped, fine, 1.5–3 µm long, depending on population. Cortex very flexible, contains closely spaced rows of colourless, minute (< 0.5 µm) granules that impregnate rather heavily with protargol, hiding the infraciliature. Cytoplasm colourless, in well-fed specimens packed with fat inclusions 3–7 µm across and some large food vacuoles. Feeds on heterotrophic flagellates (*Polytomella* sp., *Astasia* sp.) and small ciliates (*Leptopharynx costatus*), both ingested whole and thus recognizable for some time in the food vacuoles. Glides slowly on microscope slide and soil particles, showing great flexibility; rarely swims rather rapidly by rotation about main body axis.

Cilia about 10 µm long in vivo, rather closely spaced, especially in mid-body, probably due to some contraction of cells during fixation (see above); arranged in an average of 11 (Namibian population) to 14 (Kenyan population) rows following body curvature and abutting on both halves of circumoral kinety in anterior and posterior quarter of cell; rows slightly wider spaced in midline of organism, two of them inconspicuously shortened above excretory pores of contractile vacuole. All or most left side kineties anteriorly differentiated to short and thus inconspicuous dorsal brush composed of about 3 µm long, closely spaced bristles (Fig. 78a, r, s, u; 331c, d; Table 63); no second brush in mid-body of dorsal side, as described by GELEI (1934) in some species.

Oral apparatus occupies entire body length and curves around posterior end onto dorsal side for about 10 µm. Oral bulge about 5 µm high and glossy due to the many extrusomes contained, thus very distinct in vivo; slightly widened and opened anteriorly. Circumoral kinety at base of oral bulge, very elongate elliptical, composed of closely spaced dikinetids each associated with a cilium and a long nematodesma in anterior body half, while only each third to fifth dikinetid has a short and thin rod in posterior half; oral basket thus distinct only in anterior body half (Fig. 78a, g, h, k, l, r–w; 331c, d; Table 63).

Occurrence and ecology: *Bryophyllum paucistriatum* is likely distributed globally and oligo- to mesohaline because we found it not only in Kenya (type locality; dark grey, very hard savannah soil, pH 6.5), but also in Namibia (Table 4; Fig. 78c, m–q), Utah, USA (slightly saline soil from a swamp near the village of Brigham; Fig. 78f), Spain (Toledo; Fig. 78e), and Austria (beech litter from the surroundings of Salzburg; Fig. 78d). Abundances were usually low, except at Namibian site (56), where high numbers developed in the non-flooded Petri dish culture.

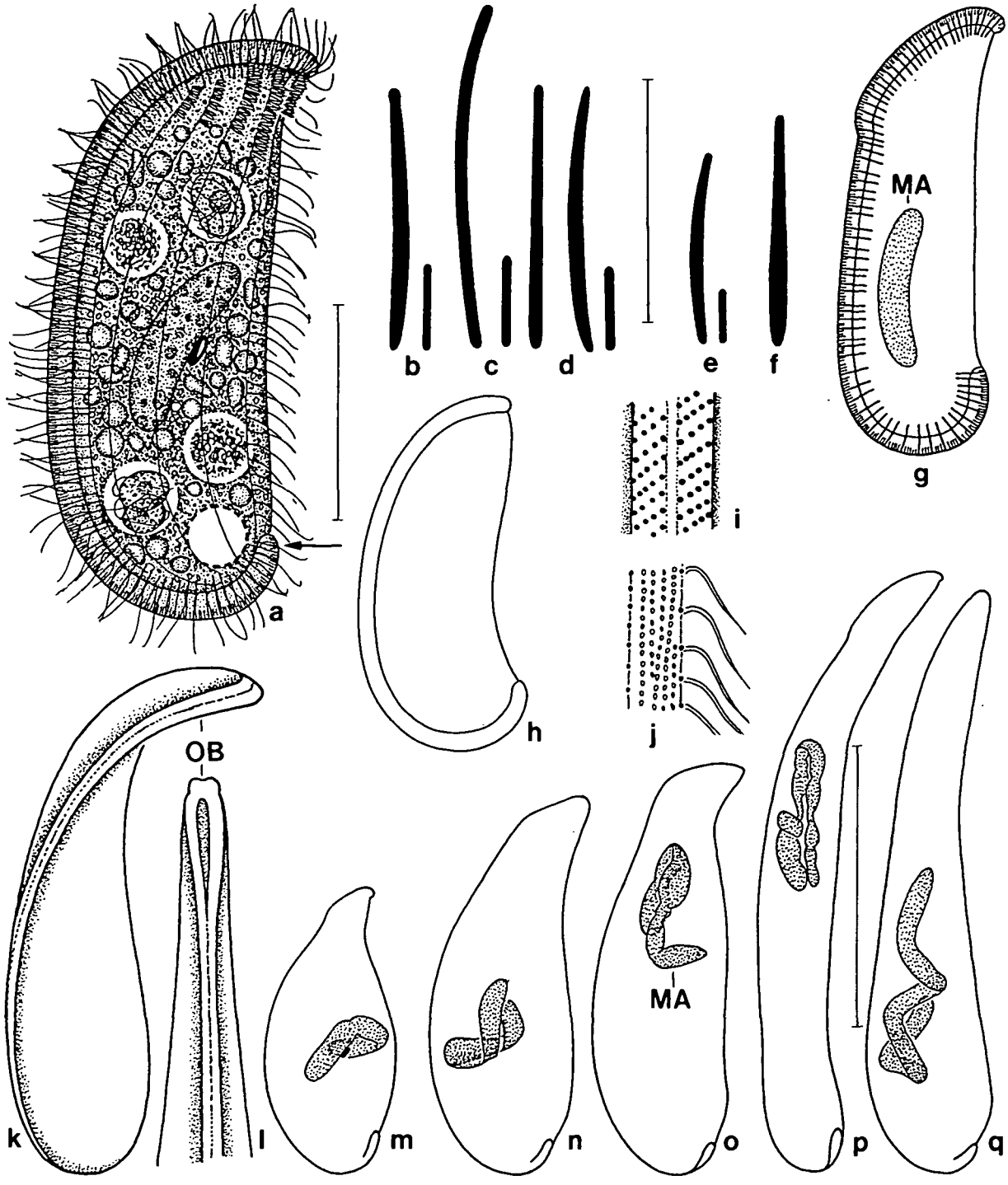

Fig. 78a–q. *Bryophyllum paucistriatum* from life (a–l) and after protargol impregnation (m–q). **a:** Left side view of a representative specimen from Kenya. Arrow marks rear end of oral bulge. **b–f:** Large and small oral bulge extrusomes from Kenyan (b), Namibian site 49 (c), Austrian (d), Spain (e), and USA (f) specimens; drawn to scale (7 µm). **g, h:** Spathidiid and hatchet-like shape variants from Kenya. **i.** The oral bulge contains oblique rows of extrusomes. **j:** Surface view showing cortical granulation. **k:** Ventrolateral view of a swimming specimen. **l:** Anterior ventral portion of oral bulge. **m–q:** Variability of size and shape of body and macronucleus in specimens from Namibian site (56); most frequent are those shown in figures (n, o). B – dorsal brush, MA – macronucleus, OB – oral bulge. Scale bars 40 µm (a), 7 µm (b–f), and 80 µm (m–q).

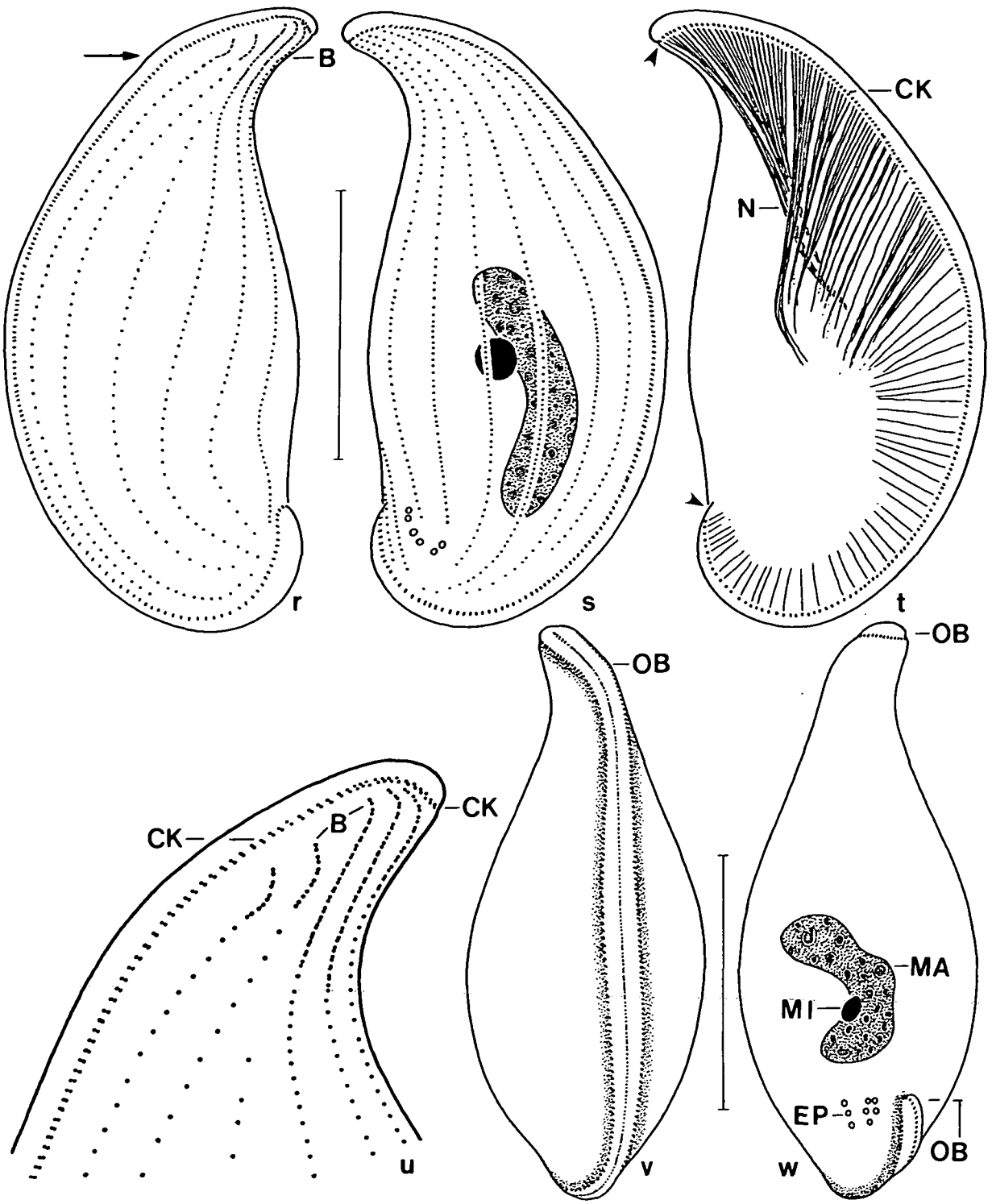

Fig. 78r–w. *Bryophyllum paucistriatum*, somatic and oral ciliary pattern and nuclear apparatus of Kenyan specimens after protargol impregnation. **r–u:** Left (r, u) and right (s) side views of ciliary and nematodesmal pattern of holotype specimen. Arrow denotes spathidiid portion of oral bulge; arrowheads mark ends of oral bulge. The specimen has five short dorsal brush rows. **v, w:** Ventral and dorsal view. B – dorsal brush, CK – circumoral kinety, EP – excretory pores, MA – macronucleus, MI – micronucleus, N – nematodesmata (oral basket rods), OB – oral bulge. Scale bars 40 μm.

Table 63. Morphometric data on *Bryophyllum paucistriatum* from Kenya (type location, upper line) and Namibian site 56 (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	86.5	84.0	9.1	2.7	10.5	75.0	102.0	11
	129.5	130.0	29.6	6.8	22.9	76.0	172.0	19
Body, width	40.5	38.0	6.5	1.9	16.1	34.0	55.0	11
	36.3	38.0	8.8	2.0	24.2	22.0	53.0	19
Body length:width, ratio	2.2	2.2	0.4	0.1	16.1	1.5	2.7	11
	3.9	3.2	1.7	0.4	42.7	1.7	7.8	19
Anterior body end to end of longest dorsal	17.6	17.5	2.5	0.8	14.2	14.0	21.0	10
brush row, distance	18.1	18.0	4.0	0.9	21.8	11.0	24.0	19
Posterior body end to dorsal end of oral bulge,	12.6	12.0	2.4	0.7	19.1	10.0	18.0	11
distance	8.6	8.0	3.4	0.8	39.0	4.0	17.0	19
Macronucleus, length (spread if coiled; values	34.4	35.0	–	–	–	28.0	40.0	10
thus approximations)	71.3	65.0	–	–	–	40.0	120.0	19
Macronucleus, width	7.8	8.0	–	–	–	7.0	8.0	10
	6.4	6.0	1.1	0.2	16.7	5.0	8.0	19
Micronucleus, length	5.6	5.6	0.9	0.3	16.6	4.0	7.0	10
	5.0	5.0	0.7	0.2	13.9	4.0	7.0	19
Micronucleus, width	4.1	4.0	1.2	0.4	28.8	3.0	6.0	10
	3.3	3.0	0.8	0.2	24.4	2.0	5.0	19
Ciliary rows, number (including brush rows)	14.4	14.5	1.4	0.5	9.8	12.0	16.0	10
	10.9	11.0	0.8	0.2	7.2	10.0	12.0	19
Dorsal brush rows, number	4.6	5.0	–	–	–	4.0	5.0	10
	4.6	5.0	0.7	4.2	14.9	4.0	6.0	19
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
Nodes in macronucleus, number	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11
	3.9	4.0	2.7	0.6	68.6	0.0	8.0	19
Micronuclei, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Comparison with related species: *Bryophyllum paucistriatum* is most similar to *B. hyalinum* GELEI, 1936, although this species is considerably narrower (100–110 × 18 µm), because it has the same body length, nuclear pattern, and number of ciliary rows. However, GELEI (1936) definitely states that *B. hyalinum* has three dorsal brush rows, while *B. paucistriatum* has four to six, usually five (Table 63). This difference looks inconspicuous. However, there are two groups of bryophyllids: one with three dorsal brush rows, as is typical for *Spathidium*, e.g., *B. tegularum* (FOISSNER 1984) and *B. loxophylliforme* (KAHL 1931b), and another with four or more rows, such as *B. paucistriatum* (four to six rows), → *B. lingua* (ten rows), and *B. carinatum* GELEI, 1934 (twenty rows). As the number of brush rows is

apparently independent of that of ciliary rows, as shown by *B. paucistriatum* and → *B. lingua*, this feature should not be under-estimated. *Bryophyllum paucistriatum* is also highly similar to *B. vorax* (STOKES, 1886b) KAHL, 1931b, differing only in the shape of the macronucleus, which is elongate reniform in the former and ovate in the latter. This difference is stable because we never saw an ovate macronucleus in several populations of *B. paucistriatum*. *Bryophyllum spathidioides* GELEI, 1954 has 35 ciliary rows, of which seven are differentiated to brush kineties, while *B. paucistriatum* has a maximum of 16 ciliary rows, of which only 4–6 form the brush.

Bryophyllum lingua GELEI, 1934

Improved diagnosis: Size about 160–250 × 40–120 µm in vivo; slenderly to broadly lanceolate with posterior end of oral bulge in last dorsal fifth of cell and distinctly set off from body proper. Many (≥ 50) ellipsoidal macronuclear nodules. About 16–50 ciliary rows, approximately 10 anteriorly differentiated to dorsal brush.

Remarks and comparison with related species: We split this species into two subspecies differing distinctly in some main morphometrics. Unfortunately, GELEI (1934) does not provide details on the extrusomes. Thus, the classification of our population is somewhat doubtful and the feature cannot be included in the diagnosis. Further, GELEI described dorsal brush rows anteriorly **and** in mid-body in all the *Bryophyllum* species he investigated. However, later and the present investigations could not confirm the mid-body brush rows. Likely, this was a misobservation, or GELEI observed dividers, which produce the dorsal brush very early, that is, before cell furrowing commences.

Bryophyllum lingua is similar to *B. loxophylliforme* KAHL, 1931b, which, however, has only three dorsal brush rows and the oral bulge less distinctly set off from the dorsal surface. As explained under → *B. paucistriatum*, the main distinguishing feature is the dorsal brush, viz., three rows in *B. loxophylliforme* vs. about ten in *B. lingua*. Unfortunately, a detailed redescription of *B. loxophylliforme* is not available.

Bryophyllum lingua lingua GELEI, 1934 **nov. stat.** (Fig. 79t–v)

Diagnosis (after GELEI): Size about 160–200 × 40–50 µm in vivo; slenderly lanceolate with a length:width ratio near 4:1. 16–18 ciliary rows.

Type location: Soda pools near Szeged, Hungary.

Bryophyllum lingua multistriatum **nov. sspec.** (Fig. 79a–s; 332a–d; Table 64)

Diagnosis: Size about 220 × 80 µm in vivo; lanceolate with an average length:width ratio

of 2.5:1. Two types of extrusomes: type I acicular, about 8 × 0.5 µm in size; type II rod-shaped, fine, about 1.5 µm long. On average 40 ciliary rows.

Type location: Mud from granitic rock-pools of a stream in the Daan Viljoen Game Park near Windhoek, Namibia, 22°35'S 17°05'E (site 73 in figure 2 and chapter 2.1.2).

Etymology: The Latin adjective *multistriatum* (many striae) refers to the high number of ciliary rows this subspecies possesses.

Description: Size 180–250 × 50–120 µm in vivo, usually near 220 × 80 µm; length:width ratio 1.6–3.5:1, on average 2.5:1 in protargol preparations; highly flexible and somewhat contractile, as indicated by slight shape changes. Shape as is typical for genus, but rather variable, that is, slenderly to broadly lanceolate, sometimes with spathidiid anterior region and often with an irregular, undulate outline; anterior third flattened leaf-like and thus hyaline, central and posterior region usually dark at low magnification (≤ ×100) and only slightly flattened because packed with food inclusions (Fig. 79a, f, i–p; 332a; Table 64). Most macronuclear nodules scattered in posterior body half; individual nodules with minute nucleoli and highly variable in size and shape, on average ellipsoidal. Many minute, ellipsoidal micronuclei scattered between and attached to macronuclear nodules (Fig. 79a, c, f). Contractile vacuole and excretory pores subterminal near left dorsal margin of cell (Fig. 79a, h, j, k, n, p). Two types of extrusomes in oral bulge and cytoplasm, impregnate heavily with silver carbonate but not with protargol (Fig. 79a, b, e, i; 332c, d): type I conspicuous, forms short, transverse, bright rows in the oral bulge, acicular and slightly curved, about 8 × 0.5 µm in size; type II very inconspicuous, rod-shaped, fine, about 1.5 µm long. Cortex very flexible, contains closely spaced rows of colourless, minute (< 0.5 µm) granules that do not impregnate with protargol. Cytoplasm colourless, in well-fed specimens packed with fat globules up to 10 µm across and small and large food vacuoles containing up to 110 µm long rotifers and indeterminable matter, likely remnants from ciliates. Glides slowly on microscope slide and soil particles showing great flexibility.

Cilia about 10 µm long in vivo, very closely spaced in rows along right body margin, while loosely so in anterior body third and left posterior body margin, arranged in an average of 40 rows following body curvature and abutting to both halves of circumoral kinety anteriorly and posteriorly; many rows interrupted and/or shortened anteriorly and/or posteriorly without any regularity. On average nine left side kineties anteriorly differentiated to rather conspicuous dorsal brush composed of closely spaced dikinetids bearing slightly inflated bristles increasing in length from about 2.5 µm in right rows to 5 µm in leftmost row, which has a monokinetidal bristle tail extending to mid-body; left three brush rows distinctly longer than others (Fig. 79a, g, h, r, s; 332a, b; Table 64). No second brush in mid-body of dorsal side, as described by GELEI (1934).

Oral apparatus occupies entire body length and curves around posterior end onto dorsal side for an average of 40 µm in protargol preparations (Table 64). Oral bulge about 10 µm high and 5 µm wide anteriorly, glossy due to the many extrusomes contained, and thus very distinct in vivo; becomes narrower posteriorly. Circumoral kinety at base of oral bulge, very elongate elliptical, composed of closely spaced dikinetids each associated with a cilium and a nematodesma decreasing in length from anterior to posterior; cilia so closely spaced that a membranoid structure is formed, especially in anterior body half, where the nematodesmata are long and form distinct bundles (Fig. 79a, d–h, s; 332a, c).

Occurrence and ecology: To date found at type location and in a soil sample from the Cape Peninsula, Republic of South Africa, indicating that it is a true terrestrial species. It was rare in the non-flooded Petri dish cultures from both sites.

Comparison with related species (see "Remarks" by → *B. lingua* above) and nominal subspecies: At first glance, *Bryophyllum lingua multistriatum* looks like a distinct species. However, a more detailed analysis shows transitions to *B. lingua lingua* in size and shape (Fig. 79k, t) and number of macronuclear nodules (about 50 according to GELEI, which matches the lower limit of our specimens). Thus, only one firm feature remains, viz., the number of ciliary rows (16–18 vs. 33–50). This matches the narrower length:width

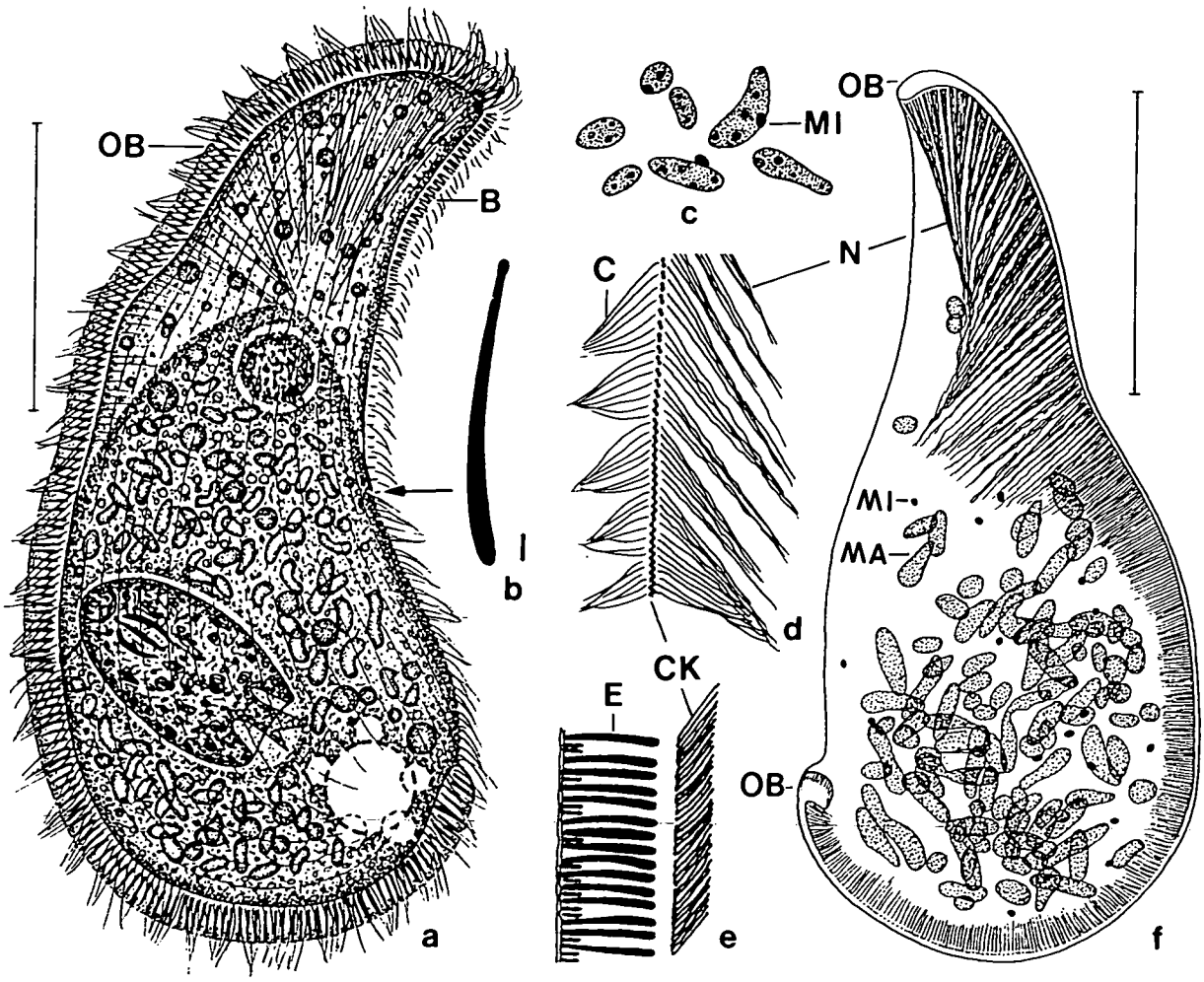

Fig. 79a–f. *Bryophyllum lingua multistriatum* from life (a, b, e) and after protargol impregnation (c, d, f). **a:** Left side view of a representative specimen having ingested a rotifer (redrawn from video records). Arrow marks end of monokinetidal bristle tail of last dorsal brush row. **b:** Type I (length 8 µm) and type II (1.5 µm) extrusomes, drawn to scale. **c:** Part of nuclear apparatus. **d:** Structure of circumoral kinety. **e:** Part of oral bulge packed with extrusomes and bordered on left by the circumoral kinety, whose very closely spaced cilia form a membranoid structure. **f:** Nuclear and nematodesmal apparatus of the specimen shown in figures 79g, h. This specimen has 113 macronuclear nodules and several micronuclei. The nematodesmata form a conspicuous basket, especially in anterior body half. B – dorsal brush, C – cilia, CK – circumoral kinety, E – extrusomes, MA – macronuclear nodules, MI – micronuclei, N – nematodesmata, OB – oral bulge. Scale bars 70 µm.

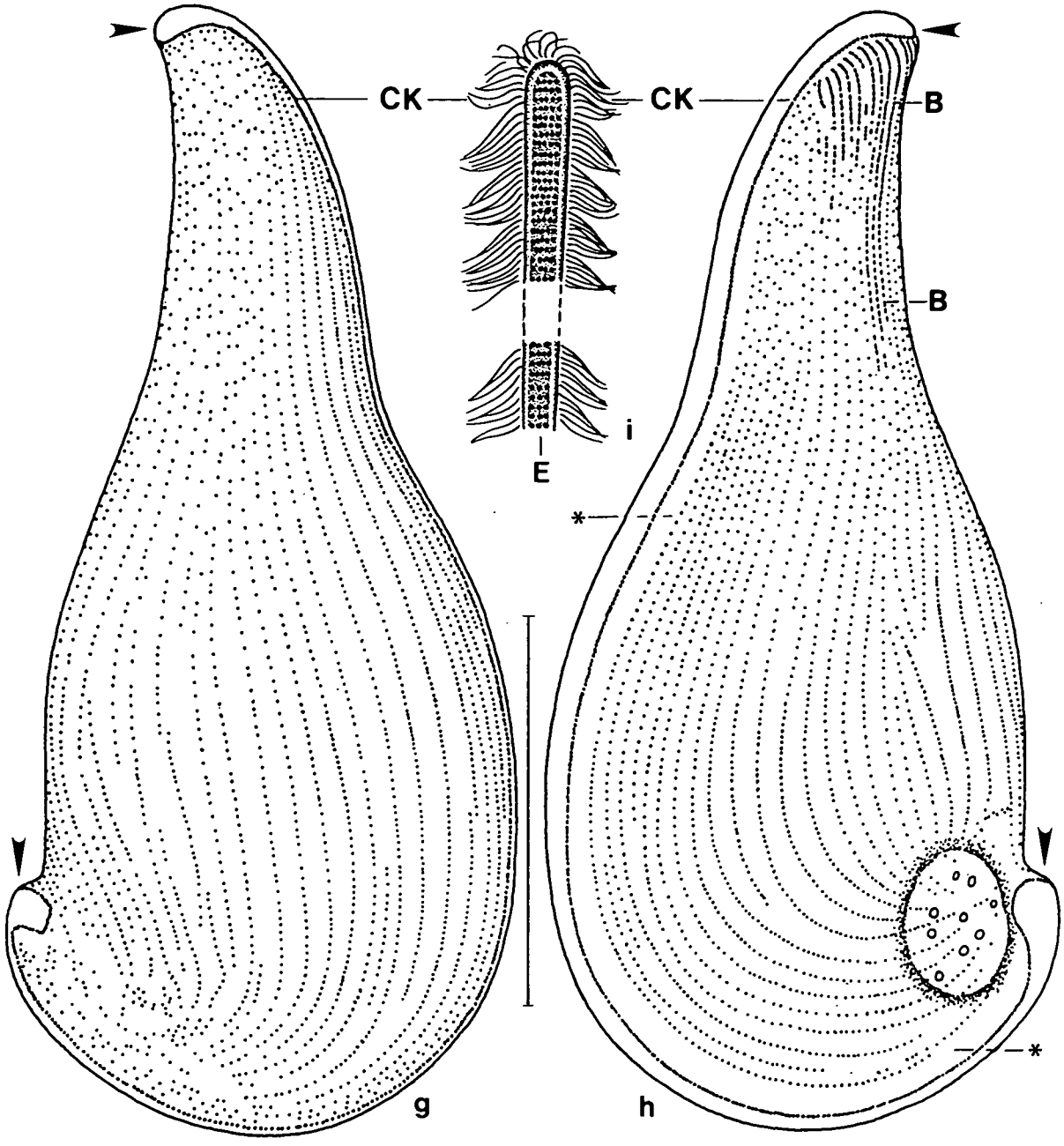

Fig. 79g–i. *Bryophyllum lingua multistriatum* from life (i) and after protargol impregnation (g, h). **g, h:** Ciliary pattern of right and left side of holotype specimen. The nuclear and nematodesmal apparatus are shown in figure 79f, and a detail of the dorsal brush (B) is depicted in figure 79s. The asterisks mark a blank stripe left of the circumoral kinety. Arrowheads denote anterior and posterior end of oral bulge. **i:** Frontal view of oral bulge at anterior end and in posterior region. The extrusomes form short, transverse rows (cp. figures 79b, e). B – dorsal brush, CK – circumoral kinety, E – extrusomes. Scale bar 70 µm.

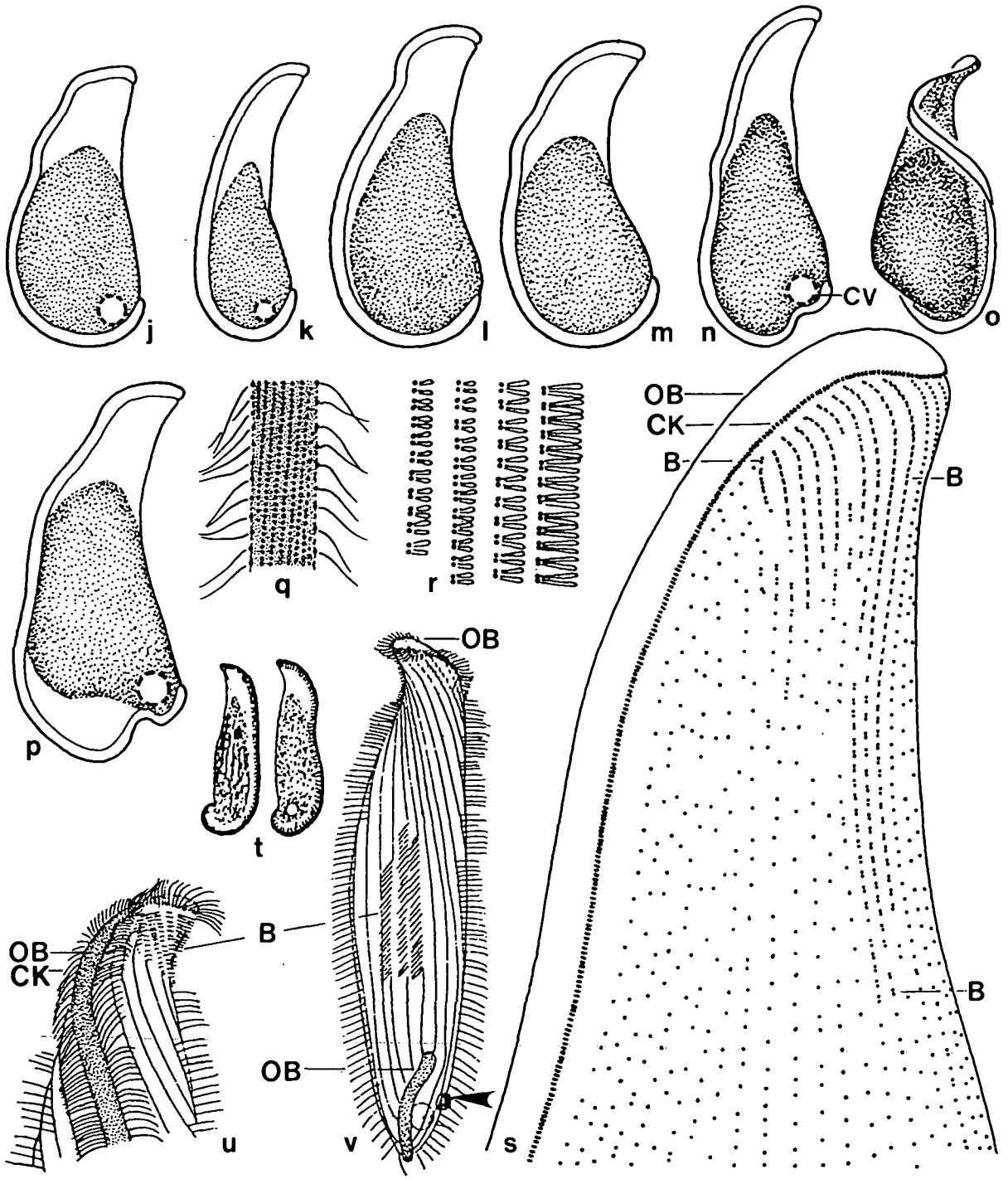

Fig. 79j–s. *Bryophyllum lingua multistriatum* from life (j–r) and after protargol impregnation (s). **j–p:** Left side views (j–n, p) and ventral view (o) of several specimens (redrawn from video records). Figures (l, m) show different aspects of the same specimen. **q:** Surface view showing rows of minute, cortical granules. **r:** Structure of the four last dorsal brush rows, longest bristles 5 µm. **s:** Dorsal brush area of holotype specimen shown in figures 79g, h; the specimen has 10 brush rows.

Fig. 79t–v. *Bryophyllum lingua lingua* from life (t; length 160 and 200 µm) and after mercuric chloride fixation (u, v). Arrowhead marks cytopyge. From GELEI (1934).

B – dorsal brush, CK – circumoral kinety, CV – contractile vacuole, OB – oral bulge.

ratio (4:1 vs. 2.5:1) making, on average, *B. lingua multistriatum* distinctly broader than *B. lingua lingua*. On the other hand, GELEI (1934) observed only two, possibly under-developed specimens. Thus, little is known about variability, although the low number of ciliary rows strongly suggests that *B. lingua lingua* is indeed more slender than *B. lingua multistriatum*. Considering this incomplete knowledge and the similarities mentioned above, subspecies than species rank is likely appropriate for our population.

Table 64. Morphometric data on *Bryophyllum lingua multistriatum*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	187.3	188.0	20.8	6.0	11.1	160.0	220.0	12
Body, width	77.9	77.0	17.3	5.0	22.2	51.0	115.0	12
Body length:width, ratio	2.5	2.5	0.5	0.1	19.0	1.6	3.5	12
Anterior body end to end of longest dorsal brush row, distance	45.6	45.0	9.3	3.1	20.4	35.0	60.0	9
Posterior body end to dorsal end of oral bulge, distance	40.5	40.0	5.9	1.9	14.6	32.0	50.0	10
Macronuclear nodules, length	12.6	11.5	4.5	1.3	35.6	5.0	20.0	12
Macronuclear nodules, width	5.7	6.0	1.2	0.3	20.4	4.0	8.0	12
Macronuclear nodules, number (approximate)	78.5	77.5	–	–	–	50.0	130.0	10
Ciliary rows, number (approximate)	39.9	37.5	–	–	–	33.0	50.0	10
Dorsal brush rows, number	9.2	9.0	1.3	0.4	13.6	7.0	11.0	11
Dikinetids in last brush row, number (approximate)	51.2	50.0	–	–	–	40.0	65.0	5

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Bryophyllum penardi KAHL, 1931 (Fig. 80a–v; 318i, j, 333i; Table 65)

1922 *Loxophyllum armatum* CLAP. et LACHM. 1859 — PENARD, Infusoires, p. 74.
1931 *Bryophyllum penardi* KAHL, Tierwelt Dtl., 21: 185.
1934 *Bryophyllum spathidioides* GELEI, Arch. Protistenk., 81: 206 (new synonym).

Synonymy: KAHL (1931b) recognized that PENARD's species is different from *Loxophyllum armatum* CLAPARÈDE & LACHMANN, 1859, and thus described it as a species novum, *Bryophyllum penardi*. We agree. However, KAHL (1931b) also mentioned that *B. penardi* is rather similar to *B. tegularum*, which he established in the same paper, differing mainly by the left side, which is barren in *B. penardi* and ciliated in *B. tegularum*. GELEI (1934) described *B. spathidioides*, but mentioned that it is so similar to *B. penardi* that "ich die Art überhaupt als provisorisch betrachten möchte". Indeed, the six distinguishing features provided by GELEI are indistinct or highly variable, according to our data, except of the ciliated/unciliated left side (see above). However, it is now clear that all *Bryophyllum* species

have both sides ciliated and PENARD's statement likely was influenced by the generic misplacement, viz., *Loxodes*, whose left side indeed lacks ordinary cilia. Likewise, the second, subequatorial dorsal brush described by GELEI (1934) in his four *Bryophyllum* species must be a misobservation because we did not find it in the four species we investigated (this paper and FOISSNER 1984).

Accordingly, the present state of knowledge can be summarized as follows: *Bryophyllum penardi*, *B. tegularum*, and *B. spathidioides* cannot be distinguished by their original descriptions, if the pronounced variability the species of this genus have is taken into account (see descriptions in this book). However, if our identification and neotypification is accepted, *Bryophyllum tegularum* and *B. penardi* are distinct species differing in an important feature, viz., the number of dorsal brush rows: three vs. six to eight. By contrast, reliable distinguishing features are lacking in *B. penardi* and *B. spathidioides*, suggesting synonymy.

Neotype material: Neotypified from Madagascan population, according to reasons 1–4, 6 in chapter 2.4.2.

Improved diagnosis: Size about 140 × 45 µm in vivo; slenderly to broadly lanceolate with posterior end of oral bulge in last dorsal sixth of cell and distinctly set off from body proper. Macronucleus about 100 µm long and more or less tortuous. Two types of scattered extrusomes: type I acicular and about 6 × 0.8 µm in size; type II rod-shaped and 1.5 µm long. On average 23 ciliary rows, about 6 of them anteriorly differentiated to dorsal brush.

Description of Madagascan neotype population (Fig. 80a–g, n–t; 318i, j): Size 100–160 × 30–70 µm in vivo, usually near 140 × 45 µm, prepared cells rather strongly shrunken (Table 65); length:width ratio highly variable, viz. 1.5–4.1, on average 2.9:1 in protargol preparations; highly flexible, but not contractile. Shape as typical for genus, but rather variable, that is, slenderly to broadly lanceolate depending on food supply, frequently *Trithigmostoma*-like, but with beak dorsally; anterior quarter and ventral cell margin leaf-like flattened and thus hyaline, central and posterior region usually dark at low magnification (≤ ×100) and only slightly flattened because packed with food inclusions (Fig. 80a–d, n, s). Nuclear apparatus in middle body third. Macronucleus on average about 100 µm long and more or less distinctly C-shaped or tortuous, contains many small, globular nucleoli. Micronucleus attached or near macronucleus in variable positions, discoidal. Contractile vacuole with about 15 excretory pores subterminal near left dorsal margin of cell. Two types of extrusomes scattered in oral bulge and cytoplasm, do not impregnate with the protargol method used (Fig. 80a, g, p–r; 318i, j): type I conspicuous because acicular and about 6 × 0.8 µm in size, produces distinct ventral fringe; type II very inconspicuous, rod-shaped, fine, about 1.5 µm long. Cortex highly flexible, contains about 10 rows of minute (0.3 µm) granules between each two kineties; rows oblique and composed of slightly larger granules in oral bulge cortex (Fig. 80e, f). Cytoplasm colourless, in well-fed specimens packed with fat globules up to 10 µm across and food vacuoles containing flagellates (*Peranema*), ciliates, and rotifers (Fig. 80a). Glides slowly on microscope slide and debris showing great flexibility.

Cilia about 8 µm long in vivo, rather loosely spaced in anterior and posterior region of cell, leaving blank a small area along left posterior portion of oral bulge, arranged in an average of 23 rows following body curvature and abutting to both halves of circumoral kinety anteriorly and posteriorly; some rows interrupted and/or shortened anteriorly and/or posteriorly without any regularity. On average six left side kineties anteriorly differentiated to inconspicuous dorsal

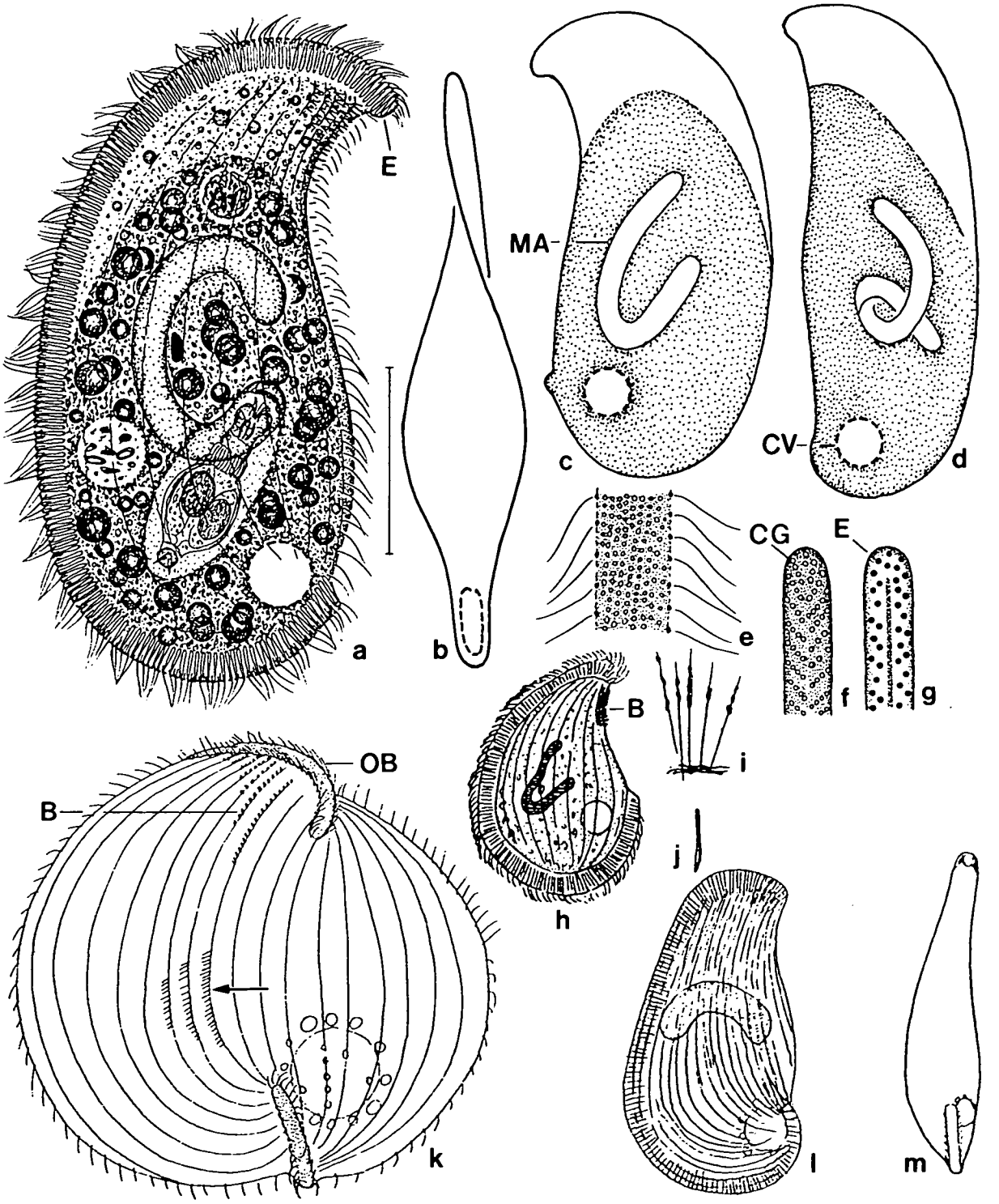

Fig. 80a–m. *Bryophyllum penardi*, Madagascan neotype population (a–g), PENARD's (1922) type population (h–j), and the presumed junior synonym, *B. spathidioides* GELEI (k–m) from life (a–j, l, m) and after Toluidin blue staining (k). **a, b:** Left side and ventral view of a well-fed specimen. Scale bar 40 µm. **c, d:** Ordinary and slender specimen. **e:** Cortical granulation. **f, g:** Anterior region of oral bulge showing bulge granulation and, at a slightly deeper focal plane, the extrusomes. **h–j:** PENARD's figures, left side view (h; length 100–150 µm) and extrusomes. **k–m:** Dorsal (k, m) and left side views. B – dorsal brush, CG – cortical granules, CV – contractile vacuole, E – extrusomes, MA – macronucleus, OB – oral bulge.

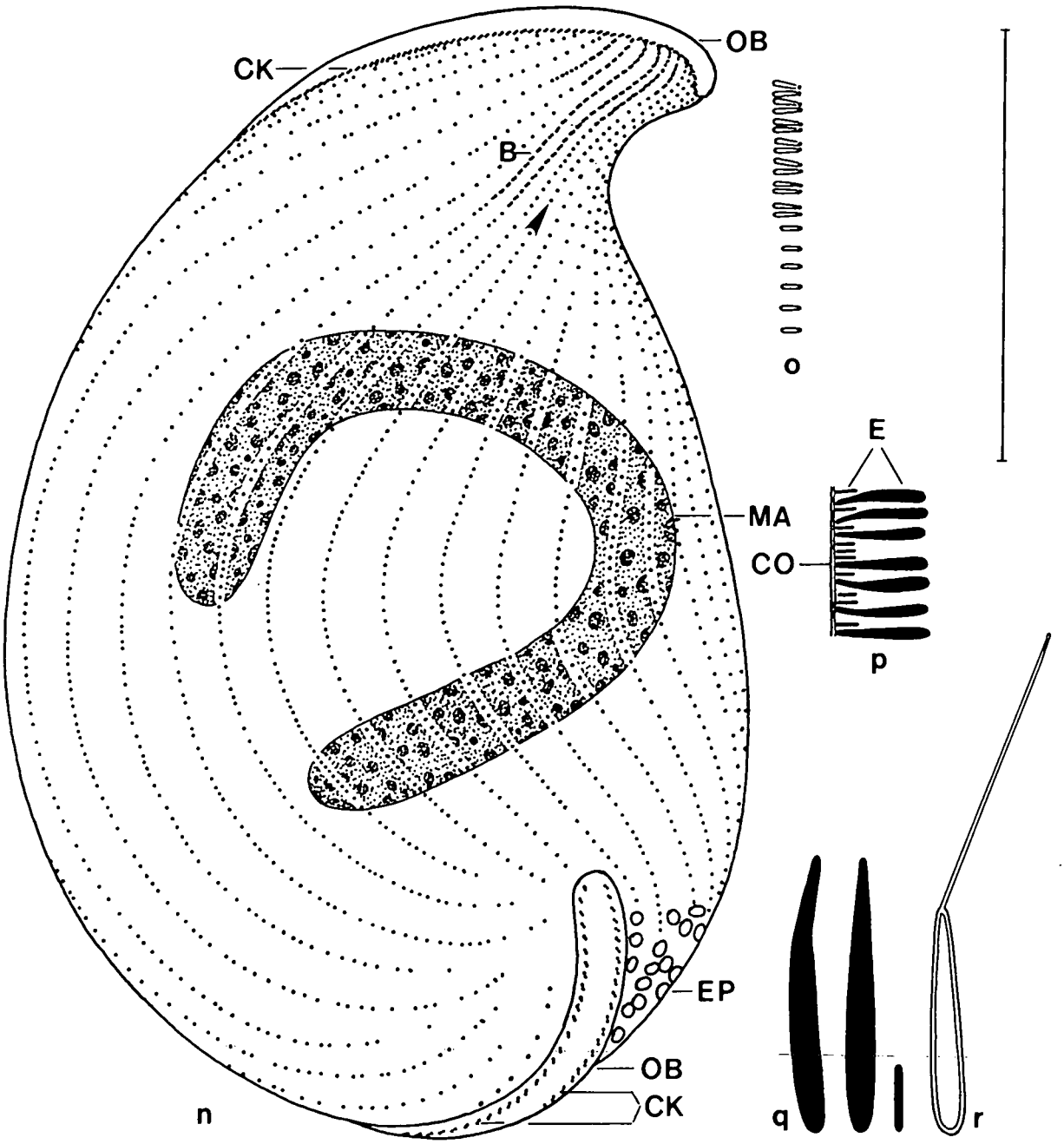

Fig. 80n–r. *Bryophyllum penardi*, Madagascan neotype population from life (o–r) and after protargol impregnation (n). **n, o:** Oral and somatic ciliary pattern of left dorsal side and nuclear apparatus of a broad specimen. The dorsal brush (B) consists of six rows of narrowly spaced dikinetids with about 3 µm long, slightly inflated bristles; the last row (n, arrowhead) has a monokinetidal bristle tail extending to mid-body (o). Note the loosened ciliature left of the anterior and posterior end of the circumoral kinety, which is composed of basal body pairs more narrowly spaced anteriorly than posteriorly. Scale bar 40 µm. **p, q:** Arrangement and shape of type I and type II extrusomes in oral bulge, where they produce a conspicuous fringe (Fig. 80a). Type I extrusomes, which have a size of about 6 × 0.8 µm, are acicular and slightly asymmetrical. Type II extrusomes are 1.5 µm long, inconspicuous rods. **r:** Exploded type I extrusome showing typical toxicyst structure, length about 15 µm. B – dorsal brush, CK – circumoral kinety, CO – oral bulge cortex, E – type I and type II extrusomes, EP – excretory pores of contractile vacuole, MA – macronucleus, OB – oral bulge.

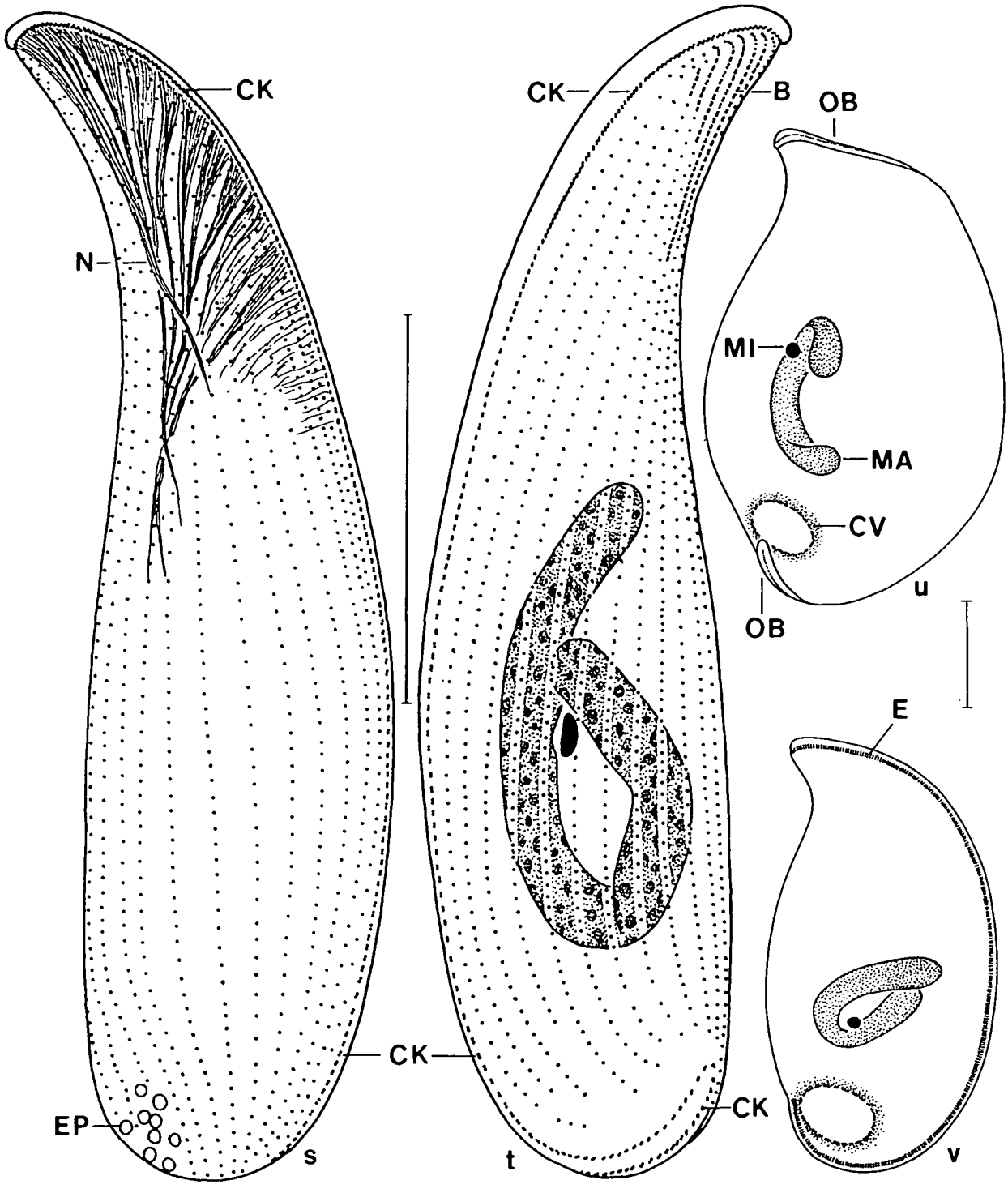

Fig. 80s–v. *Bryophyllum penardi*, Madagascan (s, t) and Namibian site 49 (u, v) specimens after protargol impregnation. **s, t:** Ciliary pattern of right and left side and nuclear apparatus of a slender specimen. Nematodesmata (N) shown only in right side view. The dorsal brush (B) consists of six rows of dikinetids. **u, v:** A broad and ordinary shape variant of the Namibian population. The short extrusomes (E) impregnated strongly and form a distinct, black stripe in the oral bulge. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuole, E – extrusome fringe, EP – excretory pores of contractile vacuole, MA – macronucleus, MI – micronucleus, N – nematodesmata (oral basket rods), OB – oral bulge. Scale bars 40 μm.

brush composed of narrowly spaced dikinetids bearing slightly inflated, 2–3 µm long bristles; kineties increase in length from right to left, and the last row has a monokinetidal bristle tail extending to mid-body (Fig. 80a, n, s, t; Table 65). We did not find any ciliary specialisations in mid-body, as described by GELEI (1934).

Oral apparatus occupies entire body length and curves around posterior end onto dorsal side for an average of 18 µm in protargol preparations (Table 65). Oral bulge rather flat, but about 10 µm wide anteriorly and 5 µm posteriorly, glossy due to the many extrusomes contained, and thus conspicuous in vivo. Circumoral kinety at base of oral bulge, very elongate cuneate, composed of dikinetids each associated with a cilium and a nematodesma decreasing in length from anterior to posterior; dikinetids so closely spaced in anterior body half that their cilia form a membranoid structure. Oral basket rods distinct only in anterior body third, where they form long bundles (Fig. 80a, f, g, n, p, s–v; Table 65).

Namibian population (Fig. 80u, v; 333i; Table 65): The Namibian site (49) specimens were also studied in detail and analyzed morphometrically. The general organization and the ciliary pattern are very similar to the Madagascan specimens, and are thus not shown. However, the Namibian specimens are considerably larger and broader than those from Madagascar, and thus have more ciliary and dorsal brush rows. Some additional observations from protargol-impregnated specimens: (i) Shape rather constant, flattened ventral margin without undulations; (ii) The short type II extrusomes impregnate heavily, producing a conspicuous black stripe in the oral bulge (Fig. 80v; 333i); (iii) Feeds mainly on the ciliate *Epistylis alpestris*; (iv) Oral bulge very flat, that is, only ~ 2 µm high; (v) Circumoral cilia about 15 µm long.

Occurrence and ecology: PENARD (1922) discovered this species in a Swiss *Sphagnum* pond, and described in detail the ingestion of a rotifer. GELEI (1934) found only few specimens of *B. spathidioides* in a eutrophic pond in Hungary; in the laboratory aquarium, they survived at 27–29° C, but obviously did not, or only slowly reproduce. We found *B. penardi* in Madagascar (Nosy Be Island, brown leaves from a streamlet in the rain forest, pH 6.1; sample kindly provided by Gerd STEINBERG, Kiel, in 1988) and at Namibian site (49), that is, in the mud of astatic pools. These records show that *B. penardi* likely is a limnetic cosmopolitan, possibly preying mainly rotifers and ciliates.

Identification and comparison with related species: The Madagascan neotype matches PENARD's original description almost perfectly, even in the size and shape of the extrusomes ("Trichocystes 6 µm et sont en forme de baguettes courtes, très légèrement recourbées."), hardly leaving any doubt about conspecificity; only the oral bulge is slightly shorter dorsally which is, however, of minor importance because it is a highly variable feature (~ 30%, Table 65). Likewise, our specimens match *B. spathidioides* GELEI (1934), especially those from Namibia, which are considerably larger than those from Madagascar, and thus have slightly more ciliary and dorsal brush rows (Table 65). However, size is highly variable in *Bryophyllum* and thus of minor importance.
Bryophyllum penardi is highly similar to *B. tegularum* KAHL, 1931b, as redescribed by FRYD-VERSAVEL et al. (1975) and FOISSNER (1984), except of the dorsal brush, which comprises six to eight rows in the former and three rows in the latter, an important difference, as explained above. Further, the macronucleus is nodulated only in *B. tegularum*. → *Bryophyllum paucistriatum* is, on average, distinctly smaller than *B. penardi* and thus has much fewer kineties (11–15 vs. 23–28 in two populations each) and dorsal brush rows (4–6 vs. 5–11).

Further, the oral bulge extrusomes are rod-shaped to slightly acicular and arranged in distinct rows in *B. paucistriatum*, while conspicuously acicular and scattered in *B. penardi*. Accordingly, only extreme specimens might pose identification problems.

DRAGESCO & DRAGESCO-KERNÉIS (1986) described a "*Bryophyllum spathidioides* GELEI, 1933" from a pond near Cotonou, Benin (Africa). With a length of 180–220 µm and a boomerang-shaped macronucleus, it is obviously very similar to our Namibian population. Unfortunately, DRAGESCO & DRAGESCO-KERNÉIS (1986) do not provide details on the ciliary pattern and extrusomes, but mention that the ciliate highly resembles *B. penardi* and the identification as *B. spathidioides* is provisional.

Table 65. Morphometric data on *Bryophyllum penardi* from Madagascar (upper line) and Namibian site 49 (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length [b]	117.6	120.0	13.0	3.9	11.0	92.0	140.0	11
	165.9	170.0	29.3	8.1	17.7	123.0	210.0	13
Body, width [b]	44.6	37.0	15.3	4.6	34.4	30.0	70.0	11
	97.2	95.0	16.3	4.5	16.8	68.0	122.0	13
Body length:width, ratio	2.9	2.6	1.0	0.3	34.9	1.5	4.1	11
	1.7	1.7	0.2	0.1	11.3	1.4	2.1	13
Posterior body end to dorsal end of oral bulge, distance	18.5	17.0	5.2	1.6	28.1	12.0	28.0	11
	22.5	20.0	6.9	1.9	30.5	15.0	40.0	13
Anterior body end to end of longest dorsal brush row,	27.2	27.0	3.3	1.0	12.3	22.0	32.0	11
distance	31.3	30.0	5.1	1.3	16.2	25.0	42.0	15
Oral bulge, height	2.0	2.0	–	–	–	1.5	2.5	10
	1.9	2.0	–	–	–	1.0	2.0	13
Macronucleus, length (spread; values thus approximate)	82.7	90.0	–	–	–	50.0	120.0	11
	88.9	90.0	–	–	–	55.0	140.0	13
Macronucleus, width	7.4	7.0	1.0	0.3	14.0	6.0	9.0	11
	11.9	12.0	1.1	0.3	9.7	10.0	14.0	13
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13
Micronucleus, length	4.8	5.0	–	–	–	4.0	5.0	8
	6.1	6.0	1.5	0.4	24.6	4.5	10.0	13
Micronucleus, width	2.5	2.5	–	–	–	2.0	3.0	8
	5.4	5.0	1.8	0.5	34.2	4.0	10.0	13
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	9
	1.2	1.0	–	–	–	1.0	1.0	13
Somatic kineties, total number	23.2	24.0	2.1	0.6	9.0	20.0	26.0	11
	27.7	28.0	2.2	0.6	7.8	24.0	32.0	15
Dorsal brush rows, number	6.1	6.0	0.8	0.3	13.7	5.0	8.0	11
	8.3	8.0	1.0	0.3	11.6	7.0	11.0	15

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Madagascan specimens more distinctly shrunken (~ 20%) than Namibian ones (~ 10%).

Apobryophyllum vermiforme nov. spec. (Fig. 81a–o; Table 66)

Diagnosis: Size about 220 × 20 µm in vivo; narrowly lanceolate to linear. Macronucleus filiform and indistinctly nodulated, about 100 µm long. Micronuclei conspicuously slender, viz., 5 × 1 µm on average. Extrusomes rod-shaped and very fine, about 5 × 0.2 µm. On average 9 ciliary rows (including circumoral kinety), those on left and dorsal side anteriorly differentiated to complex, three-rowed brush.

Type location: Highly saline terrestrial material from the dry bed of the Löwen River about 100 m downstream the Nautedam, Namibia, 26°55'S 17°55'E (site 8 in figure 2 and chapter 2.1.2).

Etymology: The Latin adjective *vermiforme* (worm-like) refers to the slender shape.

Description: Protargol impregnation did not work well, and thus the type slides are mediocre. Indeed, they look unusable at first glance because they are rather opaque and dark due to the cortical granules, which impregnated heavily. However, closer inspection reveals that the cilia are well-impregnated and show details of the dorsal brush with perfect clarity.

Size about 130–310 × 10–30 µm in vivo, usually about 220 × 20 µm, as calculated from measurements of live specimens and values shown in table 66, smallest cells might be post-dividers; length:width ratio 6.8–19.3:1, on average near 11:1 both in vivo and protargol preparations; slightly to up to 3:1 flattened laterally and then often sigmoidally twisted about main body axis; very flexible, but acontractile. Outline narrowly lanceolate to linear, anterior ventral side curved dorsally and bluntly pointed, posterior end narrowly rounded, usually widest in mid-body (Fig. 81a, e–g, m–o). Macronucleus in central body portion, about 100 µm long and indistinctly moniliform, somewhat tortuous in one third of specimens; nucleoli globular to lobate, depending on specimen. Micronuclei along and near macronuclear strand, about 5 × 1 µm and thus conspicuously slender showing a variety of shapes, viz., fusiform, lanceolate, or elongate ellipsoidal (Fig. 81a, i, n). Contractile vacuole in posterior body end, excretory pores not recognizable in the preparations. Extrusomes about 5 × 0.2 µm, that is, very fine, recognizable only under interference contrast illumination in strongly flattened specimens; thus, and because they did not impregnate with the protargol method used, we could not recognize their location, except in the anterior portion of the oral bulge; the great number indicates that they might be arranged as in → *A. etoschense*; released extrusomes about 10 µm long and of typical toxicyst structure (Fig. 81a, b, h). Cortex very flexible, contains innumerable, 0.3 µm-sized granules in closely spaced rows, which usually impregnate with protargol. Cytoplasm colourless, contains few to many fat globules 3–5 µm across. Creeps slowly, winding like a nematode.

Cilia 8–9 µm long in vivo, arranged in an average of seven equidistant, loosely ciliated rows plus the right and left branch of the circumoral kinety, which are indistinguishable from ordinary ciliary rows in mid-body. Dorsal brush at anterior end of three dorsal and left lateral kineties, short, composed of pairs of bristles somewhat inflated distally, anterior bristles of rows 1 and 2 slightly longer than posterior ones. Brush row 1 composed of 2–3 µm long bristles interspersed between ordinary somatic cilia, a specific feature also found in → *A. etoschense*. Brush row 2 slightly longer than rows 1 and 3, composed of up to 6 µm long bristles decreasing in length anteriorly and posteriorly. Brush row 3 similar as row 2, but with

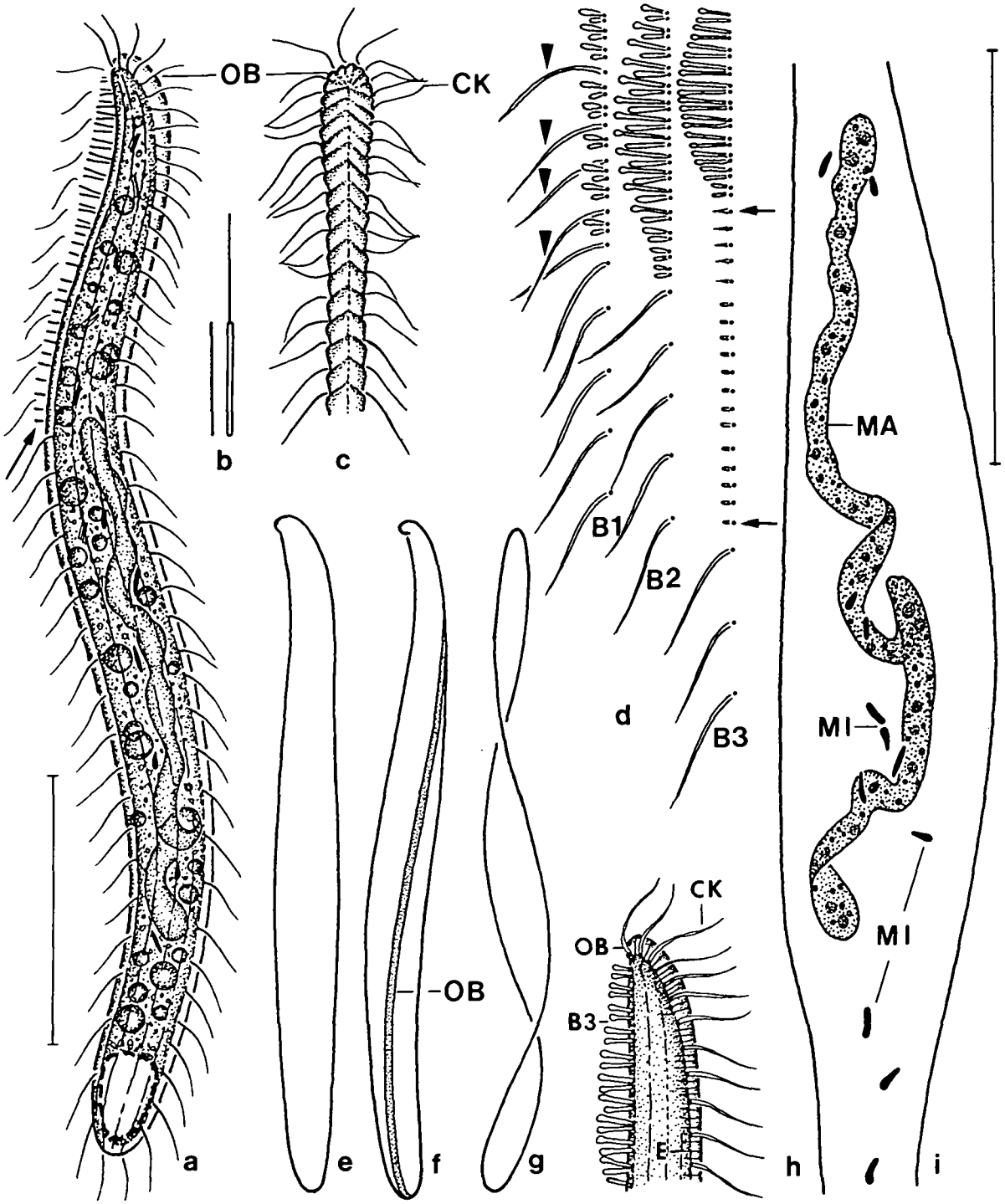

Fig. 81a–i. *Apobryophyllum vermiforme* from life (a–h) and after protargol impregnation (i). **a:** Right side view of a representative specimen. Arrow marks end of monokinetidal bristle tail of brush row 3. Extrusomes too fine to recognize at this magnification. **b:** Resting and exploded toxicyst; length 5 µm and 10 µm. **c:** Frontal view of anterior portion of oral bulge. **d:** Fine structure of dorsal brush, cilia drawn to scale. Arrowheads mark ordinary cilia between bristle dikinetids in row 1; arrows denote monokinetidal tail of row 3. **e, f:** Right side and ventral view of shape variant. **g:** A strongly flattened, twisted specimen. **h:** Right side view of anterior body portion. **i:** Nuclear apparatus. Note the slender micronuclei, B1-3 – dorsal brush rows, CK – circumoral kinety, MA – macronucleus, MI – micronuclei, OB – oral bulge. Scale bars 50 µm.

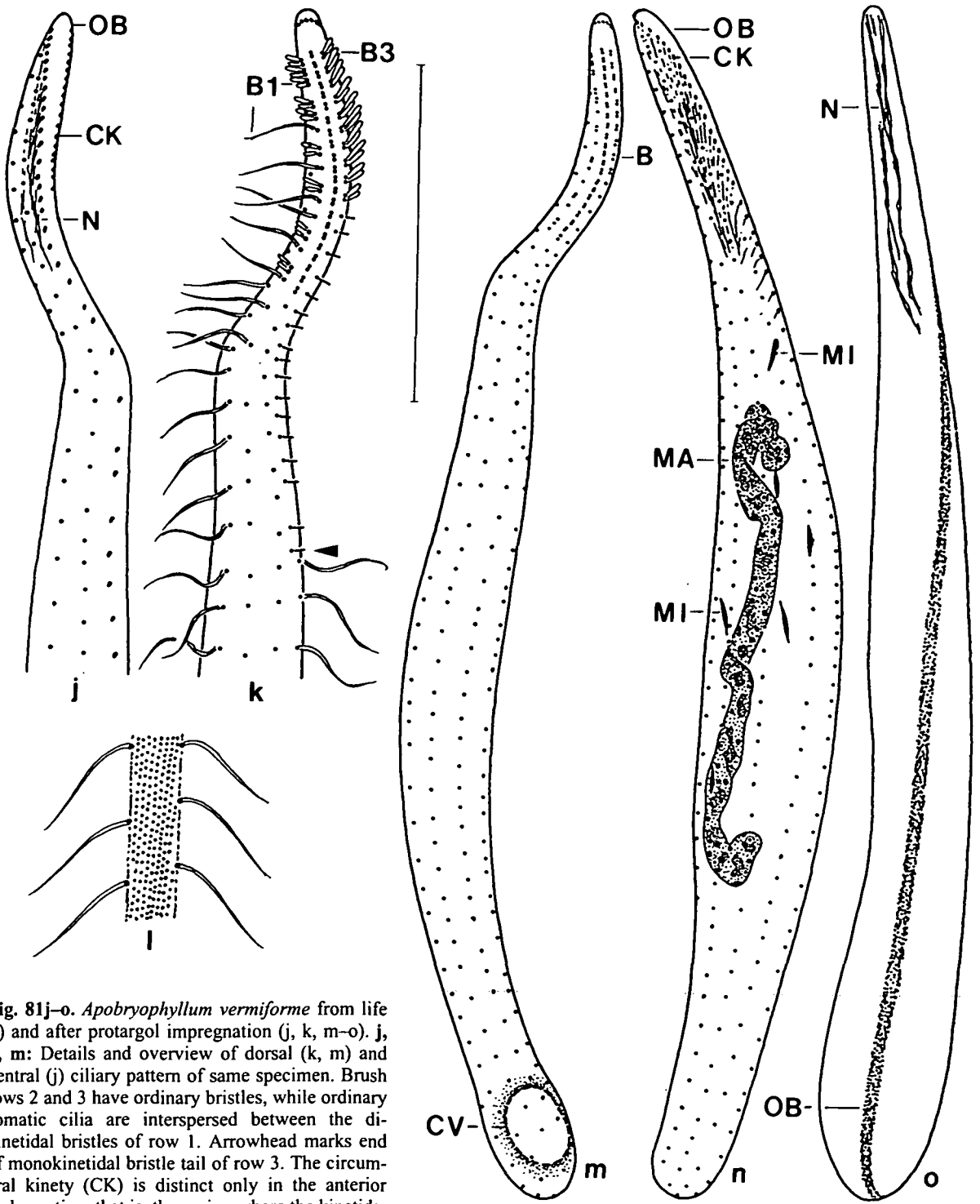

Fig. 81j–o. *Apobryophyllum vermiforme* from life (l) and after protargol impregnation (j, k, m–o). **j, k, m:** Details and overview of dorsal (k, m) and ventral (j) ciliary pattern of same specimen. Brush rows 2 and 3 have ordinary bristles, while ordinary somatic cilia are interspersed between the dikinetidal bristles of row 1. Arrowhead marks end of monokinetidal bristle tail of row 3. The circumoral kinety (CK) is distinct only in the anterior body portion, that is, the region where the kinetids are associated with fine nematodesmata. **l:** Surface view showing cortical granulation. **n:** Ciliary pattern of right side. **o:** A specimen in which the cortical granules of the oral bulge impregnated selectively. B – dorsal brush, B1–3 – dorsal brush rows, CK – circumoral kinety, MA – macronucleus, MI – micronuclei, N – nematodesmata, OB – oral bulge. Scale bar 50 µm (m, o).

a monokinetidal bristle tail extending to second third of cell (Fig. 81a, d, h, k, m; Table 66).

Oral bulge extends on whole ventral surface, hardly set off from body proper, in vivo distinct only in anterior third of cell, in protargol preparations occasionally rather conspicuous because the cortical bulge granules impregnate somewhat differently (Fig. 81o); about 5 µm high and wide anteriorly, decreasing to 2–3 µm posteriorly; bulge surface arrowhead-like patterned (Fig. 81a, c, f, h). Circumoral dikinetids comparatively widely spaced, even in anterior body third, each kinetid associated with an about 9 µm long cilium and a fine nematodesma recognizable only in anterior body portion; oral basket thus inconspicuous and visible only in protargol preparations (Fig. 81j, k, n, o).

Occurrence and ecology: To date found only at type location, where it was rather numerous, but disappeared after collecting the soil percolate for protargol preparation. As this is a dry river bed, we cannot decide whether *A. vermiforme* is a terrestrial or limnetic species. As yet, we found ciliates of this type only in soils from Kenya and Namibia, which indicates a restricted geographic distribution.

Table 66. Morphometric data on *Apobryophyllum vermiforme*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length in vivo	214.3	230.0	23.0	8.7	10.7	170.0	230.0	7
Body, width in vivo	19.0	20.0	2.5	1.0	13.2	15.0	22.0	7
Body length:width, ratio in vivo	11.4	11.5	1.6	0.6	14.2	8.5	13.3	7
Body, length	213.4	210.0	48.4	10.1	22.7	125.0	305.0	23
Body, width	19.4	20.0	4.3	0.9	22.4	10.0	27.0	23
Body length:width, ratio	11.4	10.9	3.2	0.7	28.4	6.8	19.3	23
Anterior body end to macronucleus, distance	68.8	67.0	16.3	3.4	23.6	40.0	112.0	23
Anterior body end to end of brush row 3, distance	29.7	30.0	6.4	1.3	21.6	20.0	43.0	23
Nuclear figure, length	99.5	95.0	32.5	6.8	32.6	49.0	180.0	23
Macronucleus, width	4.4	4.0	0.8	0.2	19.1	3.0	6.0	23
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	23
Micronuclei, length	4.7	5.0	1.0	0.2	22.1	3.0	7.0	23
Micronuclei, width	0.9	1.0	–	–	–	0.7	1.0	23
Micronuclei, number	8.6	8.0	2.7	0.6	31.9	3.0	15.0	23
Ciliary rows in mid-body, number [b]	9.2	9.0	0.7	0.1	7.3	8.0	10.0	23
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	23

[a] Data based, if not otherwise stated, on mounted, protargol-impregnated (FOISSNER's method), and selected (obviously inflated cells excluded) specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Including circumoral kinety, which is indistinguishable from ordinary ciliary rows in mid-body.

Comparison with related species: *Apobryophyllum vermiforme* is a distinct species easily distinguished from → *A. etoschense* FOISSNER, 1998b (size 220 × 20 µm vs. 130 × 30 µm; macronucleus filiform vs. reniform; extrusomes conspicuous vs. almost invisible; 16 vs. 9 ciliary rows) and *A. terricola* FOISSNER, 1998a (size 220 × 20 µm vs. 160 ×

25 µm; extrusomes rather distinct vs. almost invisible; micronuclei slender vs. globular; 16 vs. 9 ciliary rows; three vs. four brush kineties, with rightmost brush row(s) of different fine structure).

However, there is another terricolous ciliate, viz. *Arcuospathidium vlassaki* FOISSNER, 2000d, which highly resembles *A. vermiforme* in body size and shape, number of ciliary rows, and structure of the nuclear apparatus, including the slender micronuclei. Fortunately, *A. vlassaki* has conspicuous, oblanceolate extrusomes, and can thus be distinguished from *A. vermiforme* even in vivo; in protargol preparations, the different shape of the circumoral kinety is a reliable marker.

Apobryophyllum etoschense FOISSNER, 1998 (Fig. 82a–o; 333a–h; Table 67)

As the original description (FOISSNER 1998b) was carelessly edited, we repeat the description.

Diagnosis: Size about 130 × 30 µm in vivo; spatulous. Macronucleus reniform. Two types of extrusomes in oral bulge and somatic cortex, where they form minute bundles arranged to about 10 distinct, longitudinal rows: type I fusiform and 5 µm long; type II rod-shaped and 3 µm long. On average 16 somatic kineties, those of left side anteriorly differentiated to complex dorsal brush.

Type location: Soil from margin (*Sporobolus* grass girdle) of Etosha Pan, Namibia, 19°S 16°E (site 60 in figures 2, 3 and chapter 2.1.2).

Etymology: Named after the area discovered.

Description: Size 100–160 × 25–45 µm in vivo, usually about 130 × 30 µm, as calculated from measurements of live specimens and values shown in table 67, assuming a shrinkage of 10–15% due to the preparation procedures; length:width ratio 3:1–6:1, on average 4.3:1. Spatulous to broadly knife-shaped, that is, anterior ventral half distinctly curved and gradually narrowing to form bluntly pointed, slightly projecting dorsal anterior end: blade flattened leaf-like and thus hyaline, slightly broadened; handle evenly rounded posteriorly and unflattened in mid-portion, cells thus fusiform in ventral and dorsal view (Fig. 82a, d, e, h, n; 333a). Macronucleus subequatorial in posterior body half, reniform in 75%, dumb-bell-shaped in 10%, spiralized in 10%, and irregular in 5% of specimens (n = 20). Several micronuclei attached to macronucleus, about 3 µm across in vivo, difficult to distinguish from globular fat inclusions in protargol preparations. Contractile vacuole in posterior end, about four excretory pores in midline of right posterior surface (Fig. 82a, e). Two types of extrusomes (type I slightly fusiform and about 5 µm long, type II rod-shaped and about 3 µm long; both impregnate with silver carbonate and protargol, but shape and size differences become indistinct) in oral bulge and somatic cortex, where they form about 10 distinct, longitudinal rows each composed of small extrusome bundles contained in minute warts (Fig. 82a, b, i, j; 333b, c, g, h); released extrusomes about 20 µm long and of typical toxicyst structure (Fig. 333c). Cortex flexible, contains about six rows of colourless granules (about 1 × 0.3 µm) between each two ciliary rows (Fig. 333o, p). Cytoplasm usually packed with colourless globular and irregular fat inclusions 1–7 µm across, which often impregnate with protargol making cells very opaque. Feeds on ciliates, e.g., *Colpoda inflata*. Glides slowly on microscope slide and soil particles.

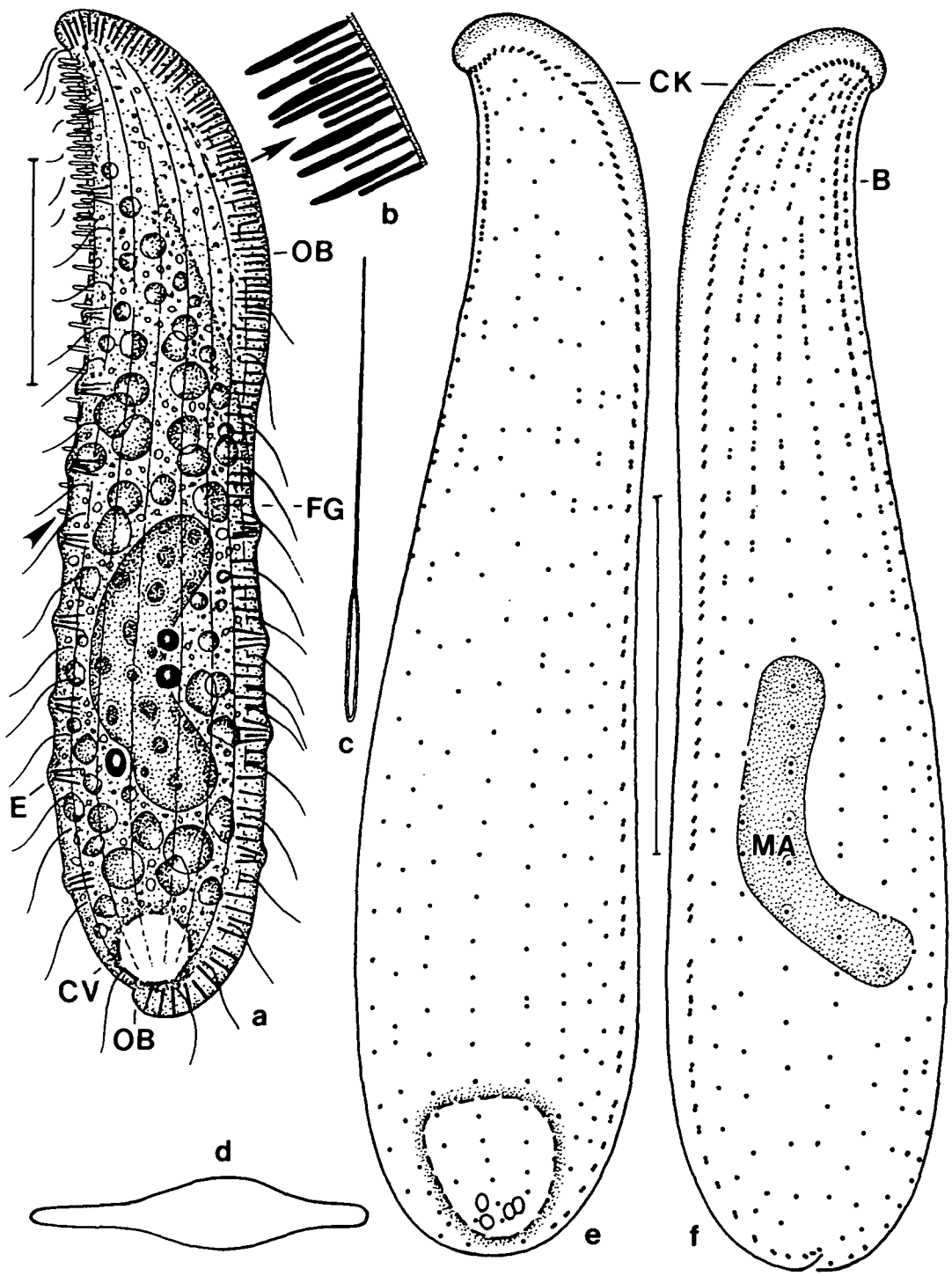

Fig. 82a–f. *Apobryophyllum etoschense* from life (a–d) and after protargol impregnation (e, f). **a:** Right lateral view of a representative specimen with many fat globules. Arrowhead marks posterior end of monokinetidal bristle tail of last dorsal brush row. **b:** Type I (5 µm) and type II (3 µm) extrusomes in oral bulge. **c:** Exploded extrusome, 20 µm. **d:** Dorsal view of a well-nourished specimen (anterior end left). **e, f:** Ciliary pattern of right and left side and nuclear apparatus of holotype specimen. OB – oral bulge, B – dorsal brush, CK – circumoral kinety, CV – contractile vacuole, E – extrusomes, FG – fat globules, MA – macronucleus. Scale bars 30 µm.

Cilia about 10 µm long, loosely spaced, especially in anterior body third, arranged in equidistant, meridional rows distinctly separate from circumoral kinety (Fig. 82a, e, f). Dorsal brush at anterior end of left lateral kineties, about as long as blade of knife (1/3 body length; Table 67), complex, that is, composed of cilia of different length (anterior cilia of dikinetids 1–2 µm, posterior 3–4 µm long) and shape (clavate or rod-shaped), as shown in figures 82k–n and 333d–f: leftmost two rows at dorsal margin of cell, of "usual" haptorid structure, last row extends with single, rod-shaped bristles to almost posterior body end; in rows 1–5, dikinetidal bristles irregularly alternate with ordinary somatic cilia; anterior basal body of dikinetids smaller than posterior (Fig. 82 l).

Oral bulge 2–3 µm thick throughout and thus inconspicuous in live specimens (Fig. 82h), hardly distinct from body proper in posterior half, extends from anterior dorsal to posterior dorsal end, where it forms a small but distinct notch filled with extrusomes (Fig. 82a, b, e, f; 333a, b, e, h). Circumoral kinety at base of oral bulge, composed of dikinetids having only one (anterior?) basal body ciliated; dikinetids associated with fine nematodesmata and more closely spaced in anterior than posterior half of kinety (Fig. 82e, f, g, k).

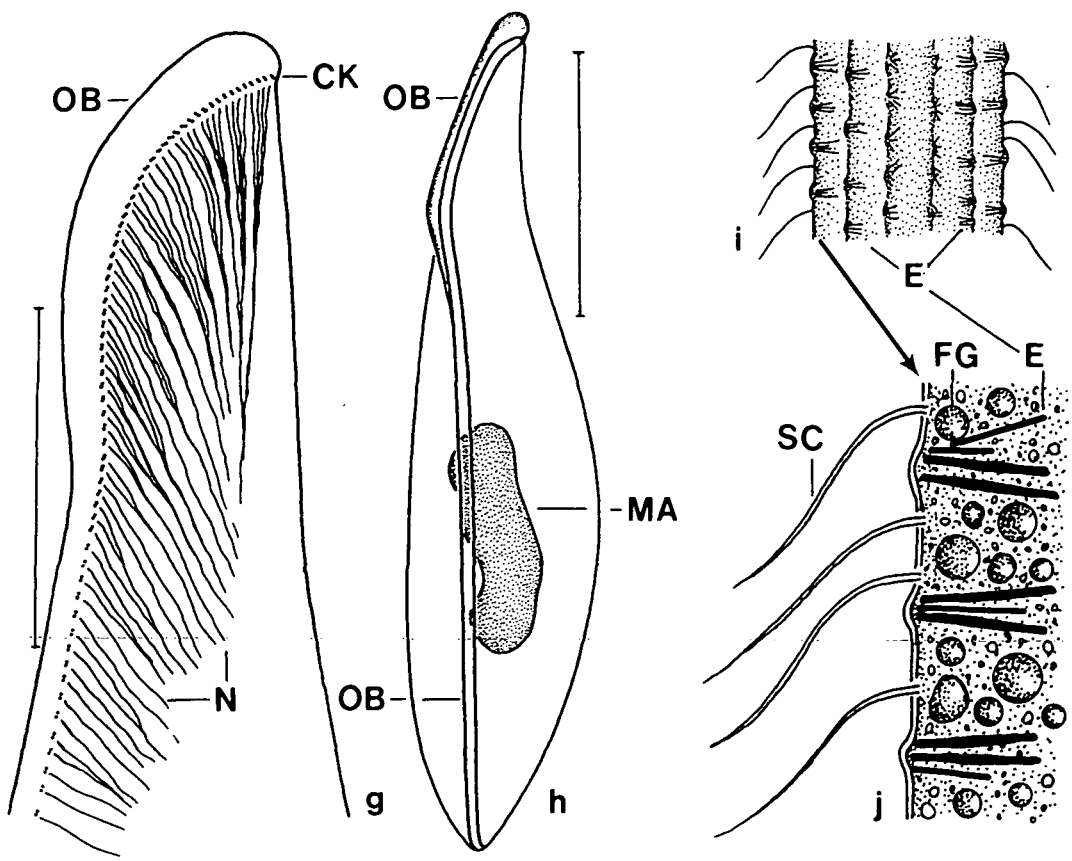

Fig. 82g–j. *Apobryophyllum etoschense* from life (i, h) and after protargol impregnation (g, h). **g:** Oral infraciliature in left anterior portion of cell. **h:** Ventral view showing general organization. **i, j:** Surface view in mid-body and optical section of dorsal cell margin, showing that *Apobryophyllum etoschense* has about 10 rows of bundled body extrusomes (cp. figures 333g, h). CK – circumoral kinety, E – extrusomes, FG – fat globule, MA – macronucleus, N – nematodesmata, OB – oral bulge, SC – ordinary somatic cilium. Scale bars 30 µm.

Occurrence and ecology: To date found only at type location and a site nearby, that is, slightly to highly saline soil from the *Sporobolus–Suaeda* girdle surrounding the Pan.

Generic classification and comparison with related species: *Apobryophyllum etoschense* matches the genus diagnosis rather well: "Spathidiidae with oral bulge extending to and around posterior end of organism. Dorsal brush on anterior left side of cell, left brush kineties regular and dikinetidal, right brush kineties fragmented and very likely monokinetidal (FOISSNER 1998a)". However, the structure of the dorsal brush is obviously slightly different. Whether this is of generic or subgeneric significance must await the discovery of further, related species.

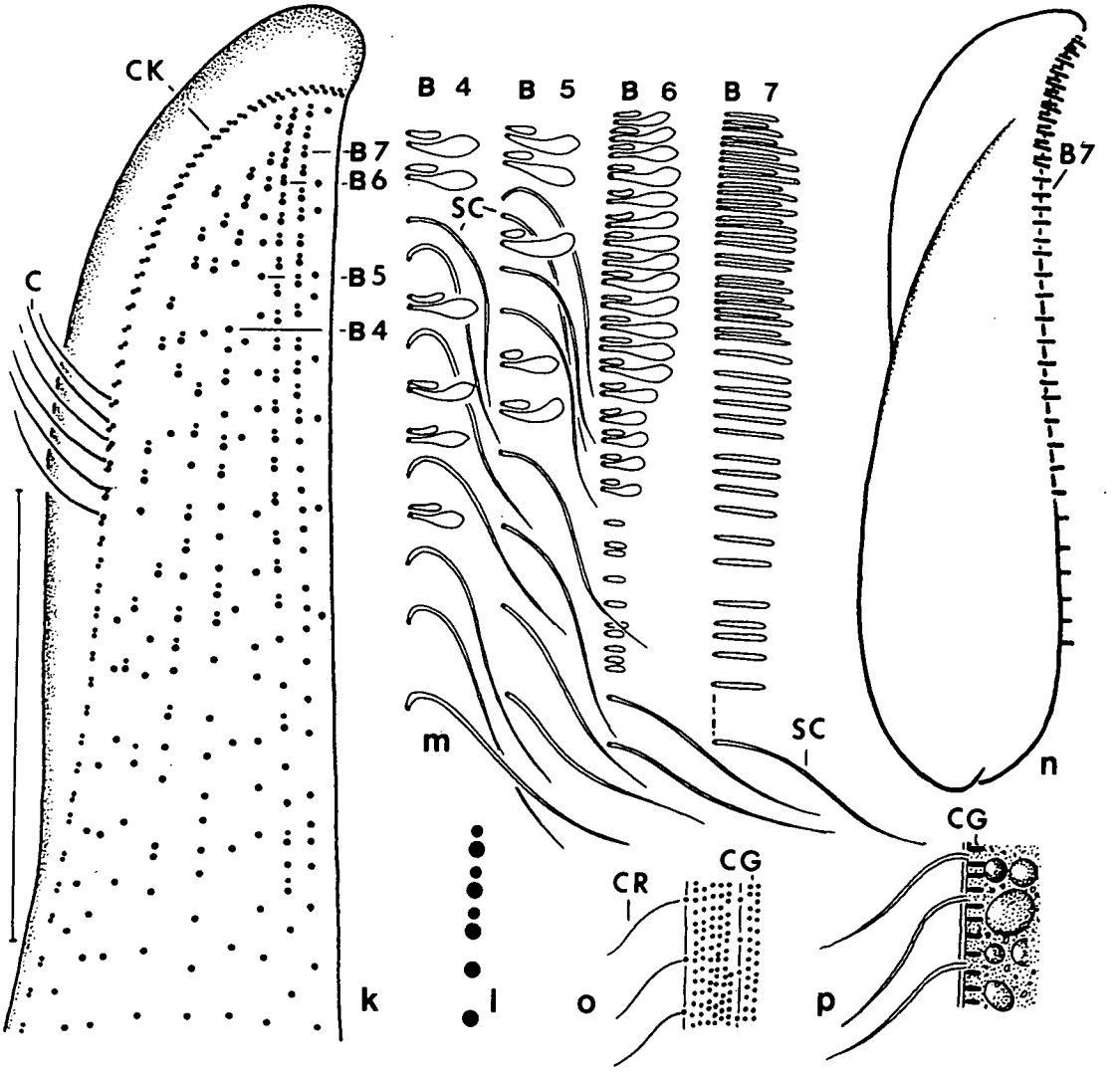

Fig. 82k–p. *Apobryophyllum etoschense* from life (m–p) and after protargol impregnation (k, l). **k, m, n:** The anterior left portion of the cell is occupied by the dorsal brush, whose cilia are highly differentiated (cp. figures 333d–f). Note, especially, ordinary somatic cilia (SC) between brush dikinetids in the right brush rows and the long monokinetidal bristle tail of brush row 7. Cilia drawn to scale, largest brush cilia about 3 µm, ordinary somatic cilia about 10 µm long. **l:** The brush is composed of dikinetids whose anterior basal body is smaller than the posterior. **o, p:** Surface view and optical section of cortex, showing rod-shaped cortical granules. B4-7 – dorsal brush rows, C – cilia of circumoral kinety, CG – cortical granules, CK – circumoral kinety, CR – ciliary row, SC – ordinary somatic cilia. Scale bar 30 µm.

Table 67. Morphometric data on *Apobryophyllum etoschense.*

Characteristics [a]	$\bar{x}$	M	SD	CV	Min	Max	n
Body, length	115.9	110.0	20.7	17.9	86.0	148.0	15
Body, width	27.4	27.0	4.2	15.4	22.0	36.0	15
Anterior body end to last brush dikinetid, distance	36.0	35.0	5.6	15.5	25.0	47.0	15
Macronucleus, length (length of chord)	30.8	29.0	7.6	24.6	19.0	43.0	15
Macronucleus, width	8.2	8.0	0.9	11.5	7.0	10.0	15
Somatic kineties, number (including brush rows)	15.7	16.0	1.8	11.4	13.0	20.0	15
Dorsal brush rows, number	6.8	7.0	0.6	8.2	5.0	8.0	15

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

No species has been found in the literature which might be identical to *A. etoschense*. It is easily distinguished from *A. terricola* FOISSNER, 1998a by the macronucleus (reniform vs. filiform) and, in silver slides, by the structure of the dorsal brush. *Apobryophyllum vermiforme* is much more slender (11:1 vs. 4.3:1) and has a filiform macronucleus, very fine extrusomes, and only three dorsal brush rows. The particular arrangement of the extrusomes and the brush structure are highly reminiscent of *Prorodon armatides*, a freshwater species with a small, anteriorly located oral opening (FOISSNER 1997b). Live specimens of *A. etoschense* are easily confused with medium-sized and large *Arcuospathidium* species, for instance, → *A. cultriforme lionotiforme*, which have a similar shape and nuclear apparatus. The best in vivo character for separating these species is the arrangement of the extrusomes, which are restricted to the oral bulge in *Arcuospathidium* and distributed in a peripheral girdle in *Apobryophyllum.*

Apobryophyllum terricola FOISSNER, 1998 (Fig. 83a–h; 328j–m)

Observations on Namibian populations: (i) Size in vivo about 200 × 40 µm (site 49) and 200 × 35 µm (site 56), thus stouter (5–5.7:1) than type specimens (7.3:1); (ii) Macronucleus of site (49) specimens considerably shorter, especially in the young culture, than in Kenyan type (Fig. 83a, h); (iii) Extrusomes of site (49) specimens distinctly fusiform (Fig. 83e; 328k–m), while rod-shaped in type and Namibian site (56) specimens which, additionally, likely lack dorsal extrusome rows and have a second extrusome type, viz. 1–1.5 µm long rods, similar to → *A. etoschense*; (iv) Dorsal brush of site (49) specimens usually as in Kenyan type (Fig. 83a, b), rarely similar to that of → *A. etoschense* (Fig. 83g, i; 328j).

FOISSNER (1998a) described a "conspicuous peripheral extrusome fringe" in *A. terricola*, and rows of extrusome bundles in → *A. etoschense* (FOISSNER 1998b). Careful in vivo observations on specimens from Namibian site (49) showed that *A. terricola* also has the extrusomes arranged in about six rows, but not in bundles (Fig. 83c). Likely, extrusome rows are an

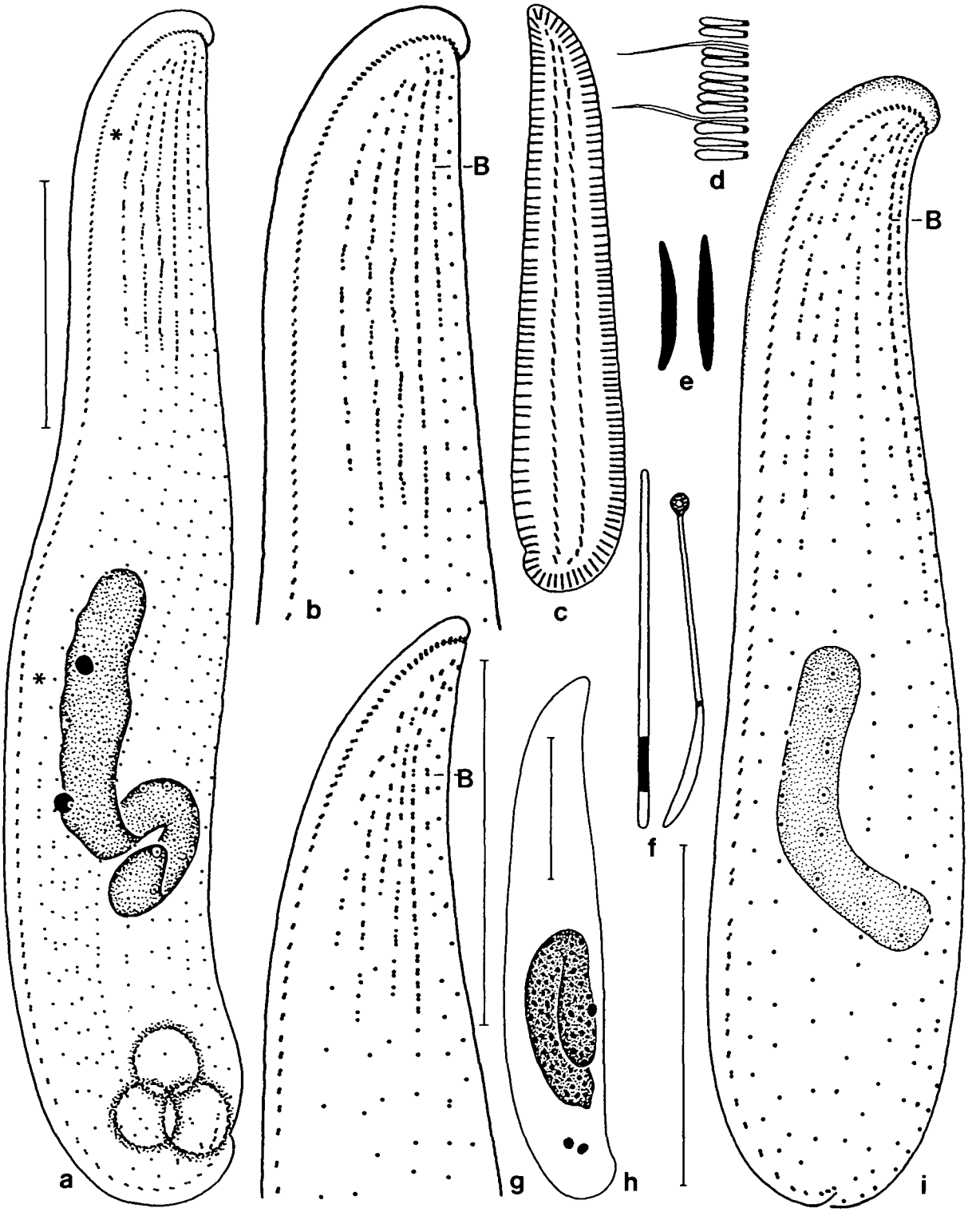

Fig. 83a–i. *Apobryophyllum terricola* (a–h) from Namibian site (49) and → *A. etoschense* (i) from life (c–f) and after protargol impregnation (a, b, g–i). **a, b, i:** Ciliary pattern of left side. Asterisks mark blank stripe, lacking in *A. etoschense*. **c:** Arrangement of extrusomes. **d:** Dorsal brush detail. **e, f:** Resting (length 6 µm) and exploded (20 µm) toxicysts. **g, h:** A small specimen (114 µm) resembling *A. etoschense* in size as well as the dorsal brush and nuclear pattern. B – dorsal brush. Scale bars 30 µm.

additional generic feature of *Apobryophyllum*. FOISSNER (1998a) suggested that both basal bodies of the circumoral dikinetids are ciliated in the right half of the circumoral kinety of *A. terricola*. However, this could be not confirmed by detailed in vivo observations on site (49) specimens, which show that each circumoral dikinetid has only one cilium (Fig. 328j).

All these new observations show that *Apobryophyllum terricola* is rather variable and thus more difficult to distinguish from → *A. etoschense* than stated by FOISSNER (1998b). However, both are still "good" species differing considerably in many features, such as body size (on average 160 × 25 µm vs. 130 × 30 µm in vivo), body shape (5–7.3:1 vs. 4.2:1 on average), macronucleus (usually long and tortuous vs. short and reniform), extrusomes (rows vs. rows of bundles; one type vs. two types, but see above), somatic ciliary pattern (with vs. without blank stripe between circumoral kinety and left side ciliature; Fig. 83a, i), and dorsal brush details (with vs. without somewhat irregularly arranged monokinetids).

Dileptus breviproboscis FOISSNER, 1981 (Fig. 84a–m; Table 68)

Material: Soil from a floodplain rain forest of an island in the Amazon River, Brazil.

Improved diagnosis (contains original and present data): Size usually 140–160 × 14–18 µm in vivo. Slenderly fusiform with both ends bluntly pointed, proboscis occupies about 23% of body length. Two ellipsoidal to distinctly spiral macronuclear segments with a globular micronucleus in between. Usually a series of 4–6 contractile vacuoles in dorsal side of trunk. Two types of extrusomes, viz., 3–4 µm long, fine rods and thick, oval to rod-shaped organelles with a size of 2–3 × 1 µm. On average 9–10 ciliary rows, 2 anteriorly differentiated to inconspicuous dorsal brush with up to 4 µm long bristles. Preoral kineties orientated almost in parallel to circumoral kinety, each composed of two cilia.

Description of Brazilian site (30) population: Size 120–220 × 15–25 µm in vivo, usually near 160 × 18 µm; length:width ratio highly variable, viz., 7–14:1, on average 9–10:1 in protargol preparations (Table 68); not or slightly flattened laterally. Shape inconspicuous because of the short proboscis and the lacking tail, usually slenderly fusiform with both ends gradually narrowed and bluntly pointed; posterior end occasionally rather broadly rounded, providing cells with a cylindroidal outline; proboscis short, that is, occupies only 22% of body length on average (Fig. 84a, c, j–m; Table 68). Nuclear apparatus in middle third of cell, invariably composed of two macronuclear segments with a globular to slightly ellipsoidal micronucleus in between; rarely specimens, likely reorganizers, with two macronuclear groups each composed of four to six globular nodules occur. Shape of macronuclear segments varies from ellipsoidal to conspicuously spiral; nucleoli globular to irregularly lobate (Fig. 84a, c, j, k, m). Three to six, usually four small contractile vacuoles each with one to three excretory pores in dorsal cortex of trunk; never in proboscis; occasionally, a pair of contractile vacuoles each occur near anterior and posterior end of trunk. Two types of extrusomes in oral bulge: type I rod-shaped and fine, 3–4 × ≤ 0.5 µm, numerous also in cytoplasm; type II conspicuously thick, viz., 2–3 × 1 µm and shell-shaped to ovate in Brazilian site (30) specimens, while rod-shaped in Brazilian site (28) individuals, less numerous than type I and restricted to oral bulge (Fig. 84a–f). Cortex very flexible, contains rows of colourless granules about 0.3 µm across. Cytoplasm colourless, contains many 0.5–5µm-

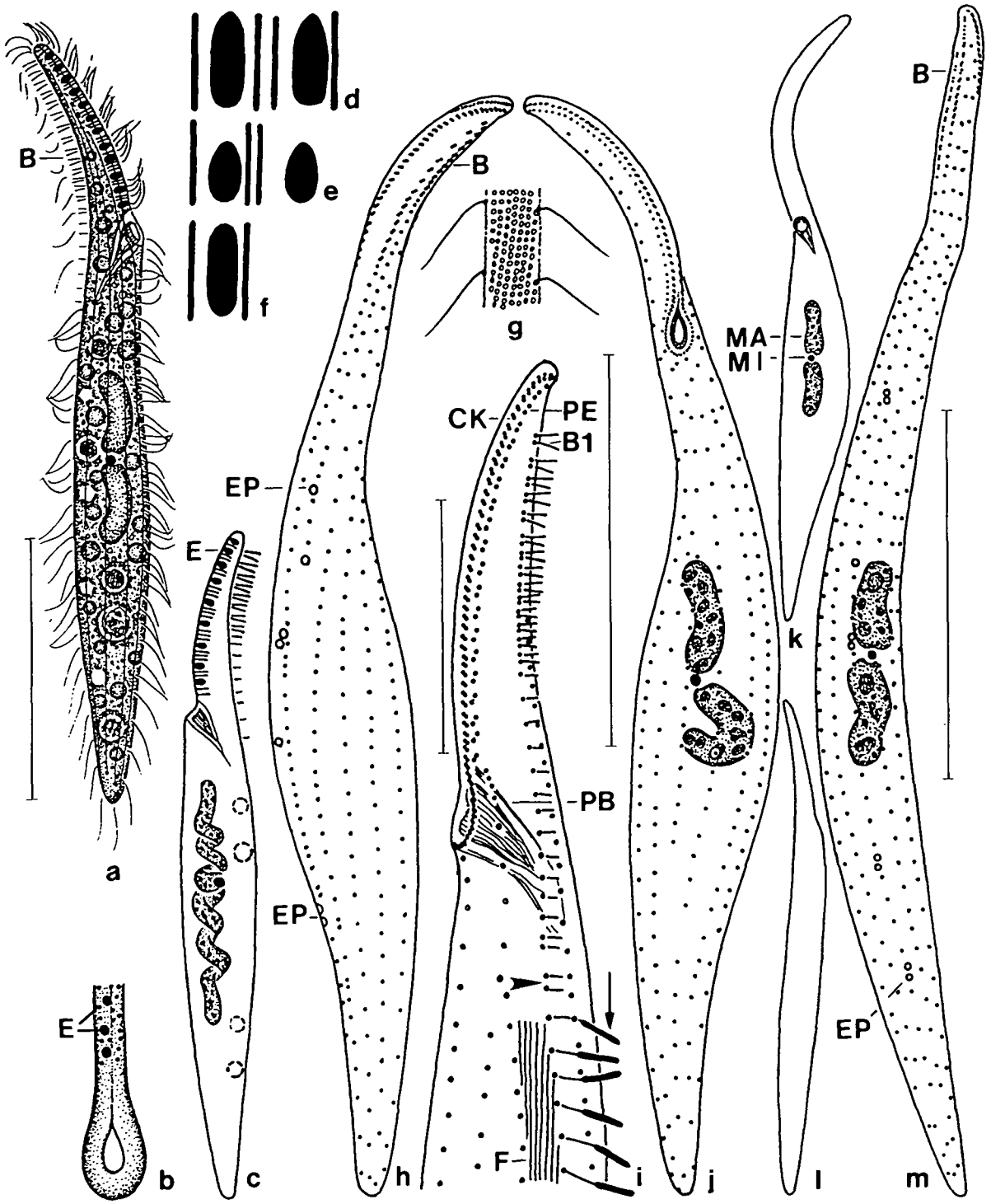

Fig. 84a–m. *Dileptus breviproboscis* from life (a–g, l) and after protargol impregnation (h–k, m). **a:** Right side view of a representative specimen. **b:** Frontal view of oral opening. **c, k, l:** Variability of shape, nuclear apparatus, and contractile vacuoles. **d–f:** Oral bulge extrusomes from populations of Brazilian sites 30 (d, e) and 28 (f). Drawn to scale, length 3 µm. **g:** Cortical granulation. **h, j:** Infraciliature of dorsal and ventral side. **i:** Left side view. Arrowhead marks end of monokinetidal bristle tail. Arrow denotes heavily impregnated distal half of cilia. **m:** Dorsal view of a slender specimen. B(1) – dorsal brush (row 1), CK – circumoral kinety, E – extrusomes, EP – excretory pores, F – fibres, MA – macronuclear segments, MI – micronucleus, PB – pharyngeal basket, PE – preoral kineties. Scale bars 50 µm (a, h, j, m) and 20 µm (i).

sized fat globules and food vacuoles with compact or loose content up to 7 µm in diameter. Swims and glides rather rapidly showing great flexibility among soil particles.

Somatic and oral cilia 7–8 µm long in vivo, show the same curious impregnation attribute as in other species of the genus, that is, have a thick, heavily impregnated distal half; somatic basal bodies associated with conspicuous (postciliary?) fibres obliquely extending backwards on right side of kineties (Fig. 84i). Ciliary rows meridionally and equidistantly arranged, leave blank a rather broad stripe each right and left of oral bulge; two of them anteriorly differentiated to inconspicuous dorsal brush having about 4 µm long, distally slightly inflated bristles anteriorly, decreasing in length to 2 µm posteriorly, both rows continue to anterior trunk portion with a tail of 1–2 µm long, monokinetidal bristles; row 1 commences subapically and is posteriorly slightly longer than row 2, which commences apically (Fig. 84a, h–j, m).

Oral apparatus as in congeners, proboscis, however, conspicuously short, occupying on average only 22% of body length. Oral opening elliptical, indistinctly set off from body proper, supported by an outer and inner rod basket. Preoral kineties, each composed of only two cilia, difficult to recognize because arranged almost in parallel with circumoral kinety (Fig. 84a, c, i, j).

Table 68. Morphometric data on *Dileptus breviproboscis* from Brazilian site (30).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	145.0	145.0	23.2	5.1	16.0	105.0	200.0	21
Body, width	15.4	15.0	2.4	0.5	15.7	12.0	20.0	21
Body length:width, ratio	9.5	9.2	2.0	0.4	21.1	7.0	13.8	21
Proboscis length, % of body length	22.2	22.0	3.6	0.8	16.4	17.0	33.0	21
Anterior body end to oral basket, distance	32.1	32.0	6.4	1.4	19.9	23.0	45.0	21
Oral basket opening, length [b]	8.4	9.0	1.5	0.3	17.4	6.0	11.0	18
Oral basket opening, width [b]	5.6	5.0	1.0	0.2	17.7	4.0	7.0	18
Anterior body end to macronucleus, distance	61.4	63.0	10.2	2.2	16.6	41.0	80.0	21
Nuclear figure, length	27.1	27.0	5.9	1.3	21.8	16.0	44.0	21
Macronuclear segments, length [c]	13.8	14.0	3.0	0.7	21.6	8.0	22.0	21
Macronuclear segments, width	4.9	5.0	0.6	0.1	12.7	4.0	6.0	21
Macronuclear segments, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Micronucleus, maximum diameter	2.0	2.0	–	–	–	1.6	3.5	21
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Somatic ciliary and brush rows, number	9.9	10.0	1.0	0.2	10.3	7.0	11.0	21
Dorsal brush rows, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Cilia in mid-body in 10 µm, number	3.8	4.0	0.8	0.2	19.7	2.0	5.0	21
Excretory pore groups, number	4.4	4.0	1.0	0.4	22.0	3.0	6.0	7
Excretory pores, total number	5.7	5.0	2.3	0.9	40.1	4.0	9.0	7

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Measured as distances between circumoral kinety.

[c] Spiralized and/or curved segments not straightened; actual length thus usually larger.

Occurrence and ecology: The population described occurred in the same sample as → *Phialinides armatus*, that is, in soil from a floodplain rainforest of an island in the Amazon River. However, we found highly similar populations also in soils from Costa Rica, the USA, and Namibia, indicating a wide ecological range and cosmopolitan distribution.

Comparison with original description and related species: FOISSNER (1984) synonymized *D. breviproboscis* with *D. anguillula* KAHL, 1932 because of transitions in body shape and nuclear pattern. However, over the years we recognized that there are two *D. anguillula*-like species, highly similar in all features except for the extrusomes: fine, 3–4 µm long rods vs. thick, 2–3 × 1 µm-sized ellipsoids plus fine, 3–4 µm long rods (Fig. 84a–f). Both species likely have cosmopolitan distribution: the former was found in Austria, Canada, and Brazil, like the latter, which occurred in the USA, Costa Rica, Brazil, and Namibia.

Unfortunately, the original descriptions of *D. anguillula* and *D. breviproboscis* lack detailed data about the extrusomes. Thus, they cannot be assigned to any of the two types described above, but must be redefined. We suggest endowing *D. anguillula* with fine, rod-shaped extrusomes, while *D. breviproboscis* additionally has thick, ellipsoidal extrusomes. A detailed redescription of *D. anguillula* is in FOISSNER (1984). Alternatively, the Brazilian population described here as *D. breviproboscis* might be considered as a new species and *D. breviproboscis* kept in synonymy with *D. anguillula*. This, however, would unnecessarily increase the number of insufficiently described species.

Dileptus orientalis SONG, PACKROFF & WILBERT, 1988 also belongs to the *D. anguillula* group. However, it is considerably larger (150–250 µm, $\bar{x}$ = 192) and has 15–19 ($\bar{x}$ = 16.7) ciliary rows, of which three are differentiated to dorsal brush rows. Note that SONG et al. (1988) illustrated the proboscis longer than it is, as evident from the morphometric data. Thus, the species seemingly looks rather different to *D. anguillula* and *D. breviproboscis*. Nevertheless, *D. orientalis* is a "good" species for the differences mentioned above.

Dileptus mucronatus PENARD, 1922 (Fig. 85a–o; 334a–p, 335a–j, 336i; Table 69)

Supplementary observations: This species, which is well-known since the thorough redescription by FOISSNER (1984), is the most common middle-sized *Dileptus* in soils world-wide and occurs also in Namibia (Table 4). Later, FOISSNER's redescription was confirmed on a Chinese population (SONG 1994). Our observations on a population from a rice field soil in Zanzibar (sample kindly provided by Mag. Hubert BLATTERER) largely agree with those from the Austrian (FOISSNER 1984) and Chinese (SONG 1994) specimens. Thus, a full redescription is not necessary. However, we provide several additional observations, morphometric data, and a multitude of figures showing details as yet unknown or documented only by line drawings.

(i) *Dileptus mucronatus* is defined by the following combination of features: middle-sized, length 250–500 µm; rather distinct tail; two macronuclear segments with a single micronucleus in between; a dorsal row of contractile vacuoles; two size-types of basically rod-shaped extrusomes; 20–30 ciliary rows, of which about eight are anteriorly modified to dorsal brush rows; and an ordinary oral basket (Fig. 85a–c; 334d–i, l, 335a, d).

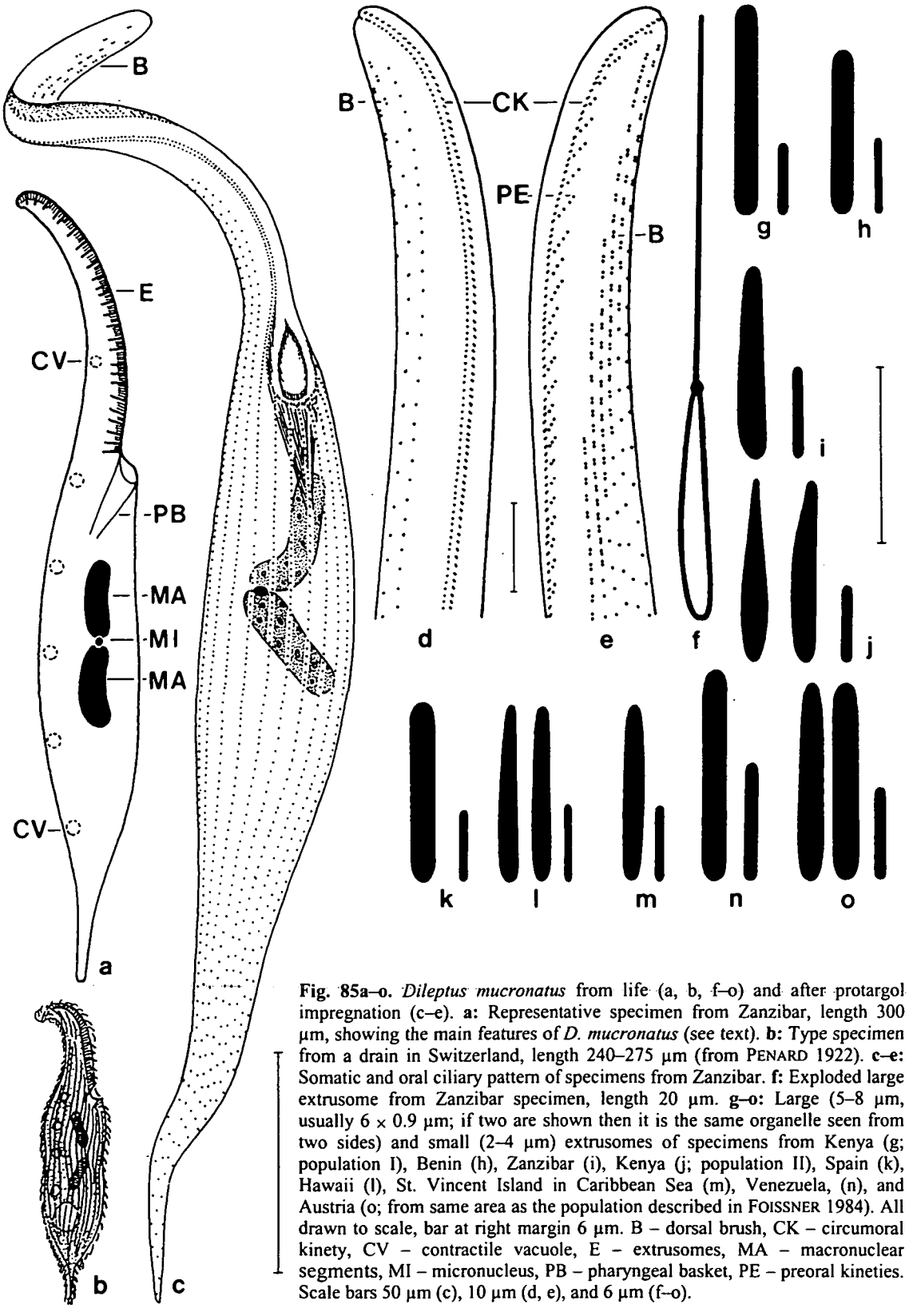

Fig. 85a–o. *Dileptus mucronatus* from life (a, b, f–o) and after protargol impregnation (c–e). **a:** Representative specimen from Zanzibar, length 300 µm, showing the main features of *D. mucronatus* (see text). **b:** Type specimen from a drain in Switzerland, length 240–275 µm (from PENARD 1922). **c–e:** Somatic and oral ciliary pattern of specimens from Zanzibar. **f:** Exploded large extrusome from Zanzibar specimen, length 20 µm. **g–o:** Large (5–8 µm, usually 6 × 0.9 µm; if two are shown then it is the same organelle seen from two sides) and small (2–4 µm) extrusomes of specimens from Kenya (g; population I), Benin (h), Zanzibar (i), Kenya (j; population II), Spain (k), Hawaii (l), St. Vincent Island in Caribbean Sea (m), Venezuela, (n), and Austria (o; from same area as the population described in FOISSNER 1984). All drawn to scale, bar at right margin 6 µm. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuole, E – extrusomes, MA – macronuclear segments, MI – micronucleus, PB – pharyngeal basket, PE – preoral kineties. Scale bars 50 µm (c), 10 µm (d, e), and 6 µm (f–o).

(ii) PENARD (1922) described the extrusomes as "courts et serrés". FOISSNER (1984) described them as "rod-shaped, about 7 µm long, and serially arranged in the oral bulge and scattered in the cytoplasm". As the extrusomes are one of the main features of *Dileptus* species, we studied them in nine populations from all over the world (Fig. 85g–n) and in a population collected from the same area (Austria, Burgenland) as that studied by FOISSNER (1984). This showed that FOISSNER (1984) recognized only the large extrusomes but overlooked the small ones (Fig. 85o; 334a, b, l). Taking all populations, the large, slightly asymmetrical extrusomes are rod-shaped to slenderly lanceolate and 5–8 µm long, mostly 6–7 µm (Fig. 85g–i,

Table 69. Morphometric data on *Dileptus mucronatus* from Zanzibar (upper line) and Austria (lower line; from FOISSNER 1984).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	286.4	300.0	33.0	10.0	11.5	220.0	330.0	11
	392.0	400.0	50.0	12.9	12.8	310.0	500.0	15
Body, width	34.1	35.0	5.7	1.7	16.7	25.0	45.0	11
	45.1	45.0	7.5	1.9	16.6	32.0	60.0	15
Anterior body end to begin of oral basket, distance	101.2	100.0	14.3	4.3	14.1	70.0	125.0	11
	117.5	112.0	17.1	4.4	14.5	90.0	145.0	15
Oral basket, maximum width	12.8	13.0	1.3	0.4	9.8	11.0	15.0	11
	13.2	14.0	1.4	0.4	10.8	10.0	15.0	15
Nuclear figure, length	57.9	55.0	10.9	3.3	18.8	45.0	85.0	11
	70.3	70.0	16.6	4.3	23.7	50.0	120.0	15
Macronuclear segments, length	33.8	32.0	5.7	1.7	16.8	29.0	48.0	11
	53.6	50.0	9.9	2.6	18.6	42.0	70.0	15
Macronuclear segments, width	9.1	9.0	1.3	0.4	14.3	7.0	11.0	11
	7.5	7.0	0.8	0.2	10.9	6.0	9.0	15
Micronucleus, largest diameter	3.3	3.0	0.7	0.2	19.8	3.0	5.0	11
	3.4	3.0	0.8	0.2	23.1	3.0	6.0	15
Macronuclear segments, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
	1.9	2.0	–	–	–	1.0	2.0	15
Micronuclei, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Somatic kineties, number in mid-body	21.6	21.0	2.2	0.7	10.0	19.0	26.0	11
	25.8	26.0	2.8	0.7	10.9	21.0	30.0	15
Basal bodies, number in 10 µm in mid-body	5.6	6.0	1.3	0.4	22.8	4.0	7.0	11
	6.6	6.0	0.9	0.2	13.8	5.0	8.0	15
Resting cysts, length with mucous layer [b]	87.4	86.0	10.7	2.9	12.3	72.0	104.0	14
Resting cysts, width with mucous layer [b]	87.1	86.0	10.8	2.9	12.4	72.0	104.0	14
Resting cysts, length without mucous layer [b]	60.7	61.0	5.8	1.6	9.6	52.0	72.0	14
Resting cysts, width without mucous layer [b]	57.8	59.0	5.0	1.3	8.7	48.0	64.0	14

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] From cultivated Kenyan population, as described in text. All in vivo.

k–o; 334a, b, d–h); only those of Kenyan population II are distinctly lanceolate (Fig. 85j), indicating that it could be a concrete subspecies. The small extrusomes are rod-shaped and 2–4 µm long, usually 2.5–3 µm (Fig. 85a, g–o; 334b, h, i). Accordingly, the extrusomes of *D. mucronatus* are fairly constant in shape and size and thus an important feature for species identification. The real value of this feature, which is largely under-estimated, becomes obvious on comparison of the micrographs of the rod-shaped extrusomes of *D. mucronatus* (Fig. 334d–h) with, e.g., the clavate extrusomes of *D. armatus* (Fig. 49a–e in FOISSNER 2000a). One of two Venezuelan populations studied has extrusomes only in the right half of the bulge.

(iii) The about eight dorsal brush rows form a staggered pattern. Anteriorly, they consist of pairs of distinctly inflated, 2–3 µm long bristles. More posteriorly, only the anterior bristle is inflated while the posterior is rod-shaped and shorter. At the end of the rows are minute, monokinetidal bristles (Fig. 85c, e; 335e, f, i, j).

(iv) The circumoral and preoral cilia form nice metachronal waves, as previously described from light microscopic observations (Fig. 335b, g).

(v) The resting cysts of a cultivated Kenyan population (that with the deviating extrusomes, Fig. 85j) are spherical to slightly ellipsoidal, have an average diameter of 60 µm, and are surrounded by a conspicuous mucous layer, which sometimes contains extruded cyst material (Fig. 334m–p; Table 69). The cysts are conspicuously honey-yellow/brown because the about 2 µm thick cyst wall has this colour, which is clearly recognizable in squashed cysts. Thus, the resting cysts of *D. mucronatus* are very similar to those of *D. margaritifer*, as described by FOISSNER et al. (1994).

Pseudomonilicaryon massutii (KAHL, 1933) **nov. comb.** (Fig. 86a–n; 336a–h; Table 70)

1929 *Dileptus anser* O.F.M. — MASSUTÍ ALZAMORA, Notas y Resúmenes, 32: 3 (misidentification).
1933 *Dileptus massutii* KAHL, Tierwelt N.- und Ostsee, 23: 63.
1963 *Dileptus massutti* KAHL, 1933 — DRAGESCO, Bull. biol. Fr. Belg., 97: 125.

Neotype material: Neotypified from Namibian site (70) population, according to reasons 1, 2, 4, 6 given in chapter 2.4.2.

Improved diagnosis: Size about 800 × 65 µm in vivo. Slenderly fusiform with both ends gradually narrowed and bluntly pointed, proboscis occupies about 30% of body length. Macronucleus moniliform and tortuous, composed of 47 segments on average. Many contractile vacuoles in dorsal side of trunk and proximal half of proboscis. Two size types of rod-shaped extrusomes, large type about 10 µm long, small approximately 3 µm. On average 44 ciliary rows, up to 15 differentiated to dorsal brush anteriorly.

Redescription: Size of Mediterranean type population 400–1000 µm, of Namibian neotype population 550–1100 × 50–85 µm, usually about 800 × 65 µm in vivo, as calculated

from some measurements of live specimens and values shown in table 70, assuming a shrinkage of about 15% due to the preparation procedures. Length:width ratio also considerably variable, namely, 8.3–19.3:1, usually 12.6:1; trunk circular in cross section, while proboscis and rear portion distinctly laterally flattened. Shape slenderly fusiform with both ends gradually narrowed and bluntly pointed; proboscis very slender, occupies 25–36%, usually 30% of body length (Fig. 86a, m, n; Table 70). Macronucleus in trunk, moniliform and tortuous, composed of an average of 47 usually ellipsoidal segments in Namibian specimens, while of only eleven in those from Spain, as estimated from illustration in MASSUTÍ ALZAMORA (1929); nucleoli numerous and spherical (Fig. 86a, m). Several globular micronuclei adjacent to macronucleus. Many contractile vacuoles in dorsal side of trunk and proximal half of proboscis; no ventral vacuoles; excretory pores only occasionally recognizable, up to three per contractile vacuole (Fig. 86a). Extrusomes accumulated in oral bulge, especially in its right half, while lacking around pharyngeal basket, numerous and scattered in cytoplasm, immature extrusomes impregnate with protargol; two shape and size types of extrusomes attached to bulge of proboscis: type I slenderly rod-shaped with ends rounded, slightly asymmetrical, about 10–12 × 0.7–1 µm; type II like type I but only 3–4 × 0.5–0.7 µm; exploded extrusomes of typical toxicyst structure and with a refractive (toxin?) globule each at proximal end of empty ampulla and tip, large type I up to 30 µm long, small type II up to 9 µm (Fig. 86c, d, h, i; 336b–h). Cortex very flexible, contains approximately seven rows of about 1 × 0.5 µm-sized granules (mucocysts?) between each two kineties. Cytoplasm colourless, contains many glossy fat globules 1–5 µm across and some food vacuoles with loose content, for instance, remnants of *Condylostomides etoschensis*, which is killed and almost completely dissolved by exploding extrusomes before it is engulfed; usually one large defecation vacuole in rear end. Movement without peculiarities, highly flexible.

Somatic and oral cilia about 7 µm long in protargol preparations, where they have a thick, heavily impregnated distal half, as in other dileptids (→ *Dileptus breviproboscis*; Fig. 86k). Ciliary rows meridionally and equidistantly arranged, anteriorly gradually shortened along both sides of oral bulge, except for first kinety right of oral opening, which extends as perioral kinety with closely spaced cilia parallel to circumoral kinety to tip of proboscis; leave blank a rather wide stripe left of preoral kineties. Dorsal brush conspicuous, although bearing only minute bristles, because occupying almost entire dorsal side of proboscis, where up to 15 left lateral kineties are anteriorly differentiated to brush rows, forming a staggered pattern (Fig. 86g, j, l; Table 70). Bristles clavate, paired and about 2–3 µm long in anterior portion of brush rows, while single and approximately 1 µm long in posterior.

Oral apparatus as in → *Dileptus*, that is, pharyngeal basket conspicuous, about 18 µm across, and composed of an inner and outer basket. Circumoral kinety composed of dikinetids orientated perpendicularly or slightly obliquely to kinety axis in proboscis, while possibly consisting of monokinetids around pharyngeal opening. Many preoral kineties left of circumoral kinety, counter-clockwise inclined, each usually composed of four closely spaced basal bodies (Fig. 86g, l).

Occurrence and ecology: MASSUTÍ ALZAMORA (1929) discovered the species in the Bay of Palma de Mallorca, Island of Mallorca, Spain. We found it only at Namibian site (70), that is, in highly saline soil and litter covered by a crust of cyanobacteria.

Generic classification and comparison with related species: JANKOWSKI (1967b) spilt the genus *Dileptus* into three subgenera solely based on the

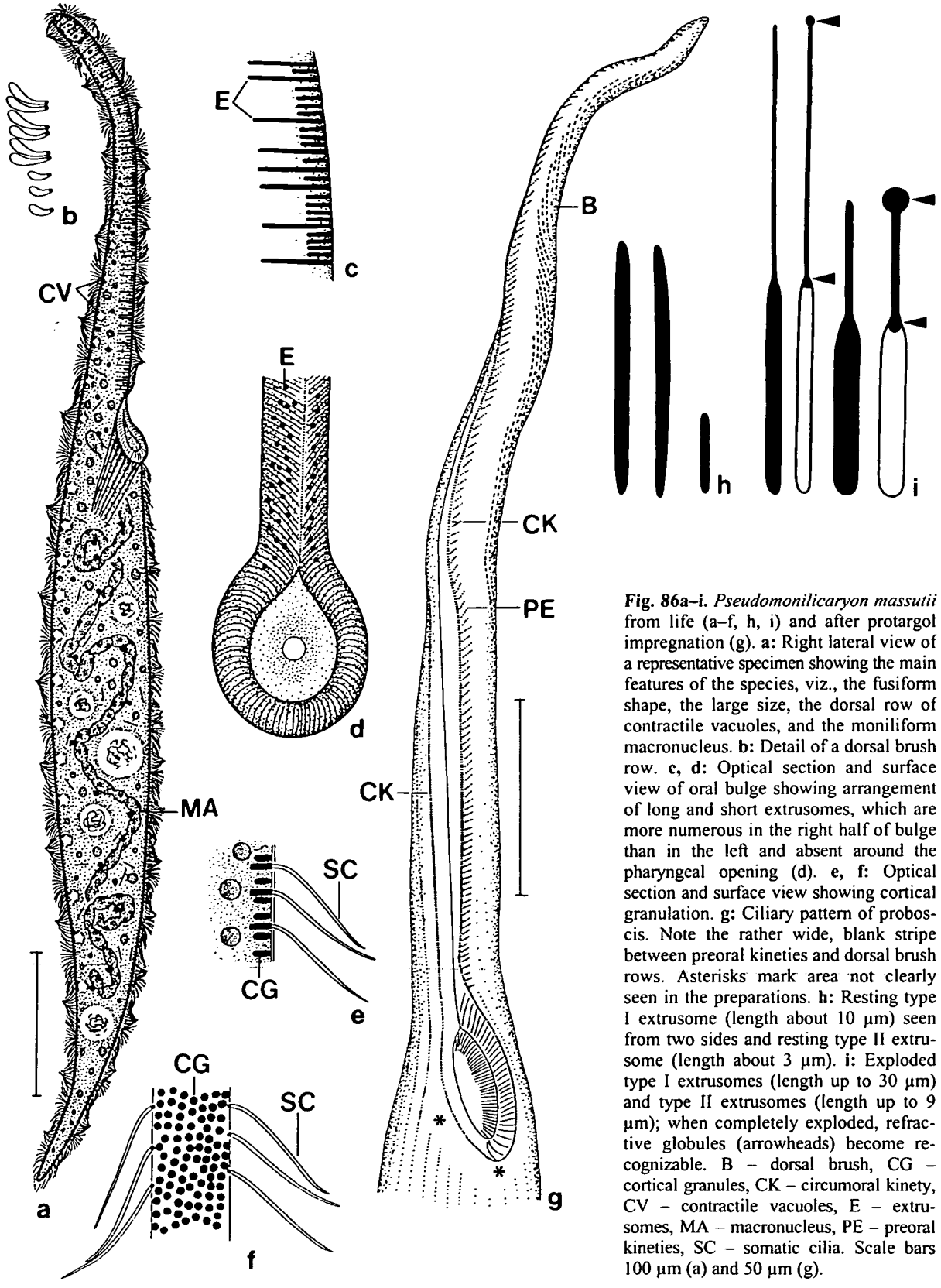

Fig. 86a–i. *Pseudomonilicaryon massutii* from life (a–f, h, i) and after protargol impregnation (g). **a:** Right lateral view of a representative specimen showing the main features of the species, viz., the fusiform shape, the large size, the dorsal row of contractile vacuoles, and the moniliform macronucleus. **b:** Detail of a dorsal brush row. **c, d:** Optical section and surface view of oral bulge showing arrangement of long and short extrusomes, which are more numerous in the right half of bulge than in the left and absent around the pharyngeal opening (d). **e, f:** Optical section and surface view showing cortical granulation. **g:** Ciliary pattern of proboscis. Note the rather wide, blank stripe between preoral kineties and dorsal brush rows. Asterisks mark area not clearly seen in the preparations. **h:** Resting type I extrusome (length about 10 µm) seen from two sides and resting type II extrusome (length about 3 µm). **i:** Exploded type I extrusomes (length up to 30 µm) and type II extrusomes (length up to 9 µm); when completely exploded, refractive globules (arrowheads) become recognizable. B – dorsal brush, CG – cortical granules, CK – circumoral kinety, CV – contractile vacuoles, E – extrusomes, MA – macronucleus, PE – preoral kineties, SC – somatic cilia. Scale bars 100 µm (a) and 50 µm (g).

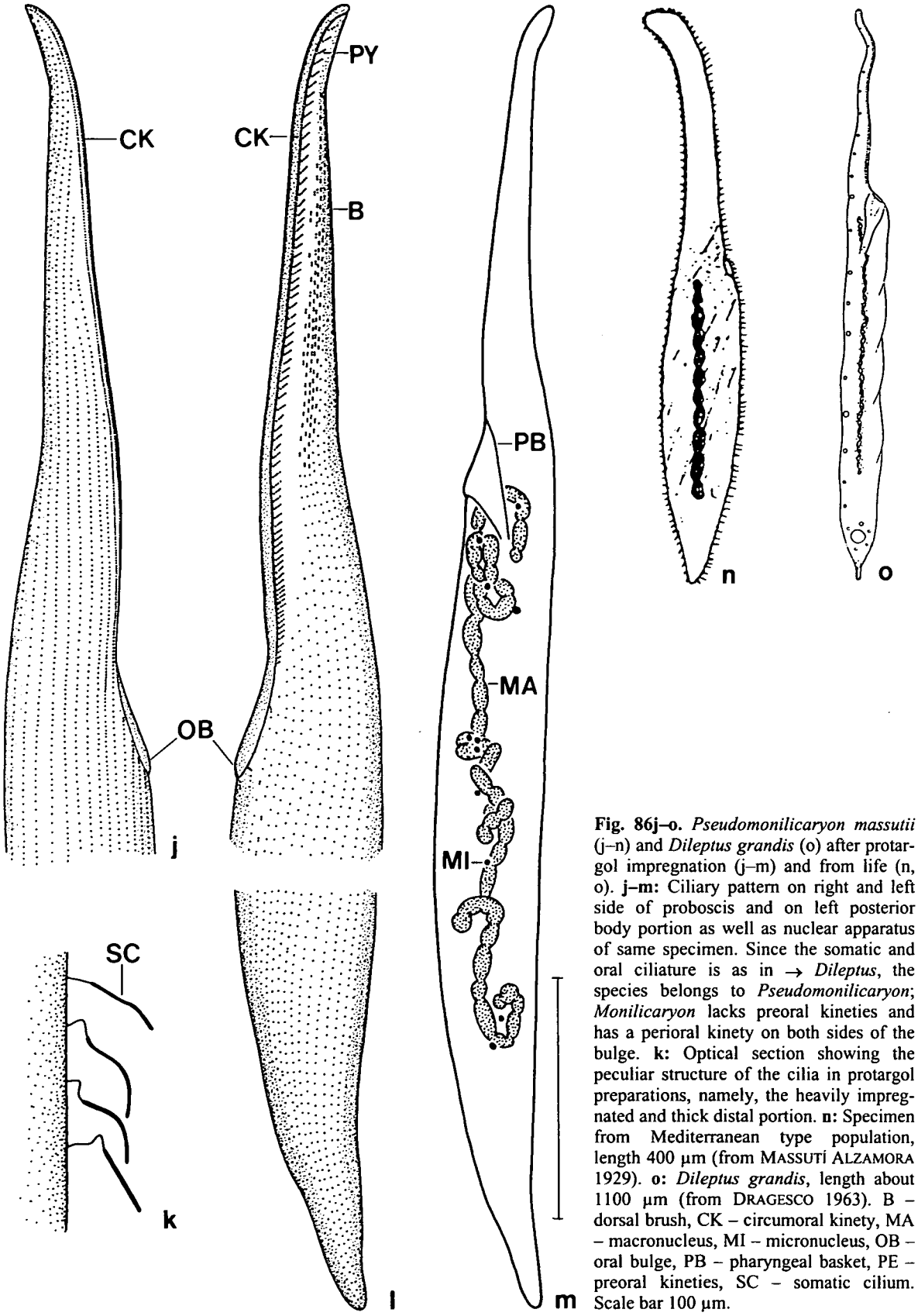

Fig. 86j–o. *Pseudomonilicaryon massutii* (j–n) and *Dileptus grandis* (o) after protargol impregnation (j–m) and from life (n, o). **j–m:** Ciliary pattern on right and left side of proboscis and on left posterior body portion as well as nuclear apparatus of same specimen. Since the somatic and oral ciliature is as in → *Dileptus*, the species belongs to *Pseudomonilicaryon*; *Monilicaryon* lacks preoral kineties and has a perioral kinety on both sides of the bulge. **k:** Optical section showing the peculiar structure of the cilia in protargol preparations, namely, the heavily impregnated and thick distal portion. **n:** Specimen from Mediterranean type population, length 400 µm (from MASSUTÍ ALZAMORA 1929). **o:** *Dileptus grandis*, length about 1100 µm (from DRAGESCO 1963). B – dorsal brush, CK – circumoral kinety, MA – macronucleus, MI – micronucleus, OB – oral bulge, PB – pharyngeal basket, PE – preoral kineties, SC – somatic cilium. Scale bar 100 µm.

macronuclear configuration: *Dileptus* with dispersed nodules; *Dimacrocaryon* with two nodules and a micronucleus in between; and *Monilicaryon* with moniliform macronucleus. FOISSNER's (1997b) reinvestigation of *Dileptus monilatus*, type of *Monilicaryon*, showed that the same nuclear pattern evolved independently in several evolutionary lines of *Dileptus* s.l. Based on this findings, he raised *Monilicaryon* to genus level and emended the diagnosis to include features of the oral ciliature, viz., a perioral kinety each along right and left side of circumoral kinety and the lack of preoral kineties. For species with a moniliform macronucleus and an ordinary dileptid oral ciliature, FOISSNER (1997b) established the genus *Pseudomonilicaryon*. According to its oral ciliature, the Namibian population belongs to this genus and is characterized by five conspicuous features, viz., the large body size (about 800 µm), the fusiform shape, the moniliform macronucleus with more than 40 segments, a dorsal row of contractile vacuoles, and two size-types of rod-shaped extrusomes. There are only two similar species, namely, *Dileptus massutii* KAHL, 1933 and *D. grandis* DRAGESCO, 1963 (Fig. 86n, o). Both have been described superficially (DRAGESCO 1963, KAHL 1933, MASSUTÍ ALZAMORA 1929). As our population is from a saline habitat, we identify it with the marine and similarly sized *D. massutii*. Likely, *D. grandis* is a junior synonym.

Table 70. Morphometric data on Namibian population of *Pseudomonilicaryon massutii*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	686.3	649.5	207.0	84.5	30.2	478.0	944.0	6
Body, width	55.2	54.5	11.2	4.6	20.4	44.0	73.0	6
Body length:width, ratio	12.6	12.2	3.6	1.5	28.9	8.3	19.3	6
Anterior body end to pharyngeal basket, distance	224.8	228.5	68.8	24.3	30.6	120.0	304.0	8
Proboscis length, % of body length	30.3	31.5	4.4	1.8	14.7	24.9	36.1	6
Anterior body end to macronucleus, distance	248.5	204.5	99.5	40.6	40.0	140.0	392.0	6
Macronucleus, length (uncoiled, approximate)	330.7	330.5	–	–	–	228.0	433.0	6
Macronuclear segments, maximum length [b]	24.2	23.5	4.8	2.0	20.0	19.0	33.0	6
Macronuclear segments, width	7.0	7.5	1.3	0.5	18.1	5.0	8.0	6
Micronuclei, length	2.5	2.5	–	–	–	2.0	3.0	8
Micronuclei, width	2.1	2.0	–	–	–	2.0	3.0	8
Anterior body end to last dikinetid of dorsal brush, distance	172.0	172.0	67.7	32.4	37.6	114.0	230.0	4
Macronuclear segments, number	47.4	46.0	7.4	3.3	15.7	39.0	59.0	5
Micronuclei, number	17.8	18.0	4.4	2.0	24.6	12.0	24.0	5
Somatic ciliary rows, number in mid-body	44.4	46.0	6.8	3.1	15.4	34.0	52.0	5
Basal bodies in 10 µm in mid-body, number	6.0	6.0	1.2	0.5	20.4	5.0	8.0	5

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Straight segments.

Pseudomonilicaryon japonicum nov. spec. (Fig. 87a–m; 337a–s; Table 71)

Diagnosis: Size about 400 × 75 µm in vivo. Fusiform with posterior end bluntly pointed, proboscis occupies about 36% of body length. Macronucleus moniliform and tortuous, composed of 28 segments on average. Many contractile vacuoles in dorsal side of trunk and proboscis, some ventrally. Two shape and size types of oral extrusomes: type I bluntly acicular and about 6 µm long; type II rod-shaped and approximately 2 µm long. On average 39 ciliary rows, up to 18 anteriorly differentiated to dorsal brush. Oral opening circular.

Type location: Tree and soil mosses from the surroundings of the "Spring of Wisdom" in Kyoto, Japan, 35°N 135°E.

Etymology: Named after the country discovered.

Description: Size 260–580 × 50–105 µm in vivo, as calculated from some measurements of live specimens and values shown in table 71, assuming a shrinkage of about 10% due to the preparation procedures. Shape fusiform to broadly fusiform, rarely cylindroidal, length:width ratio 3.8–8.4:1, on average 5.7:1 in protargol preparations; posterior end bluntly pointed, rarely widely rounded or with inconspicuous, blunt tail due to a large egestion vacuole in rear end; never with a tail sensu stricto. Proboscis occupies 22–55%, usually 36% of body length, broad and flexible, usually conspicuously curved dorsally (Fig. 87a, d, g; 337a, b, h). Macronucleus in trunk, moniliform and tortuous, composed of an average of 28 segments easily recognizable even in vivo at low magnification; individual segments usually ellipsoidal and with many small, globular nucleoli (Fig. 87a, d; 337g, l; Table 71). Several micronuclei adjacent to macronucleus, distinctly fusiform in vivo, while broadly fusiform, ovoidal or globular in protargol preparations (we cannot exclude that "globular" is caused by viewing a fusiform nucleus transversely). Contractile vacuoles numerous and conspicuous in dorsal side of entire proboscis and trunk, where they form a rather broad stripe, while sparse and thus easily overlooked in ventral side of trunk; each vacuole with one, rarely two circular excretory pores (Fig. 87a, d, e; 337a, b, h, i, k–n). Extrusomes accumulated in oral bulge, but not around and in oral opening, immature stages scattered in cytoplasm and impregnated with protargol. Two shape and size types of ripe oral bulge extrusomes: type I bluntly acicular and about 6 × 0.8 µm, type II rod-shaped and approximately 2 × 0.3 µm; exploded extrusomes of typical toxicyst structure and with a globule (toxin droplet?) on top, large type I up to 16 µm long, small type II up to 6 µm (Fig. 87a–c, h–k; 337c–f, g). Cortex very flexible, contains a sheet of refractive, comparatively large (1 × 0.5 µm) granules (mucocysts?), forming about seven oblique rows between each two kineties (Fig. 87l, m; 337g, k). Cytoplasm colourless, contains many fat globules 1–5 µm across, some 15 µm long pharyngeal baskets from ciliate prey, and up to seven vacuoles with remnants of rotifers, the preferred food of this large ciliate. Movement without peculiarities.

Somatic and oral cilia about 10 µm long in vivo, with thick, distal half in protargol-impregnated specimens, as in congeners (FOISSNER 2000a). Ciliary rows meridionally and equidistantly arranged, anteriorly gradually shortened along both sides of oral bulge, except for first kinety right of oral opening, which extends as so-called perioral kinety parallel to the circumoral kinety to tip of proboscis; cilia much more closely spaced in preoral than postoral portion of perioral kinety. Blank stripe left of preoral kineties rather wide. Dorsal brush conspicuous, although bearing only minute bristles, because occupying almost entire dorsal

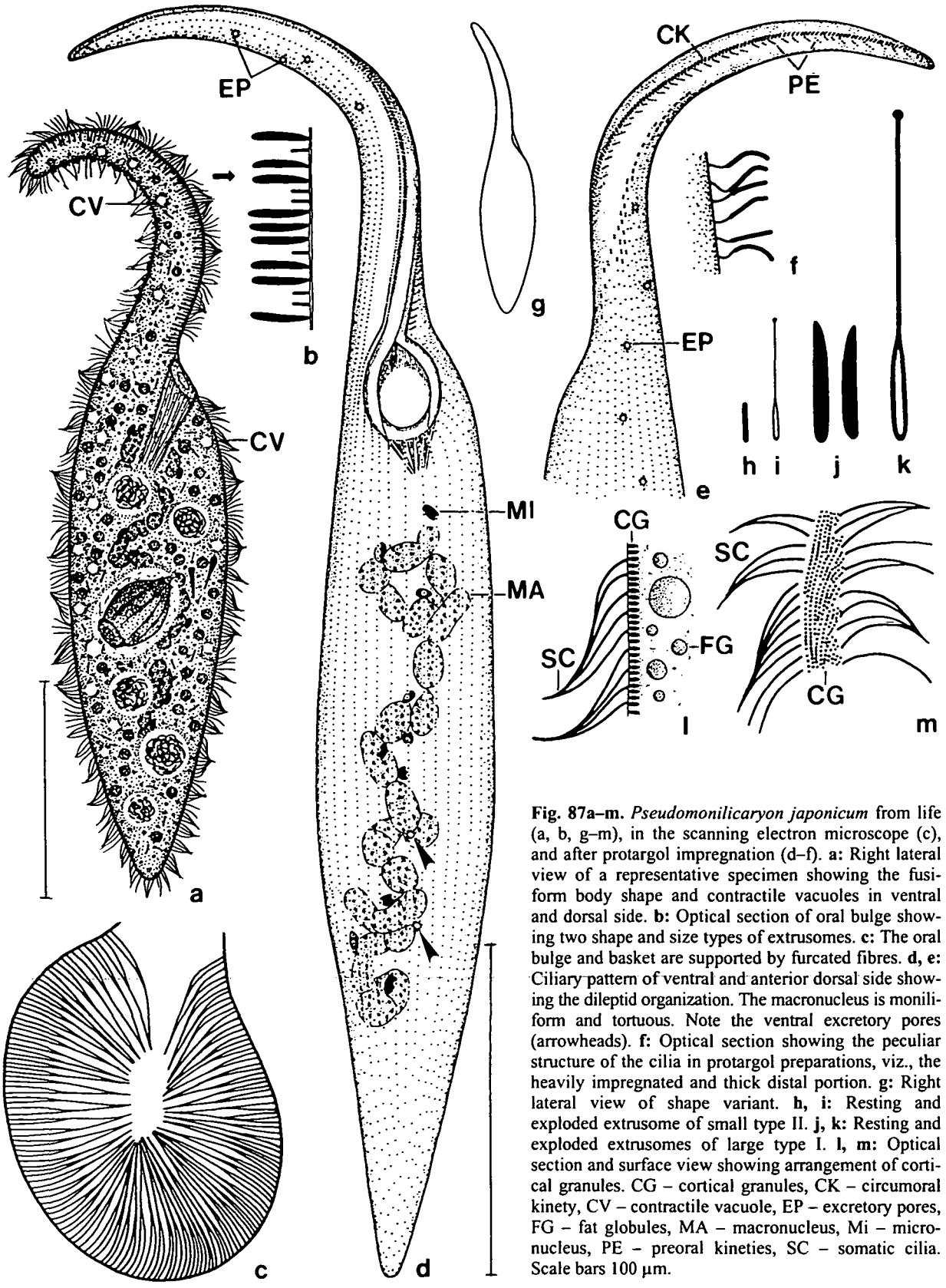

Fig. 87a–m. *Pseudomonilicaryon japonicum* from life (a, b, g–m), in the scanning electron microscope (c), and after protargol impregnation (d–f). **a:** Right lateral view of a representative specimen showing the fusiform body shape and contractile vacuoles in ventral and dorsal side. **b:** Optical section of oral bulge showing two shape and size types of extrusomes. **c:** The oral bulge and basket are supported by furcated fibres. **d, e:** Ciliary pattern of ventral and anterior dorsal side showing the dileptid organization. The macronucleus is moniliform and tortuous. Note the ventral excretory pores (arrowheads). **f:** Optical section showing the peculiar structure of the cilia in protargol preparations, viz., the heavily impregnated and thick distal portion. **g:** Right lateral view of shape variant. **h, i:** Resting and exploded extrusome of small type II. **j, k:** Resting and exploded extrusomes of large type I. **l, m:** Optical section and surface view showing arrangement of cortical granules. CG – cortical granules, CK – circumoral kinety, CV – contractile vacuole, EP – excretory pores, FG – fat globules, MA – macronucleus, Mi – micronucleus, PE – preoral kineties, SC – somatic cilia. Scale bars 100 μm.

Table 71. Morphometric data on *Pseudomonilicaryon japonicum* (upper line) and *Pseudomonilicaryon angustistoma* (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length [b]	372.7	349.0	71.5	16.4	19.2	239.0	544.0	19
	354.1	350.0	91.7	22.2	25.9	230.0	600.0	17
Body, width	66.1	64.0	12.0	2.8	18.2	46.0	93.0	19
	31.8	30.0	9.0	2.2	28.3	23.0	61.0	17
Body length:width, ratio	5.7	5.5	1.1	0.3	19.8	3.8	8.4	19
	11.4	11.0	2.6	0.6	22.8	7.9	17.4	17
Anterior body end to oral basket, distance [b]	131.9	134.0	35.0	8.0	26.6	65.0	184.0	19
	129.1	125.0	31.6	7.7	24.5	75.0	180.0	17
Proboscis length, % of body length [b]	35.5	33.5	8.1	1.8	22.7	22.0	54.9	19
	36.8	36.7	5.3	1.3	14.3	25.0	45.7	17
Anterior body end to macronucleus, distance [b]	166.7	166.0	40.7	9.3	24.4	86.0	231.0	19
	154.5	160.0	39.0	9.5	25.2	95.0	230.0	17
Nuclear figure, length	145.8	134.0	37.6	9.1	25.8	91.0	206.0	17
	108.8	94.0	54.2	13.2	49.8	45.0	250.0	17
Macronucleus, length of largest, straight segment	22.4	23.0	5.9	1.3	26.2	13.0	36.0	19
	16.9	15.0	6.6	1.6	38.9	10.0	40.0	17
Macronucleus, width of largest, straight segment	6.8	6.0	1.6	0.4	23.0	5.0	10.0	19
	6.7	7.0	1.1	0.3	16.5	5.0	9.0	17
Micronuclei, length	4.4	4.0	–	–	–	3.5	5.0	19
	2.8	3.0	–	–	–	2.0	3.5	17
Micronuclei, width	2.9	3.0	–	–	–	2.0	3.0	19
	2.8	3.0	–	–	–	2.0	3.3	17
Anterior body end to last dikinetid of dorsal brush, distance	117.1	111.0	25.4	5.8	21.7	80.0	156.0	19
	109.4	110.0	35.0	8.5	31.9	60.0	200.0	17
Macronuclear segments, number	28.1	27.0	4.5	1.0	15.9	20.0	35.0	19
	17.8	16.0	8.6	2.1	48.2	8.0	44.0	17
Micronuclei, number	20.2	21.0	4.4	1.0	21.9	12.0	27.0	19
	8.5	8.0	3.6	0.9	42.3	3.0	18.0	17
Somatic ciliary rows, number in mid-body	39.1	40.0	4.9	1.1	12.6	28.0	48.0	19
	38.9	40.0	5.2	1.3	13.3	30.0	50.0	17
Basal bodies in 10 µm in mid-body, number	7.5	7.0	1.2	0.3	15.6	5.0	9.0	19
	4.8	5.0	1.1	0.3	23.5	3.0	7.0	17
Dorsal brush rows, number	17.6	18.0	–	–	–	13.0	24.0	5
	8.7	10.0	–	–	–	5.0	10.0	15
Oral basket opening, length			about same as width					
	24.6	25.0	5.5	1.5	22.4	18.0	37.0	14
Oral basket opening, width in ventral view	18.6	18.5	2.5	0.6	13.4	15.0	25.0	18
	10.3	10.0	1.6	0.5	15.9	8.0	14.0	10

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Proboscis, if curved, not "extended".

side of proboscis, where up to 18 left lateral kineties are differentiated to brush rows anteriorly, forming a staggered pattern. Bristles rod-shaped, paired and 3–4 µm long in anterior portion of brush rows, while single and about 1.5–2 µm long in posterior (Fig. 87d–f; 337a, b, h–j, m–s; Table 71).

Oral apparatus as in → *Dileptus*, that is, conspicuous and composed of fine fibres forming an inner and outer basket about 19 µm across; a single, SEM prepared specimen has an elliptical basket opening and thus possibly belongs to another species. Circumoral kinety made of dikinetids, while apparently composed of single granules around pharyngeal opening (for details, see GRAIN & GOLINSKA 1969). Many preoral kineties left of circumoral kinety, individual kineties counter-clockwise inclined and regularly spaced, except for some irregularities distally, usually composed of three closely spaced basal bodies (Fig. 87c, d; 337o, p; Table 71).

Occurrence and ecology: To date found only at type location, that is, in a slightly acidic (pH 5.9) non-flooded Petri dish culture containing tree and soil mosses from the surroundings of the "Spring of Wisdom" in Kyoto, Japan. Recently found in forest moss from Venezuela, but with a shape rather similar to that of → *P. angustistoma*, that is, with a short tail.

Classification and comparison with similar species: This species is affiliated to *Pseudomonilicaryon* FOISSNER, 1997b, according to its *Dileptus*-like oral ciliature and the moniliform macronucleus (for genus discussion, see *P. massutii*). *Pseudomonilicaryon japonicum* highly resembles *Dileptus falciformis* KAHL, 1931b, but lacks the pharyngeal extrusomes emphasized by KAHL (1931b). The pharyngeal extrusomes are a special feature documented by micrographs in *D. costaricanus* FOISSNER, 1995. We consider pharyngeal extrusomes as relevant at species level because we know of two further, undescribed species with the same feature, showing that such species comprise a distinct evolutionary line.

According to DRAGESCO (1963) and FOISSNER (1997b), there are some other similarly sized species with a moniliform macronucleus: *Dileptus thononensis* DRAGESCO, 1960 (with distinct tail, 60–70 macronuclear segments, freshwater interstitial); *Dileptus marinus* KAHL, 1933 (450–700 µm, with distinct tail, marine); *Dileptus cygnus* (CLAPARÈDE & LACHMANN, 1859) KAHL, 1931b (400–600 µm, short and slender tail, proboscis usually distinctly longer than trunk, freshwater); *Monilicaryon monilatus* (STOKES, 1886b) JANKOWSKI, 1967b (no preoral kineties, usually 400–700 µm, with short tail).

***Pseudomonilicaryon angustistoma* nov. spec.** (Fig. 88a–f; 338a–j; Table 71)

Diagnosis: Size about 400 × 35 µm in vivo. Fusiform with distinct tail, proboscis occupies about 37% of body length. Macronucleus moniliform, composed of 18 segments on average. Many contractile vacuoles in dorsal side of trunk and proboscis. Two shape and size types of oral extrusomes: type I acicular and about 6 µm long; type II rod-shaped and approximately 2 µm long. On average 39 ciliary rows, up to 10 anteriorly differentiated to dorsal brush. Oral opening distinctly elliptical (~ 25 × 10 µm).

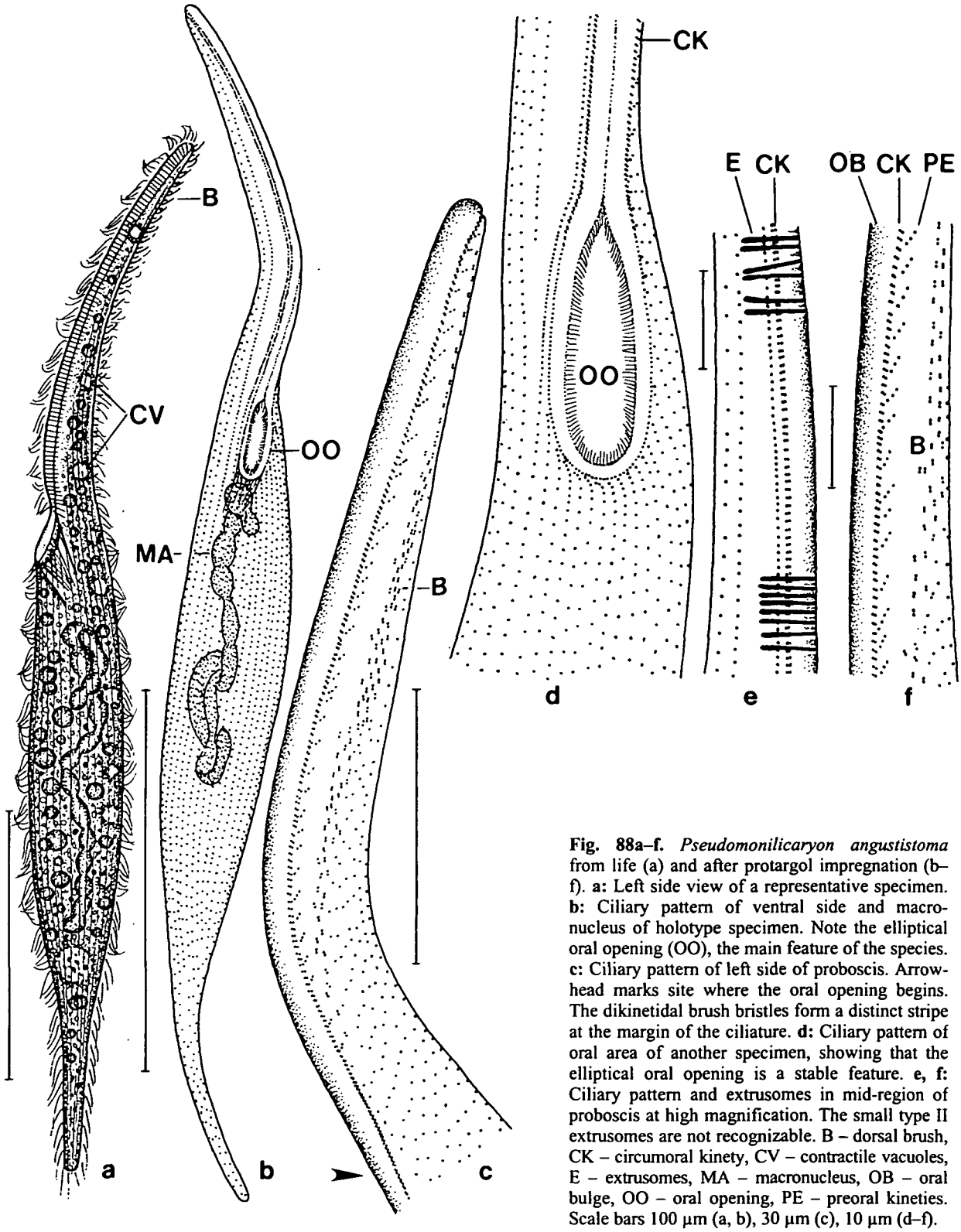

Fig. 88a–f. *Pseudomonilicaryon angustistoma* from life (a) and after protargol impregnation (b–f). **a:** Left side view of a representative specimen. **b:** Ciliary pattern of ventral side and macronucleus of holotype specimen. Note the elliptical oral opening (OO), the main feature of the species. **c:** Ciliary pattern of left side of proboscis. Arrowhead marks site where the oral opening begins. The dikinetidal brush bristles form a distinct stripe at the margin of the ciliature. **d:** Ciliary pattern of oral area of another specimen, showing that the elliptical oral opening is a stable feature. **e, f:** Ciliary pattern and extrusomes in mid-region of proboscis at high magnification. The small type II extrusomes are not recognizable. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuoles, E – extrusomes, MA – macronucleus, OB – oral bulge, OO – oral opening, PE – preoral kineties. Scale bars 100 μm (a, b), 30 μm (c), 10 μm (d–f).

Type location: Mud and soil from road puddles in the Bambatsi Guest Farm, Namibia, 20°10'S 15°25'E (site 49 in figure 2 and chapter 2.1.2).

Etymology: Apposite noun composed of the Latin adjective *angustus* (narrow) and the Greek noun *stoma* (mouth), meaning "the narrow-mouthed *Pseudomonilicaryon*", the main feature of the species.

Description and comparison with related species: *Pseudomonilicaryon angustistoma* is similar to → *P. japonicum*, except for the more slender body (length:width ratio 11.4:1 vs. 5.7:1, but about 8:1 in an Venezuelan population), a distinctly higher number of macronuclear nodules (19 vs. 28), and the elliptical (vs. circular) oral opening (Fig. 88b, d; 338a; Table 71). Thus, the reader is referred to the description of → *P. japonicum* and to the detailed figures, figure explanations, and morphometrics of *P. angustistoma*.

The most important difference between *P. angustistoma* and other species, for instance, *Dileptus marinus*, is the elliptical oral opening, a special feature resembling *Dimacrocaryon amphileptoides*, as redescribed by FOISSNER (1984), and especially, *Pelagodileptus trachelioides*, as reviewed by FOISSNER et al. (1999). Indeed, this pelagic species has remarkable similarities (size, shape, macronuclear pattern) with *Pseudomonilicaryon angustistoma*, but is distinctly stouter (5:1 vs. 11.4:1), has 120–200 ciliary rows (vs. 39), and is usually packed with symbiotic green algae (zoochlorellae). For differentiation from other, more distantly related species, see → *P. japonicum*.

Occurrence and ecology: To date found only at type location, but a similar or even the same species occurs in Venezuela, South America. The slender body indicates that *P. angustistoma* is a terrestrial species.

Actinobolina multinucleata nov. spec. (Fig. 89a–n; 339a–x, 340a–d; Table 72)

Diagnosis: Size about 85 × 55 µm in vivo; ellipsoidal. An average of 22 macronuclear nodules and 18 ciliary rows, each associated with about 8 tentacles.

Type location: Mud and soil from road puddles in the Bambatsi Guest Farm, Namibia, 20°10'S 15°25'E (site 49 in figure 2 and chapter 2.1.2).

Etymology: The Latin adjective *multinucleata* (having many nuclei) refers to the numerous macronuclear nodules, the main feature of the species.

Description: Size 70–100 × 40–70 µm in vivo, while distinctly shrunken and thus only 52–74 × 40–68 µm in protargol preparations. Well-nourished specimens ovoidal, rarely obovoidal when swimming; ellipsoidal to broadly ellipsoidal when floating; and elongate ellipsoidal to cylindroidal under prolonged cover glass stay (Fig. 89a, b, i–l; 339a–f; Table 72). Transparent, undernourished specimens, as occurring in the old Petri dish culture and used for studying the ciliary pattern, up to 2:1 flattened and with some long tentacles posteriorly. Macronuclear nodules numerous, namely 22 on average, scattered, globular, ellipsoidal or reniform; nucleoli globular. Two to eleven, usually five globular micronuclei adjacent to macronuclear nodules (Fig. 89c, h; 339i–k; Table 72). Contractile vacuole terminal, surrounded by contributory vesicles during diastole, with four to six excretory pores

in posterior pole area. Cortex basically almost smooth, but ribbed in optical section due to the bulb-like structures formed by retracting and retracted tentacles; contains loosely spaced granules about 0.4 µm across (Fig. 89b, g, h; 339f, h, k, q–s, w, x, 340a, c, d). Six to ten, usually eight almost equidistant tentacles associated with each ciliary row; individual tentacles usually at anterior left end of a small cluster of cilia and associated with a short fibre (?) extending anteriad and a granule (microtubular array and/or extrusome tip?) recognizable only in protargol preparations. Tentacles radially spread and up to 60 µm long in floating specimens, while more or less withdrawn into body in swimming and disturbed cells forming a conspicuous, ring-like array in mid-body; entrance of withdrawn tentacles into body proper surrounded by a minute collar and/or small bulbs recognizable in the scanning electron microscope; distal tentacle portion bent in rotating and tortuous in silver carbonate-impregnated specimens. Extrusomes (toxicysts) in distal portion of tentacles, rod-shaped to slightly capitate, about 11 × 0.8 µm and highly refractive in vivo; often curved in protargol preparations and occasionally with a lanceolate or rhomboidal tip in silver carbonate preparations (Fig. 89a–h, m, n; 339a–g, i, k, m, o, r, t, v–x, 340a, b). Cells dark at low magnification due to numerous fat globules, likely digested prey ciliates, such as *Halteria grandinella* occasionally identified in the food vacuoles. Swims rather rapidly by rotation about main body axis, floats for long times with more or less extended tentacles and rather fast metachronal ciliary waves when lurking for prey. Divides in freely motile (non-encysted) condition.

Ciliary rows equidistantly and meridionally to slightly spirally arranged, composed of 20–22 µm long cilia scattered in circumoral area, while forming more or less large and distinct clusters with tentacles postorally. Fine structure of individual clusters rather different in protargol and silver carbonate preparations (Fig. 89d, g, m, n; 339l–r, v, 340b). Protargol impregnation usually reveals some cilia forming a minute, slightly oblique row with a barren granule each at its anterior left end and left posterior of the tentacle, which is associated with a granule (microtubular array and /or extrusome tip?) and a short fibre (?); both granules not revealed by silver carbonate. Silver carbonate impregnation shows the ciliated basal bodies of the clusters as conspicuous, minute rods likely composed of two granules, the right of which is associated with a short, anteriorly extending structure (kinetodesmal fibre?); furthermore, a minute, oblique structure (probably the support wall according to the TEM observations of HOLT et al. 1973) often traverses or touches the anteriormost basal body complex producing an argyrophilic accumulation at anterior end of cluster. Scattered circumoral basal bodies smaller and more globular than those of clusters.

One tentacle-free, distinct dorsal brush row extends to rear quarter or fifth of cell and continues as ordinary somatic kinety posteriorly; rarely, two long rows are present; composed of single or paired, frequently slightly inflated bristles < 1–3 µm long; frequently, the anterior portion of one or two adjacent ciliary rows also bears scattered or aligned bristles between ordinary cilia and tentacles. Brush kinetids inconspicuous in silver carbonate preparations because lacking fibrillar associates and globular, that is, not rod-shaped as the somatic ordinary kinetids (Fig. 89d, g; 339m, q, s, u–x, 340c, d).

Oral opening in anterior pole centre, covered by an about 3 µm high bulge with a slight central indentation (Fig. 89a, c, d, g; 339 l, p, u, v, 340b). Circumoral ciliary row at base of oral bulge, composed of closely spaced, rather often somewhat irregularly arranged basal bodies and surrounded by scattered, likely oralized somatic monokinetids associated with fine nematodesmata in protargol preparations (minute, slightly oblique rows of 1–3 basal bodies according to the TEM observations of HOLT et al. 1973); no fibrillar associates revealed by

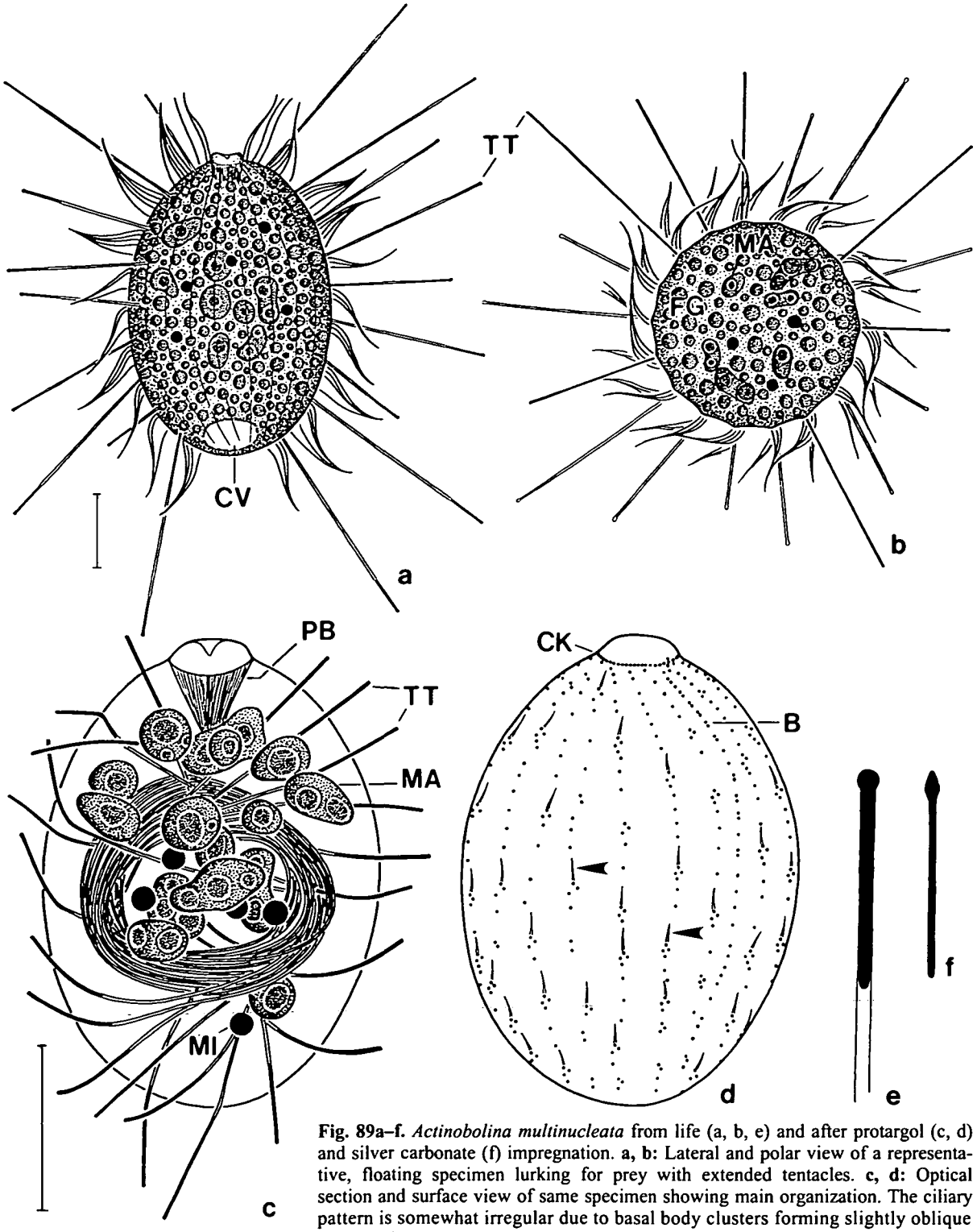

Fig. 89a–f. *Actinobolina multinucleata* from life (a, b, e) and after protargol (c, d) and silver carbonate (f) impregnation. **a, b:** Lateral and polar view of a representative, floating specimen lurking for prey with extended tentacles. **c, d:** Optical section and surface view of same specimen showing main organization. The ciliary pattern is somewhat irregular due to basal body clusters forming slightly oblique rows with two granules at the anterior left end. The anterior granule is at tentacle entrance into body proper and associated with a fibre (?; arrowheads). **e:** Tentacle containing an about 11 µm long extrusome (toxicyst). **f:** Extrusome with lanceolate tip. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuole, FG – fat globules, MA – macronuclear nodules, MI – micronucleus, PB – pharyngeal basket, TT – tentacles forming a ring-like array. Scale bars 20 µm.

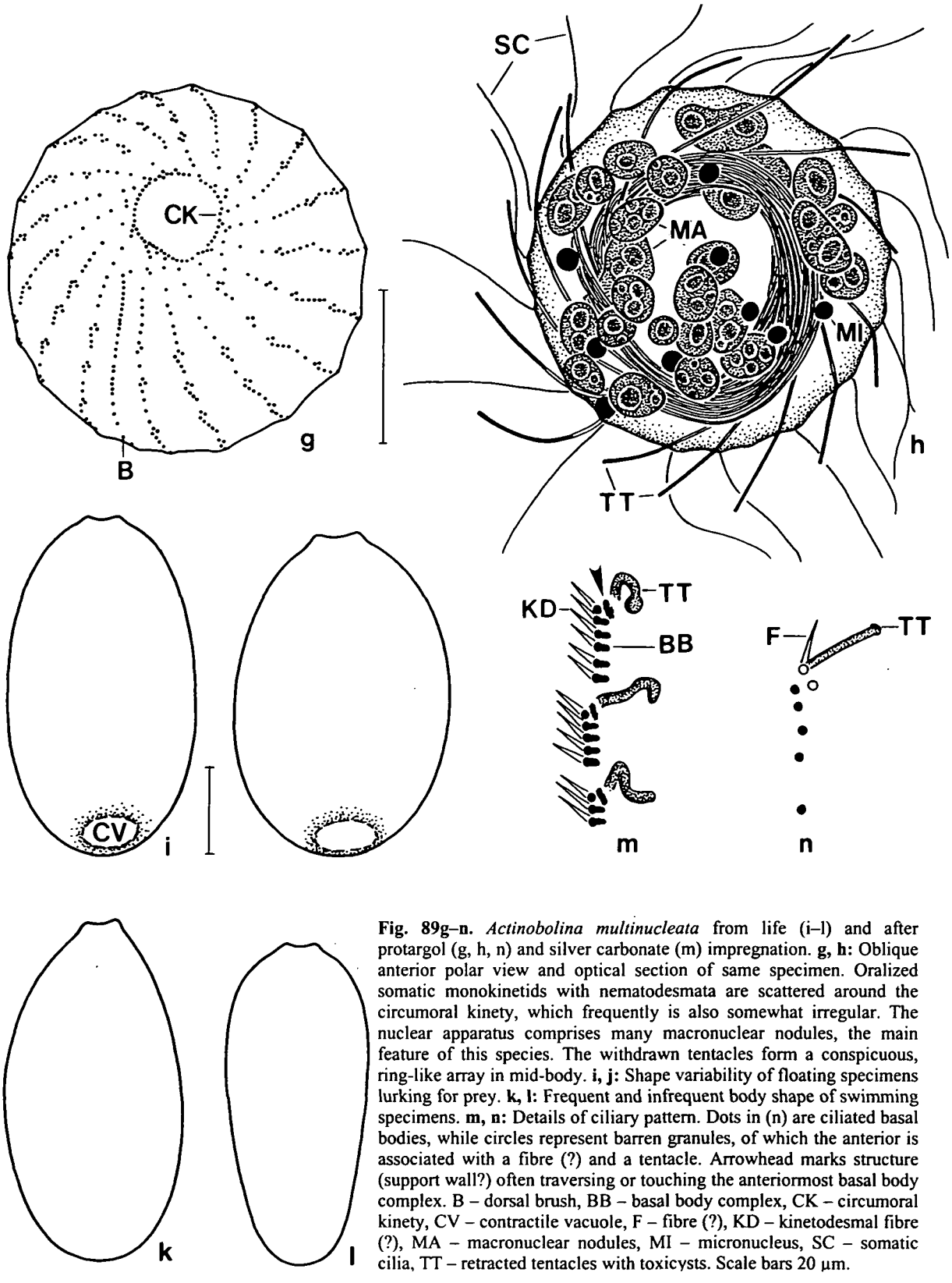

Fig. 89g–n. *Actinobolina multinucleata* from life (i–l) and after protargol (g, h, n) and silver carbonate (m) impregnation. **g, h:** Oblique anterior polar view and optical section of same specimen. Oralized somatic monokinetids with nematodesmata are scattered around the circumoral kinety, which frequently is also somewhat irregular. The nuclear apparatus comprises many macronuclear nodules, the main feature of this species. The withdrawn tentacles form a conspicuous, ring-like array in mid-body. **i, j:** Shape variability of floating specimens lurking for prey. **k, l:** Frequent and infrequent body shape of swimming specimens. **m, n:** Details of ciliary pattern. Dots in (n) are ciliated basal bodies, while circles represent barren granules, of which the anterior is associated with a fibre (?) and a tentacle. Arrowhead marks structure (support wall?) often traversing or touching the anteriormost basal body complex. B – dorsal brush, BB – basal body complex, CK – circumoral kinety, CV – contractile vacuole, F – fibre (?), KD – kinetodesmal fibre (?), MA – macronuclear nodules, MI – micronucleus, SC – somatic cilia, TT – retracted tentacles with toxicysts. Scale bars 20 μm.

silver carbonate impregnation. Oral basket conical, composed of many fine fibres and thus hardly recognizable in vivo, while usually faintly impregnated with protargol; fine structure likely as described in *Belonophrya pelagica* by FOISSNER et al. (1999).

Occurrence and ecology: Basically, *Actinobolina* spp. are planktonic ciliates, but occur also in small, ephemeral waters (DINGFELDER 1962, FOISSNER et al. 1999). Thus, our habitat, mud from ephemeral pools, is not exceptional. As yet, we found *A. multinucleata* only in a sample from the type location, where it developed a few days after rewetting the material and stayed for several weeks. However, well-nourished specimens occurred mainly during the first couple of weeks. As the genus *Actinobolina* is comparatively well-known, the Namibian species might have a restricted Palaeotropic or Gondwanan distribution.

Table 72. Morphometric data on *Actinobolina multinucleata.*

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	63.6	66.0	6.9	1.8	10.9	52.0	74.0	15
Body, width	52.4	50.0	7.7	2.0	14.8	40.0	68.0	15
Body length:width, ratio	1.2	1.2	0.2	0.0	13.7	1.1	1.7	15
Oral basket, distal diameter	9.1	9.0	1.9	0.5	20.6	5.0	12.0	15
Macronuclear nodules, length [b]	12.4	10.0	4.9	1.3	39.7	8.0	28.0	15
Macronuclear nodules, width [b]	7.2	6.0	1.6	0.4	22.4	5.0	10.0	15
Micronuclei, diameter	3.1	3.0	0.7	0.2	22.9	1.0	4.0	15
Macronuclear nodules, number [c]	22.0	23.0	6.1	1.1	27.7	4.0	31.0	30
Micronuclei, number	5.4	5.0	2.7	0.7	49.4	2.0	11.0	15
Somatic ciliary rows, number	18.6	18.0	1.1	0.3	5.7	17.0	21.0	15
Kinetids in a ciliary row, number	30.9	30.0	8.7	2.2	28.2	19.0	56.0	15
Tentacles (toxicysts) per ciliary row, number	7.7	8.0	1.2	0.3	15.3	6.0	10.0	15

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Largest nodule of each specimen.

[c] Four globular nodules in one out of 30 specimens.

Comparison with related species: The genus *Actinobolina* was revised by FOISSNER et al. (1999). *Actinobolina multinucleata* has all features of the genus and differs from its congeners mainly by the number of macronuclear nodules: about 22 in *A. multinucleata*; two in *A. wenrichii* WANG & NIE, 1933; and a long, tortuous strand in *A. radians* (STEIN, 1867) STRAND, 1928, *A. vorax* (WENRICH, 1929) KAHL, 1930a, and *A. smalli* HOLT, LYNN & CORLISS, 1973. Furthermore, *Actinobolina wenrichii* and *A. smalli* have symbiotic algae. The descriptions of *Actinóbolus rotundus*[12] and *Actinóbolus piriformis* by ESCOMEL

[12] STRAND (1928) established *Actinobolina* as replacement name for *Actinobolus* STEIN, 1867, preoccupied by a coleopteran genus.

(1929) are insufficient, especially due to the lack of illustrations. However, the author mentions one large macronucleus in *A. rotundus* and a maximum body length of about 30 µm in *A. piriformis*. Thus, both species are obviously not conspecific with our specimens, which have many macronuclear nodules and measure 70–100 × 40–70 µm.

The genus *Belonophrya*, a close relative of *Actinobolina*, was resurrected by FOISSNER et al. (1999), who redescribed the type species, *Belonophrya pelagica*. It differs distinctly from *A. multinucleata* by the number of macronuclear nodules (1 vs. about 22). Additionally, it has more ciliary rows (27 vs. 18) and lantern-shaped extrusomes in protargol preparations.

CYRTOPHORIDA

Cyrtophorida are rare in soil for unknown reasons, although some species are quite frequent, especially in leaf litter (FOISSNER 1987d, 1998a). In Namibia, we found only known species, except of the new subspecies of *Odontochlamys alpestris* described below.

Odontochlamys CERTES, 1891

Improved diagnosis: Small to medium-sized Chilodonellidae with apical dorsal brush. Ventral ciliary field depressed, composed of a left and right portion distinctly separated by a blank stripe postorally. Ciliary rows of right field curved anteriorly. Dorsal hump large, often projecting above ventral surface and conspicuously wrinkled, rarely rather regularly serrated. Encystment fast and easily induced.

Type species: *Odontochlamys gouraudi* CERTES, 1891.

Comparison with related genera: KAHL (1931b), WENZEL (1953), BUITKAMP (1977a), and DRAGESCO & DRAGESCO-KERNÉIS (1986) synonymized *Odontochlamys* CERTES, 1891 with *Chilodonella* STRAND, 1928. Based on detailed investigations of the type species and *O. alpestris*, FOISSNER (1981b, 1988b) resurrected the genus with an improved diagnosis. The reinvestigation of *O. convexa* by BLATTERER & FOISSNER (1992) and *O. wisconsinensis* by PETZ & FOISSNER (1997), as well as the new subspecies described here support FOISSNER's suggestion that the apical location of the dorsal brush is the most important feature for distinguishing *Odontochlamys* and *Chilodonella*.

Odontochlamys alpestris FOISSNER, 1981

We split this species into two subspecies according to the number of dorsal brush cilia and left field kineties. The improved diagnosis is based on the revision by FOISSNER et al. (1991) and the original descriptions of a soil and a freshwater population (BLATTERER & FOISSNER 1992, FOISSNER 1981b).

Improved diagnosis: Size about 40–50 × 20–30 µm in vivo; outline elliptical to ovoidal, dorsal hump irregularly wrinkled. Right ciliary field with 5 rows, left with 5–7. Dorsal brush composed of 2 or 3–9 cilia. Pharyngeal basket with about 8 rods.

Odontochlamys alpestris alpestris FOISSNER, 1981b **nov. stat.**

Diagnosis: Dorsal brush composed of 3–9, usually 4–7 cilia. Left ciliary field with 6–7 rows.

Locus classicus: Alpine grassland soil in the surroundings of the "Wallack-Haus" at the Grossglockner-Hochalpenstrasse (Hohe Tauern, Austria).

Odontochlamys alpestris biciliata nov. sspec. (Fig. 90a–u; 341a–h; Table 73)

Diagnosis: Dorsal brush invariably composed of 2 cilia. Left ciliary field with 5 rows.

Type location: Highly saline soil from coast of Curaçao Island at the north coast of Venezuela, 12°N 71°W.

Etymology: Composite of the Latin prefix *bi* (two) and adjective *ciliatus* (ciliated), referring to the two dorsal brush cilia. *Odontochlamys* has feminine gender, not masculine as stated by AESCHT (2001).

Description: Size highly variable, that is, 30–55 × 20–35 µm in vivo, usually about 40 × 25 µm, as calculated from measurements of live specimens and values shown in table 72, assuming a length shrinkage of about 15% due to the preparation procedures. Shape complex and rather variable (Fig. 90a, g, k–s; 341a). Outline elliptical in ventral and dorsal view, with anterior left end bluntly pointed and posterior broadly rounded; distinctly dorsoventrally flattened in preoral area (up to 8:1), while less so in vaulted postoral portion (about 1.7:1); very flexible but acontractile, except for thin preoral portion, which contracts slightly when specimens touch an obstacle. Ventral side with conspicuous postoral depression, left margin straight to slightly sigmoidal, right distinctly convex. Dorsal side flattened in preoral portion, while conspicuously vaulted in postoral, producing a bowl-shaped transverse view together with the hollowed ventral side. Dorsal hump about 13% back from anterior body end, conspicuous, distinctly set off from thin preoral region, elliptical, laterally usually projects distinctly above ventral surface; numerous concentric, argyrophilic fibres extend on hump and probably contract ventral side during encystment. Anterior hump region often with prominent slope, occasionally with furrow parallel to anterior margin; mid-region frequently with short furrow extending obliquely anteriad from left margin; posterior region occasionally with some lobes. Macronucleus in variable position, broadly ellipsoidal, of centric heteromeric type; peripheral orthomere composed of granules in vivo, while with several nucleoli about 1 µm across in protargol preparations, surrounds paramere with central, globular endosome. Two globular macronuclei in two out of 30 specimens, of which one also has a macronuclear anlage. Although no conjugants were seen in vivo and the preparations, a quarter of the specimens had a macronuclear anlage, whose transformation to a new nucleus takes about 80 hours (PYNE et al. 1974); anlage in posterior body portion, broadly ellipsoidal and up to three times larger than the ordinary macronucleus and thus very prominent, usually impregnates more lightly and homogenously. Micronucleus in variable position, about 3 µm across and surrounded by distinct membrane in vivo, frequently not impregnated with protargol (Fig. 90a, c, h, j; 341a, c). Two contractile vacuoles usually obliquely opposed; right vacuole 25–37% (n = 4) back from anterior body end and slightly right of midline, left vacuole more posteriorly, namely, 38–58% back from anterior end and near left body margin; excretory pores recognizable neither in protargol nor KLEIN-FOISSNER silver nitrate preparations. Cytoplasm finely granulated or opaque. Food vacuoles 3–4 µm across, optically empty or containing bacterial remnants, especially spores. Glides rather quickly on large substrate

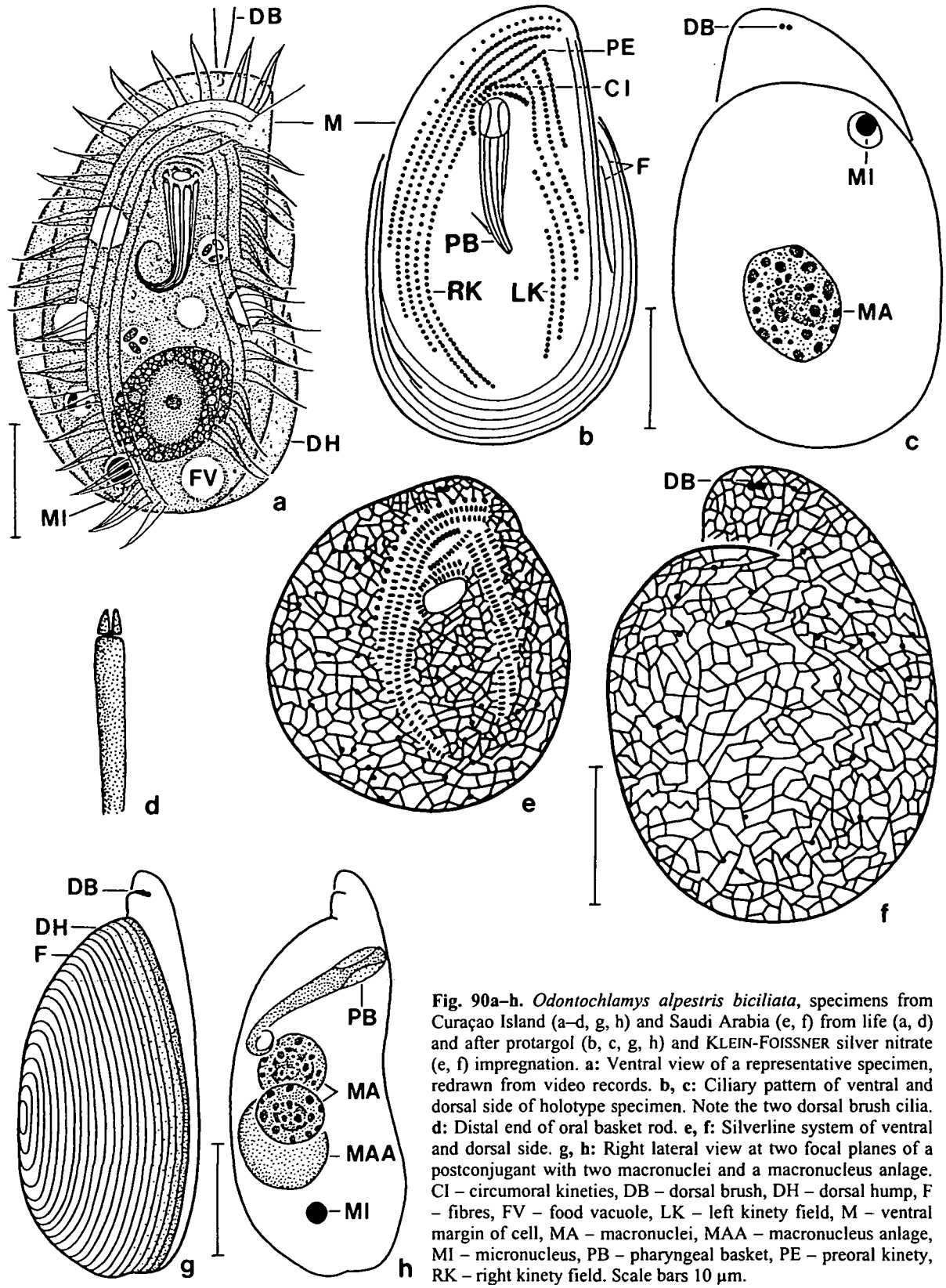

Fig. 90a–h. *Odontochlamys alpestris biciliata*, specimens from Curaçao Island (a–d, g, h) and Saudi Arabia (e, f) from life (a, d) and after protargol (b, c, g, h) and KLEIN-FOISSNER silver nitrate (e, f) impregnation. **a:** Ventral view of a representative specimen, redrawn from video records. **b, c:** Ciliary pattern of ventral and dorsal side of holotype specimen. Note the two dorsal brush cilia. **d:** Distal end of oral basket rod. **e, f:** Silverline system of ventral and dorsal side. **g, h:** Right lateral view at two focal planes of a postconjugant with two macronuclei and a macronucleus anlage. CI – circumoral kineties, DB – dorsal brush, DH – dorsal hump, F – fibres, FV – food vacuole, LK – left kinety field, M – ventral margin of cell, MA – macronuclei, MAA – macronucleus anlage, MI – micronucleus, PB – pharyngeal basket, PE – preoral kinety, RK – right kinety field. Scale bars 10 µm.

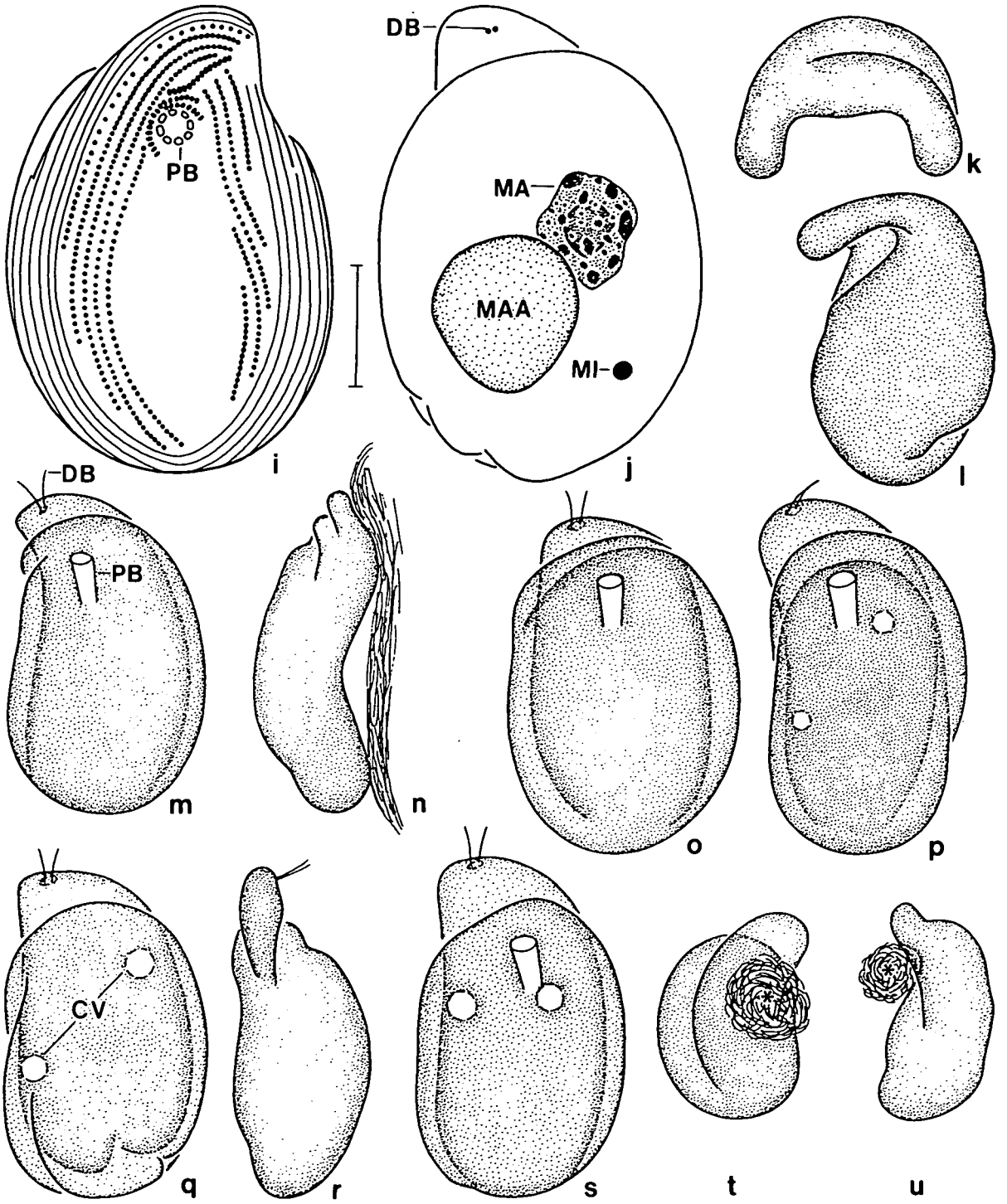

Fig. 90i–u. *Odontochlamys alpestris biciliata* from Curaçao after protargol impregnation (i, j) and from life (k–u; redrawn from video records). **i, j:** Ciliary pattern of ventral and dorsal side of a postconjugate. **k:** Transverse optical section at mid-body. **l:** Ventrolateral view showing ventrally bent, contractile anterior cell portion. **m, n:** Dorsal view and optical section of a specimen crawling over organic debris. **o, p:** Dorsal views of same specimen showing contractility of thin anterior region. **q, r:** Dorsal and left lateral view of same specimen. **s:** Dorsal view. **t, u:** Ventrolateral and lateral view of specimens handling organic debris (asterisks). CV – contractile vacuoles, DB – dorsal brush, MA – macronucleus, MAA – macronucleus anlage, MI – micronucleus, PB – pharyngeal basket. Scale bar 10 µm.

particles and microscope slide; sometimes handles small organic debris by curving around the thin, contractile anterior portion (Fig. 90t, u).

Somatic cilia about 6 µm long. Ventral ciliary rows arranged in a left and right field leaving blank broad, postoral stripe, posteriorly gradually shortened (right field) or staggering (left field) and curved towards body midline; composed of monokinetids with circular outline in protargol preparations, while elliptical in KLEIN-FOISSNER silver nitrate preparations, probably due to an associated parasomal sac. Invariably five arched kineties in right field, commence near left anterior body end above preoral kinety, except for the innermost row which commences at level of oral basket opening; outermost kinety rather loosely ciliated, especially in mid-region. Invariably five almost straight left field kineties, commence underneath preoral kinety, except for the two innermost rows, which are highly variable in length and commence near mid-body. Dorsal brush apical left of midline, in all populations composed of only two 7 µm long and stiff cilia arising from a distinct pit (Fig. 90a–c, e, f, i, j; 341d–h; Table 73).

Oral ciliature *Chilodonella*-like, that is, comprises a preoral and two circumoral kineties, all composed of closely spaced dikinetids having only the right (anterior) basal body ciliated, according to the TEM observations of *Chilodonella cyprini* by HOFMANN (1987). Preoral kinety slightly curved, commences underneath anterior end of middle kinety of right field and extends obliquely to body midline above circumoral kinety. Circumoral kineties arched, form Y-pattern, anterior row composed of about 15–18 dikinetids, posterior of circa 10–11. Oral opening in body midline about 22% back from anterior end. Oral basket cornucopia-shaped, extends obliquely to dorsal side and posteriad, composed of about eight rather thick, toothed rods; distal end bulbous in protargol preparations (Fig. 90a, b, d, e, h, i; 341a, c).

Silverline pattern of Saudi Arabian specimens as in *O. alpestris alpestris* (FOISSNER 1981b), that is, narrowly meshed with argyrophilic granules in some intersections (Fig. 90e, f; 341d–f).

Encystment as in congeners (BLATTERER & FOISSNER 1992, FOISSNER 1981b, 1988b), that is, conspicuously fast under slight cover glass pressure and when drop evaporates.

Occurrence and ecology: *Odontochlamys alpestris biciliata* was discovered in a soil sample collected by Maria WALDHÖR on 28.02.1993 at the coast of Caracas Bay, Curaçao Island. The sample was an alkaline (pH 8.1), highly saline mixture of grass litter and humus. Furthermore, we found the species in several other soils world-wide, e.g., in a slightly acidic (pH 6.0), highly saline soil from the Al-Hassa Oasis in Saudi Arabia and in the circumneutral (pH 6.7), mud and soil from Namibian site (49). Obviously, *O. alpestris biciliata* is a euryhaline and cosmopolitan ciliate preferring terrestrial habitats.

The congeners also prefer edaphic habitats, although some populations of *O. alpestris alpestris* and *O. gouraudi* have been recorded from freshwater (BLATTERER & FOISSNER 1992, BUITKAMP 1977a, CERTES 1891, FOISSNER 1981b, 1988b, WENZEL 1953).

Comparison with similar species: Our population is affiliated with *Odontochlamys*, according to the improved genus diagnosis above. The structure of the dorsal brush is an important species feature of chilodonellids (FOISSNER 1988b, KAHL 1931b). Thus, it seems justified to establish a new subspecies for our populations, which differs from all congeners and especially *O. alpestris alpestris* by the number of dorsal brush cilia: invariably 2 in all populations of *O. alpestris biciliata*; 3–6 ($\bar{x}$ = 4) in soil and 6–9 ($\bar{x}$ = 7.4) in fresh-

water populations of *O. alpestris alpestris* (BLATTERER & FOISSNER 1992, FOISSNER 1981b); 4–5 in *O. convexa* (BLATTERER & FOISSNER 1992); 11–15 in *O. gouraudi* (FOISSNER 1988b); and 3–5 ($\bar{x}$ = 4) in *O. wisconsinensis* (PETZ & FOISSNER 1997). The number of kineties in the left ciliary field also distinguishes *O. alpestris biciliata* from the congeners (invariably 5 vs. 6–7; Table 73).

At first glance, *Thigmogaster nanus* SONG & WILBERT, 1989, *T. oppositevacuolatus* AUGUSTIN & FOISSNER, 1989, and *T. potamophilus* FOISSNER, 1988b resemble *O. alpestris biciliata* because they have the same number of ventral ciliary rows and two distinct dorsal brush cilia. However, the ventral kinety fields are much closer together in *Thigmogaster* than in *Odontochlamys*, changing the overall ciliary pattern distinctly. Furthermore, *Thigmogaster* species have a peculiar third dorsal brush cilium at level of oral entrance, a flat ventral side, and live in freshwater (AUGUSTIN & FOISSNER 1989, FOISSNER 1988b, SONG & WILBERT 1989).

Table 73. Morphometric data on two populations of *Odontochlamys alpestris biciliata*: CU – from Curaçao Island, SA – from Saudi Arabia.

Characteristics [a]	Population	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	CU	35.2	35.5	5.8	1.1	16.6	26.0	48.0	30
	SA	29.5	30.0	2.4	0.6	8.2	25.0	34.0	15
Body, width	CU	26.1	25.0	5.2	1.3	19.8	20.0	35.0	15
	SA	22.0	23.0	2.9	0.7	13.2	16.0	28.0	15
Body, height	CU	13.9	14.0	1.5	0.4	11.0	11.0	16.0	15
Body length:width, ratio	CU	1.5	1.5	0.1	0.0	7.8	1.3	1.7	15
	SA	1.4	1.3	0.1	0.0	8.3	1.2	1.6	15
Body length:height, ratio	CU	2.3	2.3	0.2	0.1	10.5	1.9	2.7	15
Anterior body end to pharyngeal basket, distance	CU	7.6	8.0	1.0	0.3	13.7	6.0	10.0	15
	SA	6.3	6.0	1.3	0.3	21.3	4.0	9.0	15
Anterior body end to dorsal hump, distance	CU	4.5	5.0	0.8	0.2	18.7	3.0	6.0	15
	SA	3.1	3.0	0.9	0.3	28.2	2.0	5.0	10
Anterior body end to macronucleus, distance [b]	CU	16.4	18.0	3.9	1.0	23.9	9.0	21.0	15
Distance between right and left kinety field [c]	CU	8.5	9.0	1.9	0.5	22.3	5.0	11.0	15
Macronuclei, length [b]	CU	10.8	10.0	1.7	0.4	15.3	9.0	14.0	15
Macronuclei, width [b]	CU	7.9	8.0	1.3	0.3	16.6	6.0	10.0	15
Micronucleus, length	CU	2.7	3.0	–	–	–	1.5	4.0	15
Micronucleus, width	CU	2.3	2.5	–	–	–	1.5	3.0	15
Pharyngeal basket, distal diameter	CU	3.2	3.0	–	–	–	2.5	4.0	15
Pharyngeal basket, length [d]	CU	10.0	10.0	1.1	0.3	10.7	9.0	13.0	15
Innermost row of left kinety field, length	CU	9.3	9.0	3.4	0.9	36.4	5.0	18.0	15
2nd innermost row of left kinety field, length	CU	12.3	11.0	3.6	0.9	29.5	8.0	21.0	15
Preoral kinety, length [e]	CU	4.2	4.0	–	–	–	4.0	6.0	15
Macronuclei, number [f]	CU	1.1	1.0	–	–	–	1.0	2.0	30
Micronucleus, number	CU	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Right kinety field, number of rows	CU	5.0	5.0	0.0	0.0	0.0	5.0	5.0	15
	SA	5.0	5.0	0.0	0.0	0.0	5.0	5.0	14

(continued)

Characteristics [a]	Population	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Left kinety field, number of rows	CU	5.0	5.0	0.0	0.0	0.0	5.0	5.0	15
	SA	5.0	5.0	0.0	0.0	0.0	5.0	5.0	14
Dorsal brush, number of kinetids	CU	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15
	SA	2.0	2.0	0.0	0.0	0.0	2.0	2.0	9
Pharyngeal basket, number of rods	CU	7.7	8.0	–	–	–	6.0	8.0	15

[a] Data based on mounted, protargol-impregnated (Curaçao population) or KLEIN-FOISSNER silver nitrate-impregnated (Saudi Arabian population), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] In specimens with single, seemingly not degenerated macronucleus.

[c] At level of anterior end of innermost left kinety.

[d] Straight portion only.

[e] Measured as chord of kinety.

[f] Of 30 specimens investigated, two have 2 globular macronuclei.

SUCTORIA

As sessile organisms, suctoria and peritrichs are rare in terrestrial habitats; still, the work by PENARD (1914) is the most comprehensive study. This and our experience indicate that most terricolous suctoria are likely still undescribed. Usually, they are too rare to be studied in detail. Nevertheless, we can provide here good data from three species.

Podophrya tristriata nov. spec. (Fig. 91a–g; 342a–f, j–l; Table 74)

Diagnosis: Adults unstalked, globular, about 30 µm across in vivo, covered with thick, very hyaline mucilaginous sheath. About 50 scattered tentacles up to 120 µm long. 2 contractile vacuoles. Swarmers about 35 × 18 µm in protargol preparations, reniform, usually with 9 ciliary rows. Cysts stalked, about 30 µm across in vivo, invariably with 3 prominent transverse ribs and many small, longitudinal crests.

Type location: Soil from forest near Tinaro Dam in the surroundings of Cairns, Australia, 17°S 145°E.

Etymology: Composite of *tri* (Greek; three) and *striatus* (Latin; striated), referring to the three transverse ribs of the resting cyst.

Description: Adults unstalked, 25–60 µm, usually 30 µm across in vivo, as calculated from measurements of live specimens and values shown in table 74, assuming a shrinkage of about 10% due to the preparation procedures. Mucilaginous sheath covers body proper; although about 15–20 µm thick, inconspicuous because very hyaline and thus usually only recognizable due to attached bacteria and debris (Fig. 91a–c; 342a–c). Tentacles scattered over cell, penetrate mucilaginous sheath, numerous (about 50), all of same structure but highly variable in length (up to four-times body diameter) and about 0.5 µm thick, conspicuously zigzagging when contracting, proximal portion not conical; distal end distinctly capitate because 1–2 µm wide and 3–4 µm long, contains minute, central vacuole (?). Macronucleus in centre of cell, usually globular, packed with minute spheres in vivo, and with some nucleoli in protargol preparations. Micronucleus globular, only occasionally recognizable due to similarly sized cytoplasmic inclusions. Two opposed, peripheral contractile vacuoles surrounded by contributory vesicles during diastole (Fig. 91a; 342a); excretory pores not recognizable in protargol preparations of Australian type population, but several pores observed in live specimens from a Japanese population. Cortex about 1 µm thick and smooth. Cytoplasm colourless, packed with lipid droplets 1–4 µm across. Feeds on the heterotrophic flagellate *Polytomella* and likely also on ciliates.

Budding external by "pseudo-scissipartié" (BATISSE 1975) and as described in *P. fixa* by COLLIN (1912), that is, mother cell enlarges and forms a daughter cell bearing a ciliary stripe with usually nine rows of closely spaced basal bodies; subsequently, the daughter transforms into a motile swarmer. Aggregates of two to six cells each with a ciliary stripe, globular macronucleus, slightly fusiform (dividing?) micronucleus, and tentacles are frequent in the protargol slides (Fig. 91f); likely formed when next budding commences before previous complete.

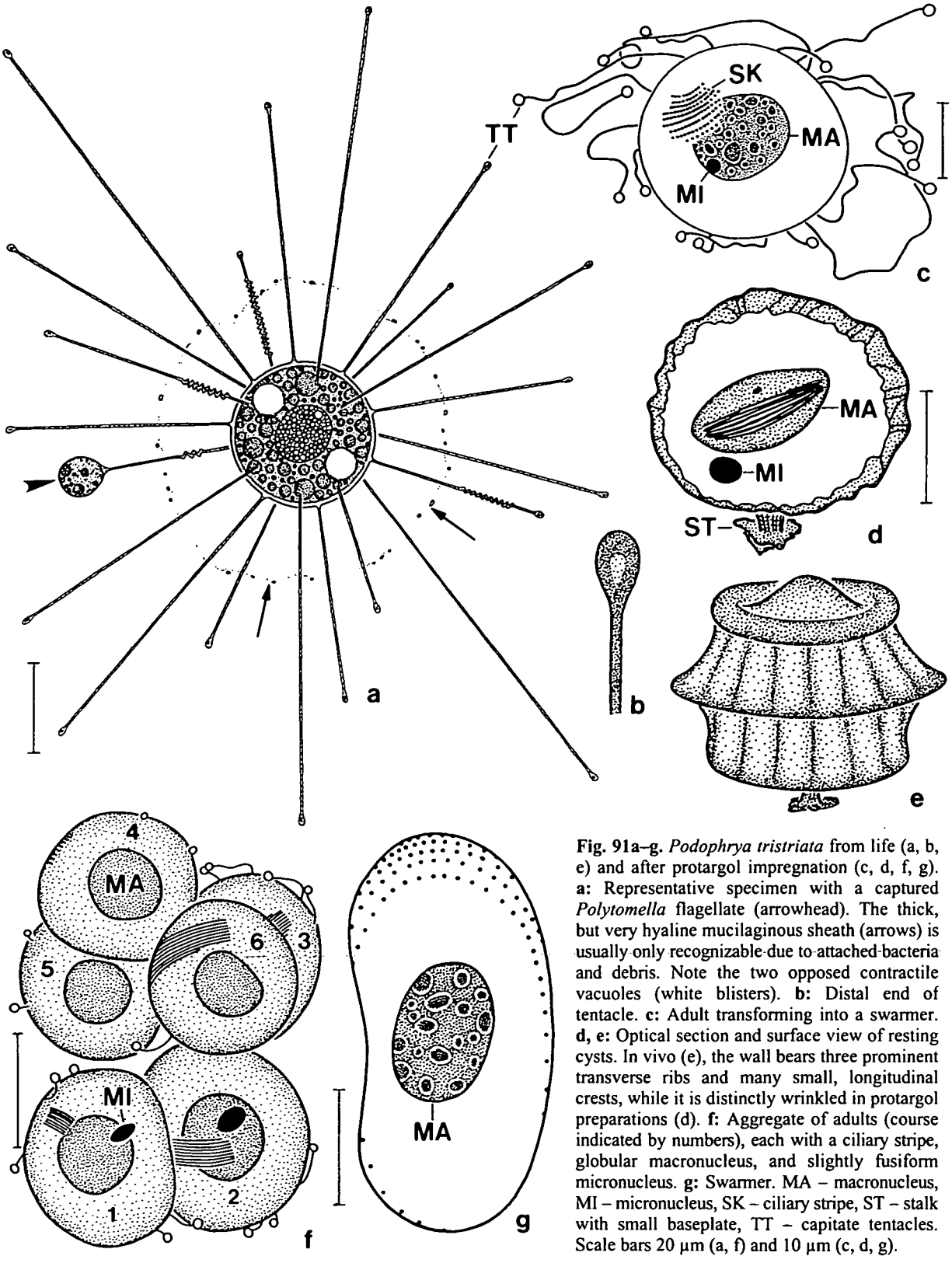

Fig. 91a–g. *Podophrya tristriata* from life (a, b, e) and after protargol impregnation (c, d, f, g). **a:** Representative specimen with a captured *Polytomella* flagellate (arrowhead). The thick, but very hyaline mucilaginous sheath (arrows) is usually only recognizable due to attached bacteria and debris. Note the two opposed contractile vacuoles (white blisters). **b:** Distal end of tentacle. **c:** Adult transforming into a swarmer. **d, e:** Optical section and surface view of resting cysts. In vivo (e), the wall bears three prominent transverse ribs and many small, longitudinal crests, while it is distinctly wrinkled in protargol preparations (d). **f:** Aggregate of adults (course indicated by numbers), each with a ciliary stripe, globular macronucleus, and slightly fusiform micronucleus. **g:** Swarmer. MA – macronucleus, MI – micronucleus, SK – ciliary stripe, ST – stalk with small baseplate, TT – capitate tentacles. Scale bars 20 μm (a, f) and 10 μm (c, d, g).

Swarmers found only in protargol preparations: 30–40 × 15–23 µm, reniform, one out of 28 specimens found had very short, capitate tentacles (Fig. 91g). Macronucleus in mid-body, broadly ellipsoidal, with globular nucleoli. Micronucleus globular, often not recognizable due to similarly sized cytoplasmic inclusions. Very likely two contractile vacuoles, one each in anterior and posterior body end; excretory pores not recognizable. Ciliature *Podophrya*-like, that is, arranged in a stripe of about nine kineties along swarmer margin, more dense anteriorly than posteriorly; detailed course of ciliary rows not recognizable.

Table 74. Morphometric data on adults (A), swarmers (S), and cysts (C) of *Podophrya tristriata* from Australia.

Characteristics [a]	Stage	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	A [b]	29.5	26.0	8.7	2.1	29.4	21.0	54.0	17
	S	34.4	35.0	2.9	0.8	8.6	30.0	40.0	15
	C [c]	17.4	18.0	1.6	0.4	9.4	15.0	20.0	15
Body, width	A [b]	27.7	25.0	7.1	1.7	25.8	21.0	46.0	17
	S	18.3	18.0	1.9	0.5	10.4	15.0	23.0	15
	C [c]	18.9	19.0	1.8	0.5	9.7	15.0	23.0	15
Body length:width, ratio	A	1.1	1.0	0.1	0.0	4.8	1.0	1.2	17
	S	1.9	1.9	0.2	0.1	11.7	1.3	2.4	15
	C	0.9	0.9	0.1	0.0	12.7	0.8	1.2	15
Stalk, length	C	4.3	4.0	1.2	0.3	28.5	3.0	6.0	15
Macronucleus, length	A	12.7	13.0	1.9	0.5	14.8	10.0	15.0	15
	S	12.3	12.0	2.2	0.6	18.1	10.0	19.0	15
	C	14.6	14.0	2.0	0.5	13.6	11.0	18.0	15
Macronucleus, width	A	11.1	11.0	1.3	0.3	12.1	9.0	13.0	15
	S	9.4	9.0	0.6	0.2	6.7	8.0	10.0	15
	C	8.9	8.0	2.2	0.6	24.8	6.0	14.0	15
Micronucleus, diameter	A	3.0	3.0	0.4	0.1	14.9	2.0	4.0	11
	S	2.9	3.0	0.6	0.2	20.8	2.0	4.0	9
	C	2.9	3.0	–	–	–	2.0	3.0	15
Macronucleus, number	A	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	S	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	C	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Micronucleus, number	A	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
	S	1.0	1.0	0.0	0.0	0.0	1.0	1.0	9
	C	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Somatic ciliary rows, number [d]	A	9.3	9.0	0.8	0.2	8.7	8.0	11.0	19

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Dividing or aggregated cells excluded.

[c] Measured without wrinkled cyst wall.

[d] From specimens transforming into swarmer.

Cysts 25–35 µm across in vivo, of typical *Podophrya* structure, that is, globular, stalked, and transversely ribbed (Fig. 91d, e; 342j–l; Table 74). Cyst wall in live specimens of eleven populations brownish and invariably with three prominent transverse ribs and many small, longitudinal crests, while distinctly wrinkled and not impregnated in protargol preparations from Australian type population; internal stalk anchoring cell to wall, as described in → *P. halophila*, not recognizable. Cyst opening (emergence pore) not recognizable either in vivo, protargol preparations or a scanning electron micrograph of a Japanese specimen, also not indicated by an apical plug as in → *P. halophila*. Stalk up to 6 µm long, with narrowed mid-portion and small, argyrophilic baseplate, frequently broken off. Macronucleus usually fusiform to elongate ellipsoidal; occasionally heavily impregnated fibres (mitotic spindle?) extend in main nucleus axis. Micronucleus adjacent to macronucleus, globular.

Occurrence and ecology: *Podophrya tristriata* was discovered in a sample from a forest near the Tinaro Dam in the surroundings of Cairns, Australia. The sample was a mixture of dry, yellow soil amended with roots and litter, pH 4.8. Adults with two contractile vacuoles and a mucilaginous sheath as well as cysts with three prominent transverse ribs and ordinary size also occurred in other terrestrial habitats of Australia: (i) slightly acidic (pH 5.2–5.7) soil samples from the Botanical Garden in Cairns; (ii) humus from decaying epiphytes accumulated in ramifications of trees; and (iii) acidic (pH 5.7) soil with grass roots taken from top of a hill near Alice Springs. In Japan, typical adults and/or cysts were found in (i) tree and soil mosses collected around the "Spring of Wisdom" in Kyoto and (ii) in some samples containing mosses, soil and bamboo litter collected in the surroundings of Tsukuba. All Japanese samples were acidic with pH between 4.3 and 5.9. Likely, *P. tristriata* occurs in edaphic habitats world-wide, preferring more or less acidic environments. Indeed, we recently found it also in an acidic forest soil near Vienna, Austria (Fig. 342e, f).

At Namibian site (73), *Podophrya* cysts were found which match those of *P. tristriata* in the three prominent transverse ribs, but were 70 µm across (Fig. 342g–i); thus, they might belong to another species. Further, a species exists that is highly similar to *P. tristriata*, but lacks the mucilaginous sheath and has only five swarmer kineties; cysts were unfortunately not found.

Besides *P. tristriata*, only three podophryids have been recorded from soil (FOISSNER 1998a): → *P. halophila* KAHL, 1934; *Sphaerophrya parva* GREEFF, 1888; and *S. terricola* FOISSNER, 1986. Of these, however, only the latter are probably confined to terrestrial habitats.

Generic assignment and comparison with related species: KAHL (1934) based the genera *Podophrya* EHRENBERG, 1834 and *Sphaerophrya* CLAPARÈDE & LACHMANN, 1859 on the presence vs. absence of a stalk in adults. However, CURDS (1986) synonymized them arguing that (i) the stalk is often lost in adults of *Podophrya*, while some adults of *Sphaerophrya* are apparently stalked; and (ii) the knowledge about these suctorians is meagre and thus cysts may also be found in *Sphaerophrya*. Furthermore, he stated a high similarity of *Podophrya* and → *Parapodophrya* adults which, however, was not confirmed by a reinvestigation of the type species, *Parapodophrya soliformis* (FOISSNER et al. 1995); the swarmer is also highly different, while resting cysts are similar (cp. figures 342g and 343g with figure 4 in FOISSNER et al. 1995). MATTHES (1988), not familiar with CURDS (1986), continued to separate *Podophrya* and *Sphaerophrya* by the stalk of the adults, but weakened the feature (**usually** present vs. lacking) and included another, namely the occurrence of cysts (present and stalked vs. lacking). Basically, the argumentation by CURDS (1986) is correct; however, as long as cysts are unknown in *Sphaerophrya*, synonymization is premature. Thus,

we follow MATTHES (1988) and affiliate our species with *Podophrya*, whose type species, *P. fixa* (O. F. MÜLLER, 1786) EHRENBERG, 1834, forms a similar-shaped swarmer and cyst. This discussion shows that affiliation of adults to *Podophrya* or *Sphaerophrya* and species identification are extremely difficult or even impossible without detailed knowledge of the life cycle.

According to CURDS (1986) and MATTHES (1988), there are only few free-living *Podophrya* s.l. adults with two contractile vacuoles: *Podophrya sandi* COLLIN, 1911 (1–5 but usually 1; cysts with five transverse ribs); *P. gracilis* CALKINS, 1902 (1–2, but cells only 8 µm across and with very long stalk); *Parapodophrya sparganium* KAHL, 1931a (2–3, but tentacles with conspicuous conical base); *P. nigricans* KAHL, 1931a (2–3, but with *Parapodophrya* swarmer); *Sphaerophrya magna* MAUPAS, 1881 (1–2, but with eccentric macronucleus and swarmers similar to those of → *Parapodophrya*); *S. natans* PENARD, 1922 (only 5–6 very long tentacles); *Gajewskajophrya melosirae* (GAJEWSKAJA, 1933) MATTHES, 1988 (about 90 µm across and with grouped tentacles). *Podophrya maupasii* BÜTSCHLI, 1889 has a gelatinous, rather compact, thin layer (pellicle?) distinctly different from the fragile, voluminous mucilaginous sheath of *P. tristriata* (only up to 9% of body diameter, as estimated from figures 68a, b in COLLIN 1912 vs. about 50% of body diameter). Furthermore, *P. maupasii* adults usually have only one contractile vacuole and the cysts lack transverse ribs (COLLIN 1912). Adults of *Mucophrya pelagica* GAJEWSKAJA, 1933 are distinctly larger (65–110 µm) than those of *P. tristriata* and have a thicker (40–70 µm) mucilaginous sheath and only a single contractile vacuole.

Although *Podophrya* cysts usually show a high variability in the number of transverse ribs (→ *P. halophila*), there are invariably three in the eleven populations of *P. tristriata*. *Podophrya fixa* is the sole congener which forms, at least occasionally in pure line cultures, cysts with only three ribs (REIBENBACH & REICH 1968). The adults, however, differ from *P. tristriata* in having only a single contractile vacuole. Longitudinal cyst crests occur also in → *P. halophila*, *P. grelli* (as estimated from DIECKMANN 1985), and *P. stylonychiae* (as estimated from FOISSNER 1980d), but they are much less distinct and more numerous than in *P. tristriata* (Fig. 91e; 342f, g, l). In → *P. halophila*, the apical opening (emergence pore) of the cyst is closed by a conspicuous plug, and the cell is anchored to the cyst wall by a short stalk. Both structures are lacking in *P. tristriata*. Thus, they can possibly be used for a meaningful splitting of the genus *Podophrya*. However, more and better data are required.

Podophrya halophila KAHL, 1934 (Fig. 92a–f; 343a–m; Table 75)

Description of Namibian site (48) population: Adults in vivo 15–35 µm, usually 25 µm across. Globular, occasionally slightly flattened in stalk attachment area. Stalk, although usually of body length, inconspicuous because only 1 µm thick and colourless, proximal end cuff-like, distal adhering to soil particles with yellowish baseplate; without transverse striation and apparently lacking in most specimens (Fig. 92a; 343a, b). Tentacles scattered over cell, all of same structure, highly variable in number (15–48; Table 75) and length (up to body diameter), 0.5–0.8 µm thick; distal end distinctly capitate because 1–2 µm wide, proximal slightly conical and thus producing somewhat angular body outline. Macronucleus usually globular, nucleolus reticular in vivo, while composed of one large (about 3

µm across) and some small (about 1 µm across) globules in protargol preparations; occasionally contains some heavily impregnated fibres (mitotic spindle?). Micronuclei not recognizable due to many similarly sized cytoplasmic inclusions. Contractile vacuole usually slightly eccentric in posterior quarter of cell; two rather distant excretory pores near beginning of ciliary ribbon in two well-impregnated specimens transforming into a swarmer, indicating that two closely spaced vacuoles might be present. Cortex about 0.8 µm thick and smooth. Cytoplasm packed with lipid droplets 1–4 µm across. Feeds mainly on *Gonostomum* spp. Ciliary ribbon of specimens transforming into a total swarmer composed of four parallel rows of closely spaced basal bodies.

Swarmers 30–45 × 15–25 µm in vivo. Shape rather variable, that is, broadly to elongate ellipsoidal or slightly reniform, flattened up to 2:1, occasionally with truncate posterior end; one broad side of cell with conspicuous furrow in midline (Fig. 92e, f; 343c, d). Tentacles scattered over unciliated portion of broad cell sides, short (< 3 µm) and distinctly capitate. Macronucleus usually in mid-body, shape highly variable, namely, globular to elongate ellipsoidal; frequently, heavily impregnated fibres (mitotic spindle?) extend parallel to main nucleus axis. Micronuclei usually not recognizable due to many similarly sized cytoplasmic inclusions; however, in one specimen three micronuclei each about 3 µm across are recognizable. Two contractile vacuoles mostly near anterior half of convex body margin, each with a single excretory pore between second and third ciliary row (n = 5). Cilia form four circumferential, posteriorly slightly opened rows on narrow sides of cell, distances between individual cilia decrease towards both ends of kineties; kinetids connected by a thin, fibrillar (?) structure. One distinctly shortened, C-shaped marginal kinety.

Cysts 20–35 × 20–40 µm in vivo; of typical *Podophrya* structure, that is, globular, stalked, and transversely ribbed; cell attached to cyst wall by a minute internal stalk (Fig. 92c, d; 343e–m; Table 75). Cyst wall probably bilaminate, honey-yellow, with five to ten, usually six conspicuous, in optical section triangular ribs very likely extending spirally from anterior to posterior; surface finely striated longitudinally, except around apical collar, where a reticular pattern is recognizable. Cyst opening (emergence pore) in anterior centre, surrounded by distinct collar, closed by a compact, structureless, slightly argyrophilic, hemispherically protruding plug intimately connected to cyst wall because it cannot be squashed off. Stalk obconical, adheres cyst to soil particles, 6–20 µm long and usually 5 µm wide proximally. Macronucleus globular to elongate ellipsoidal.

Occurrence and ecology: *Podophrya halophila* was found at Namibian site (48), that is, in a circumneutral (pH 6.7), non-saline mixture of soil and litter from *Combretum imberbe*. The other records listed in Table 4 are doubtful due to taxonomic problems (see below).

Comparison with previous descriptions and similar species: From about 1000 moss and soil samples collected world-wide, FOISSNER (1998a) recorded only a single *Podophrya* species, namely *P. halophila* KAHL, 1934, as redescribed by BLATTERER & FOISSNER (1988), from a saline soil of Australia. The Namibian population matches the Australian *P. halophila* in the edaphic habitat, the number of excretory pores in the adult and swarmer as well as the longitudinal groove of the swarmer. Thus, we pragmatically identify our population with this species, attributing the differences in size (adult: 15–35 µm vs. 25–45 µm; swarmer: 30–45 µm vs. 45–70 µm; cyst: 20–40 µm vs. 30–45 µm) and numbers of kineties (4 vs. usually 6), cyst ribs (usually 6, n = 51 vs. 12, n = 3) and contractile vacuoles (1 vs. 2 in the adult) to the ordinary intraspecific variability.

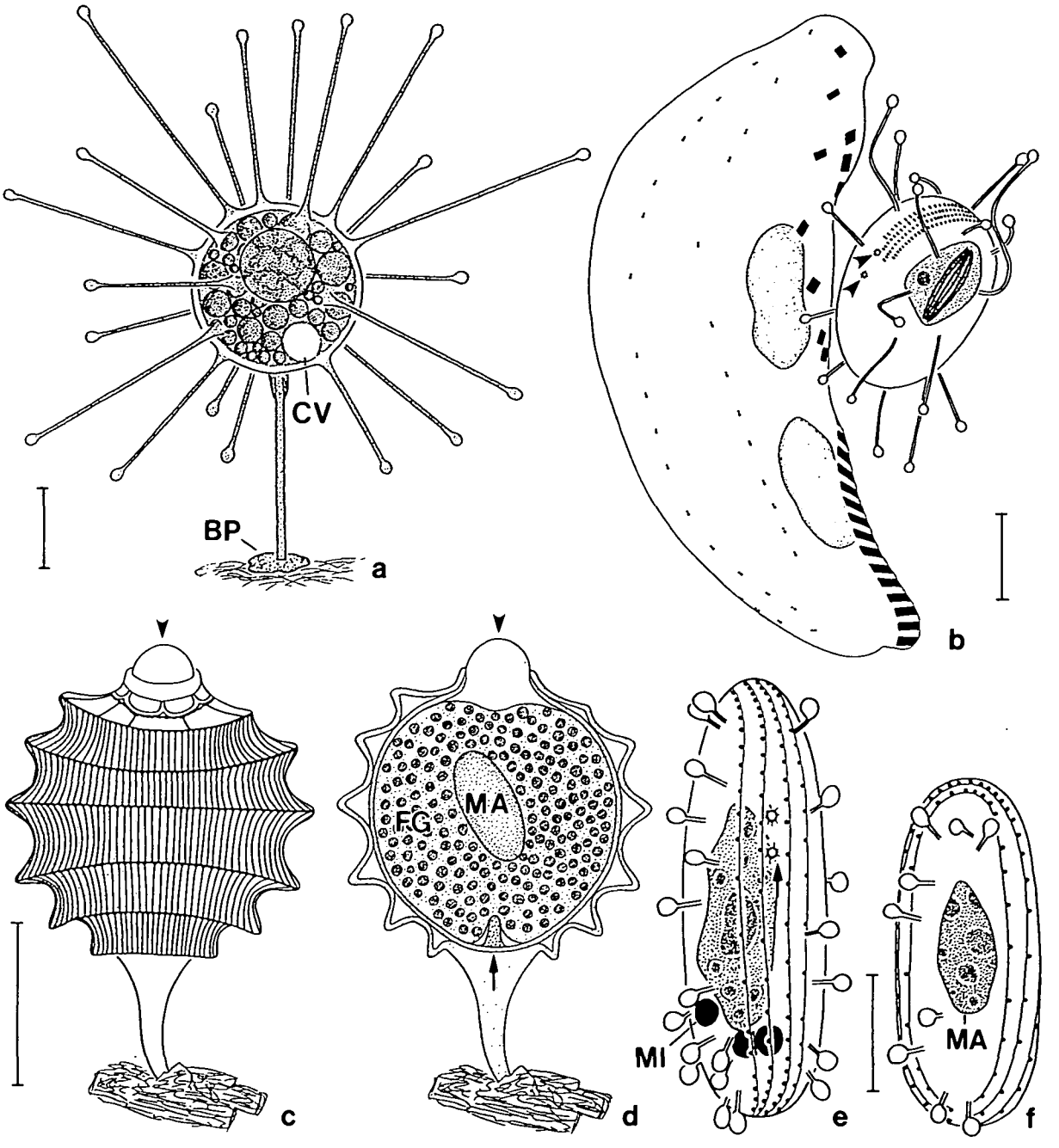

Fig. 92a–f. *Podophrya halophila* from life (a, c, d) and after protargol impregnation (b, e, f). **a:** Side view of a representative specimen. The slightly conical proximal end of the tentacles produces a somewhat angular body outline. The stalk, which is lacking in most specimens, is usually of body length and adhered to soil particles by a small baseplate. **b:** This specimen, which is just ingesting a *Gonostomum* sp., transforms into a "total swarmer". Note the two excretory pores (arrowheads) at the begin of the ciliary ribbon. **c, d:** Surface view and optical section of same resting cyst, which has a typical *Podophrya* structure. The hyaline, hemispherically protruding plug (arrowheads), which closes the apical collar, occurs in several *Podophrya* species, while the minute internal stalk (arrow) anchoring the cell to the cyst wall has not been observed in congeners. **e, f:** Ciliary pattern of narrow and broad side of swarmers. The excretory pores of the two contractile vacuoles are between the second and third ciliary row (arrow). The tentacles are short and capitate. BP – baseplate, CV – contractile vacuole, FG – fat globules, MA – macronucleus, MI – micronuclei (?). Scale bars 10 μm.

Basically, however, *Podophrya* species identification is extremely difficult; actually, the Australian, Namibian, and German populations of *P. halophila* are hardly distinguishable from, e.g., *Sphaerophrya terricola* FOISSNER, 1986 and the common *P. fixa*, as reviewed by FOISSNER et al. (1995). On the other hand, they are rather different in details, for instance, adult size: 50–90 µm (KAHL 1934), about 35 µm (BLATTERER & FOISSNER 1988), and only 15–35 µm in the Namibian population. This frustrating situation is, at least partially, caused by many poor descriptions and redescriptions. At the present state of knowledge, it is crucial

Table 75. Morphometric data on adults (A), swarmers (S), and cysts (C) of *Podophrya halophila* from Namibian site (48).

Characteristics [a]	Stage	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	A	19.3	18.0	3.9	1.0	20.0	16.0	30.0	15
	S	33.9	34.0	3.8	1.0	11.3	28.0	40.0	15
	C	19.2	19.0	3.3	0.8	17.4	14.0	26.0	19
Body, width	A	17.8	16.0	3.4	0.9	19.3	15.0	26.0	15
	S	15.7	15.0	2.8	0.7	17.7	11.0	20.0	15
	C [b]	15.9	16.0	2.2	0.5	13.7	12.0	19.0	19
Stalk, length	C	12.0	13.0	2.2	0.5	18.2	9.0	16.0	19
Stalk, width at proximal end	C	3.9	4.0	1.3	0.3	31.8	1.0	6.0	19
Transverse ribs, maximum height	C	3.0	3.0	1.0	0.2	33.8	1.0	4.0	19
Apical plug, height	C	1.6	2.0	0.6	0.1	35.2	1.0	3.0	19
Macronucleus, length	A	8.5	8.0	1.4	0.4	16.0	7.5	13.0	15
	S	13.1	13.0	4.3	1.1	32.4	7.0	20.0	15
	C	10.5	9.5	3.7	1.3	35.6	6.0	15.0	8
Macronucleus, width	A	7.9	8.0	0.9	0.2	11.0	6.0	9.0	15
	S	7.1	7.0	1.4	0.4	20.3	5.0	9.0	15
	C	4.8	4.8	0.8	0.3	17.5	4.0	6.0	8
Macronucleus, number	A	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	S	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	C	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13
Somatic ciliary rows, number	A [c]	4.0	4.0	0.0	0.0	0.0	4.0	4.0	4
	S	4.0	4.0	0.0	0.0	0.0	4.0	4.0	10
Tentacles, number [d]	A	24.4	21.0	–	–	–	15.0	48.0	15
Cyst ribs, maximum number [e]	C	5.9	6.0	1.3	0.2	22.1	4.0	10.0	51

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Without ribs.

[c] From specimens transforming into total swarmer.

[d] Rough estimation.

[e] Number can be different at both sides of a cyst because the rib is spiral, at least in the anterior portion of the cyst.

to show the features not only by line drawings but also by micrographs and morphometry, giving later investigators a chance to re-evaluate the data. For instance, the small stalk anchoring the cyst to the wall has not been described in any other *Podophrya* species, but it is impossible to know whether this is due to superficial observation or because our organism is a distinct species or even genus. Likewise, the conspicuous plug closing the cyst opening has rarely been mentioned (CANTER et al. 1990, DINGFELDER 1962, FAURÉ-FREMIET 1945, REIBENBACH & REICH 1968).

Metacineta namibiensis nov. spec. (Fig. 93a–o; 344a–k; Table 76)

Diagnosis: Globular, about 20 µm across in vivo, lorica abruptly merging into minute stalk. Tentacles distinctly capitate, emerge through 6 lorica clefts. 2 contractile vacuoles. Swarmers about 45 × 20 µm in vivo, reniform, with 5 obliquely C-shaped ciliary rows and 1 very short kinety on scopuloid bearing side.

Type location: Slightly saline sand dune from Namib Escarpment, Namibia, 23°50'S 16°E (site 33 in figure 2 and chapter 2.1.2).

Etymology: Named after the region (Namib Desert) discovered.

Description: We use anterior and posterior as well as ventral and dorsal according to GUILCHER (1951).

Adult cells 15–25 µm across in vivo; globular in lateral view, indistinctly hexagonal in top view due to six bundles of about seven tentacles each (Fig. 93a–d; 344a–c, f–h, k; Table 76). Tentacles emerge from lorica clefts only, up to 70 µm long and about 0.6–1 µm thick, distinctly capitate because of about 2 µm wide distal end containing haptocysts, conspicuously zigzagging when contracting; highly variable in number, namely, 28–51, usually 38. Occasionally, fibres (?) that impregnate with protargol spread radially into cell from tentacle bases. Macronucleus in centre of cell, globular, pyriform or fusiform, about 9 µm across in vivo and containing numerous globules up to 1.2 µm across. Probably one or two globular micronuclei difficult to distinguish from similarly sized cytoplasmic inclusions. Two contractile vacuoles opposed or slightly obliquely opposed in or above mid-body, surrounded by contributory vesicles during diastole; excretory pores not recognizable. Cytoplasm colourless. Feeds on various ciliates (*Pseudochilodonopsis mutabilis*, *Colpoda maupasi*, *Gonostomum* spp.) and the heterotrophic flagellate *Polytomella* sp. (Fig. 344d, e). Resting cysts not found.

Lorica 18–25 µm across, thin and brownish in vivo, usually does not impregnate with protargol; cup-shaped in lateral view, with hemispherical posterior portion merging abruptly into a minute and thus inconspicuous stalk; more or less distinctly hexagonal in top view because anterior half contains six almost equidistant, radial, slightly protruding and inclined clefts through which the tentacles emerge (Fig. 93a–c; 344a, c, f–h; Table 76).

Budding commences with the subapical production of six parallel ciliary rows; subsequently, the ciliated cell portion protrudes and performs a turn about main body axis causing an oblique course of the kineties (Fig. 93i, j). Swarmers 35–50 × 15–20 µm in vivo, while distinctly shrunken and thus only 28–35 × 10–14 µm in protargol preparations. Overall shape

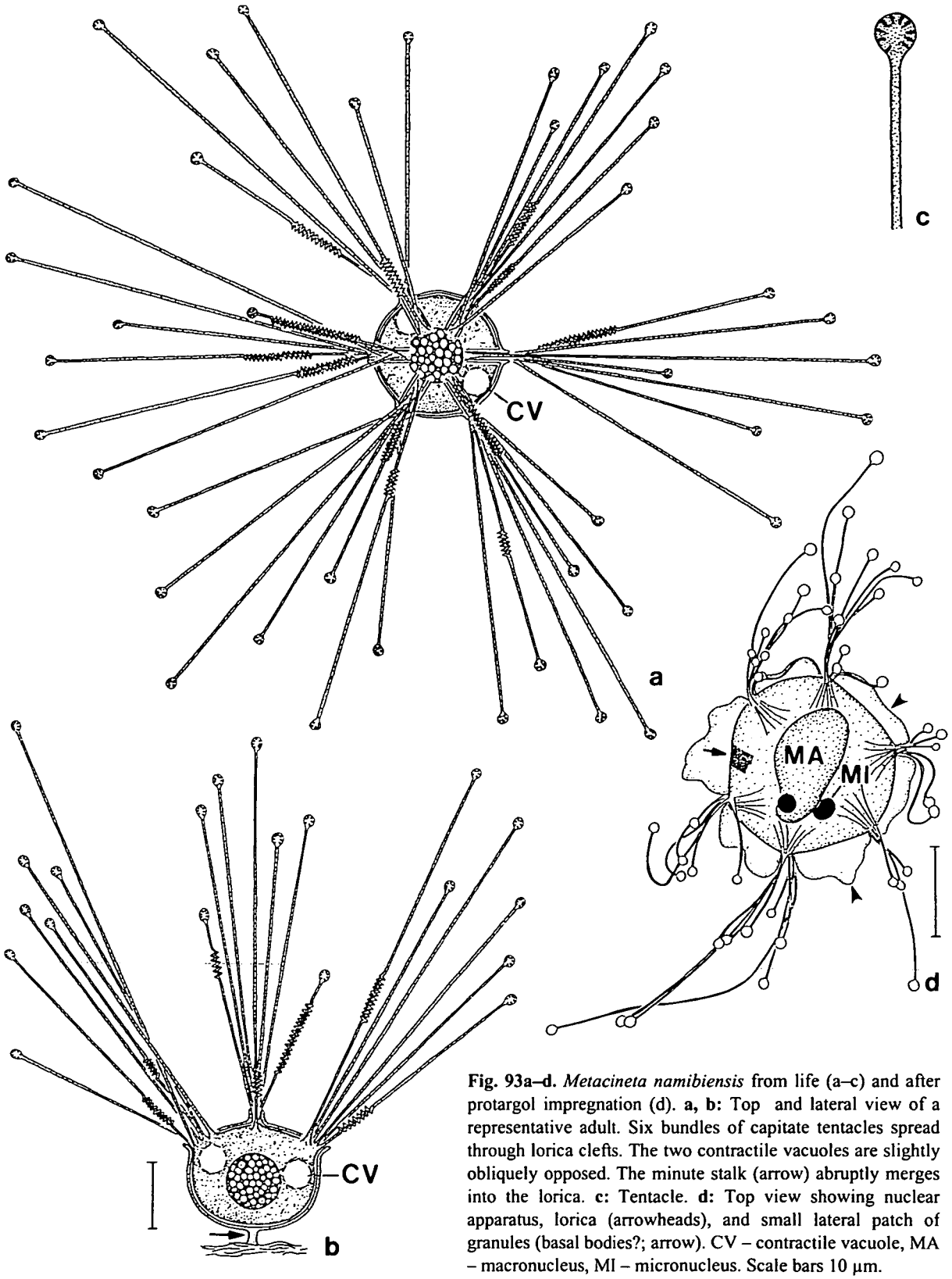

Fig. 93a–d. *Metacineta namibiensis* from life (a–c) and after protargol impregnation (d). **a, b:** Top and lateral view of a representative adult. Six bundles of capitate tentacles spread through lorica clefts. The two contractile vacuoles are slightly obliquely opposed. The minute stalk (arrow) abruptly merges into the lorica. **c:** Tentacle. **d:** Top view showing nuclear apparatus, lorica (arrowheads), and small lateral patch of granules (basal bodies?; arrow). CV – contractile vacuole, MA – macronucleus, MI – micronucleus. Scale bars 10 μm.

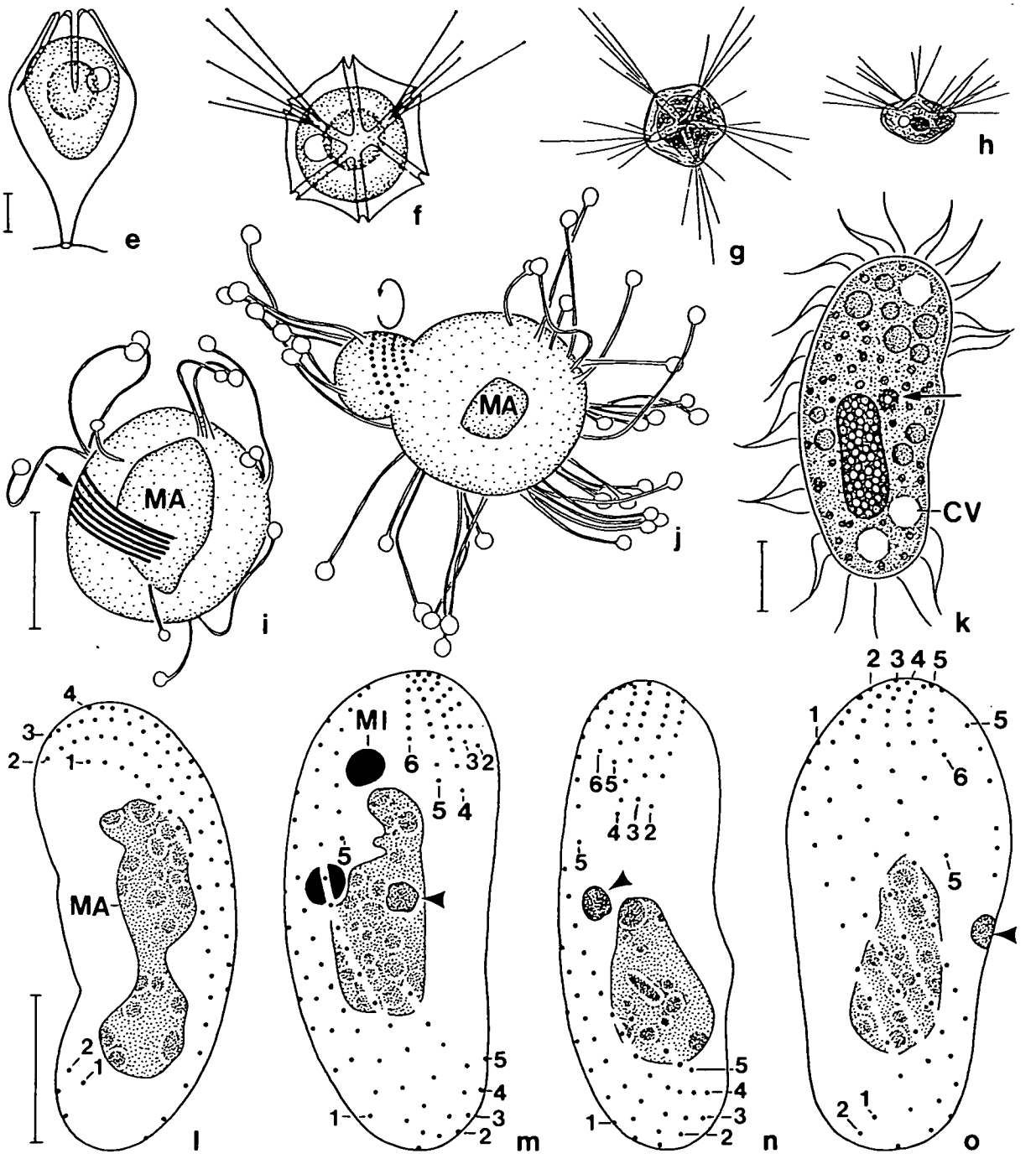

Fig. 93e–o. *Metacineta namibiensis* (i–o) and similar species (e–h) from life (e–h, k) and after protargol impregnation (i, j, l–o). **e, f:** *Metacineta mystacea* var. *brevipes* (from RIEDER 1985). **g, h:** *Metacineta micraster*, size 30–56 µm (from PENARD 1914). **i, j:** Early stages of budding showing the production of six parallel rows of basal bodies (arrow; i) and subsequent turning of the ciliated cell portion about main cell axis (j). **k:** Ventral view of a representative swarmer showing three contractile vacuoles and a small invagination, probably the scopuloid, in mid-body (arrow). **l–o:** Ciliary pattern of dorsal, ventral, left, and right side showing the obliquely C-shaped kineties 1–5 and the very short kinety 6 near the anterior end. The scopuloid (arrowheads) interrupts ciliary row 5. 1-6 – somatic ciliary rows, CV – contractile vacuole, MA – macronucleus, MI – micronucleus. Scale bars 10 µm.

reniform to elongate reniform, frequently with small bulge in or near mid-body on concave side, inconspicuously flattened; length:width ratio about 2–3:1 in vivo and protargol preparations (Table 76). About 1 µm long, finger-like tentacles were observed in one living specimen. Macronucleus highly variable in shape, namely, pyriform, elongate ellipsoidal or globular, contains numerous globules and nucleoli 1–2 µm across. Probably one or two micronuclei about 3 µm across, difficult to recognize due to numerous similarly sized cytoplasmic inclusions. Two or three contractile vacuoles in variable positions, however, usually near body ends; excretory pores not recognizable. Cytoplasm packed with fat globules 1–4 µm across. Cilia about 10 µm long in vivo, closely spaced at anterior body end, while loosely so at posterior and convex side leaving blank mid-portion of concave side and adjacent ventral and dorsal region; arranged in six obliquely C-shaped, equidistant rows (Fig. 93k–o; 344i, j): kinety 1 commences dorsally near anterior end of midline and curves slightly obliquely to dorsal posterior pole area; C-shaped kineties 2–5 form slightly oblique ribbon on convex swarmer side with anterior end curved ventrolaterally and posterior dorsolaterally; kinety 5 interrupted mid-ventrally; kinety 6 within anterior curve of C-shaped ciliary ribbon, comprises only three to five basal bodies. A small pit or wrinkled structure (scopuloid?), 1–2 µm across, near centre of ventral side where kinety 5 is interrupted; surrounded by many minute granules in vivo, impregnates heavily with protargol.

Occurrence and ecology: To date found only at type location.

Comparison with related species: Taxonomy of *Metacineta* is bewildering, likely because based only on (often poor) live observations (RIEDER 1985, MATTHES 1988). One of the most striking features of the Namibian species is its small size, possibly related to the soil habitat. *Metacineta namibiensis* is similar to *M. mystacea* var. *brevipes* SAND, 1900[13], as described by RIEDER (1985), in the number of lorica clefts and the small stalk. Both differ distinctly in lorica shape (globular vs. conical), lorica size (15–25 µm vs. 50–60 × 36–49 µm), and number of contractile vacuoles in the adult (1 vs. 2). Furthermore, the stalk is even much smaller in *M. namibiensis* (1/10 of lorica length) than in *M. mystacea* var. *brevipes* (1/6–1/5 of lorica length; Fig. 93e, f).

Metacineta namibiensis is rather similar to *M. micraster* (PENARD, 1914) BATISSE, 1967 in lorica shape and colour. However, both are distinguished by lorica size (15–25 µm vs. 30–56 µm) and number of lorica clefts (6 vs. 5) and contractile vacuoles in the adult (2 vs. 1). Furthermore, *M. micraster* lacks a stalk (Fig. 93g, h).

As concerns the swarmer, data are available only from *M. mystacea* and its many varieties and forms (COLLIN 1912, FOISSNER et al. 1995, GUILCHER 1951, PENARD 1920, SCHMITZ 1986); however, they are sparse and so contradictory that they are likely based on different species. Thus, this feature can hardly be used to differentiate species at the present state of knowledge. However, the observations of PENARD (1920) and GUILCHER (1951) match our data rather well and suggest that the Namibian species differs from *M. mystacea* varieties by the large barren area on the concave (left) side and the number of ciliary rows (6 vs. about 10). → *Podophrya* swarmers are distinguished from *M. namibiensis* swarmers by the fully ciliated concave side.

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[13] SAND (1900) did not provide a figure of his variety "*brevipes*", but designated specimens in which the stalk occupies only 1/7 of lorica length as "*brevipes*". A nomenclatural discussion of this "variety" is beyond the scope of this monograph.

Table 76. Morphometric data on adults (A) and swarmers (S) of *Metacineta namibiensis*.

Characteristics [a]	Stage	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, maximum diameter in top view	A	18.2	19.0	2.8	0.7	15.4	13.0	23.0	15
Macronucleus, length	A	11.8	11.0	2.0	0.5	17.0	8.0	14.0	15
Macronucleus, width	A	7.7	8.0	1.4	0.4	18.6	6.0	10.0	15
Micronucleus, diameter	A	2.7	3.0	0.6	0.2	21.7	1.0	3.0	15
Lorica clefts, number [b]	A	6.0	6.0	0.0	0.0	0.0	6.0	6.0	30
Macronucleus, number	A	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Tentacles, total number [c]	A	37.8	38.0	–	–	–	28.0	51.0	5
Tentacles, maximum number per cleft [c]	A	6.7	6.5	–	–	–	6.0	8.0	6
Body, length	S	30.7	29.0	2.6	0.7	8.5	28.0	35.0	15
Body, width	S	11.5	11.0	1.4	0.4	11.8	10.0	14.0	15
Body length:width, ratio	S	2.7	2.7	0.2	0.1	9.2	2.2	3.1	15
Macronucleus, length	S	13.7	13.0	3.6	0.9	26.5	8.0	21.0	15
Macronucleus, width	S	6.3	6.0	1.2	0.3	18.6	5.0	8.0	15
Macronucleus, number	S	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Somatic ciliary rows, number	S	6.0	6.0	0.0	0.0	0.0	6.0	6.0	12

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Counted in top view of properly orientated specimens.

[c] Approximations.

Parapodophrya sp. (Fig. 344 l–n)

At Namibian site (4) a few swarmers occurred which, according to the characteristic shape and structure, belong to the suctorian genus *Parapodophrya*. Unfortunately, no adults were found; thus, a reliable identification was impossible. Several *Parapodophrya* species have been described (MATTHES 1988). However, only the type of the genus, *P. soliformis*, has been reliably documented (FOISSNER et al. 1995).

NASSULIA

The nassulids, as classified by DEROUX (1994), are a rather homogenous group united by two strong apomorphies, viz., the cortical alveolocysts and the mixokinetal stomatogenesis (EISLER & BARDELE 1983, 1986, FOISSNER 1996c). Although nassulids are rare in terrestrial habitats (FOISSNER 1998a), several new species were described over the years: *Colpodidium caudatum* WILBERT, 1982; *Nassula terricola* FOISSNER, 1989; *Obertrumia kahli* FOISSNER, 1989; *Urliella terricola* FOISSNER, 1989; *Parafurgasonia terricola* FOISSNER, 1999b; *Pedohymena australiensis* FOISSNER, 1995; *Drepanomonas pauciciliata* FOISSNER, 1989; and *D. exigua bidentata* FOISSNER, 1999b. Several other species were redescribed in the studies cited above and in FOISSNER (1998a, 1999b): *Nassula citrea* KAHL; *N. picta* GREEFF; *Parafurgasonia sorex* (PENARD); *P. protectissima* (PENARD); *Drepanomonas sphagni* KAHL; *D. exigua exigua* PENARD; *Microthorax simulans* (KAHL); and *Stammeridium kahli* (WENZEL).

In the present monograph, which contains all other not yet published nassulids (except for four new microthoracids) found in soils world-wide, the 16 species listed above are increased by 11 new species and the redescription of 7 poorly known species. The data obtained from these investigations cause important changes in the familial and suprafamilial classification of the group, including the new order Colpodidiida, whose members obviously prefer soil and semiterrestrial (e.g., mud from ephemeral waters) habitats.

Taken together, 24 new nassulids were described from terrestrial habitats world-wide during the past 20 years, increasing the 62 species listed in KAHL (1931b) by more than one third. This is a considerable gain, especially in a group which obviously does not prefer terrestrial habitats, indicating that there must be many more free-living ciliate species than the 3000 estimated by FINLAY (2001). See chapter 3.1.7 for a more detailed discussion of this matter.

Family Nassulidae FROMENTEL, 1874

Improved diagnosis (Fig. 94a–g): Small to very large Nassulida JANKOWSKI, 1967a with conspicuous pharyngeal basket extending posteriorly. Nassulid organelles composed of three ciliary rows and usually numerous, forming distinct frange extending leftwards and splitting somatic ciliary rows. Paroral membrane often inconspicuous, in *Rhinakis* possibly even lacking.

Type genus: *Nassula* EHRENBERG, 1834.

Remarks: To our knowledge, nobody ever fixed a type genus for the Nassulidae; however, FROMENTEL (1874) used the stem "Nassul-" for the family group name, indicating that he based it on the genus *Nassula*. For the sake of stability and in accordance with article 64 of the ICZN (1999), we agree with CORLISS (1961) in suppressing the older name Liosiphonidae DIESING and crediting the family not to BÜTSCHLI (1889) but to FROMENTEL, who first proposed a family "Nassuliens (Nassulina)".

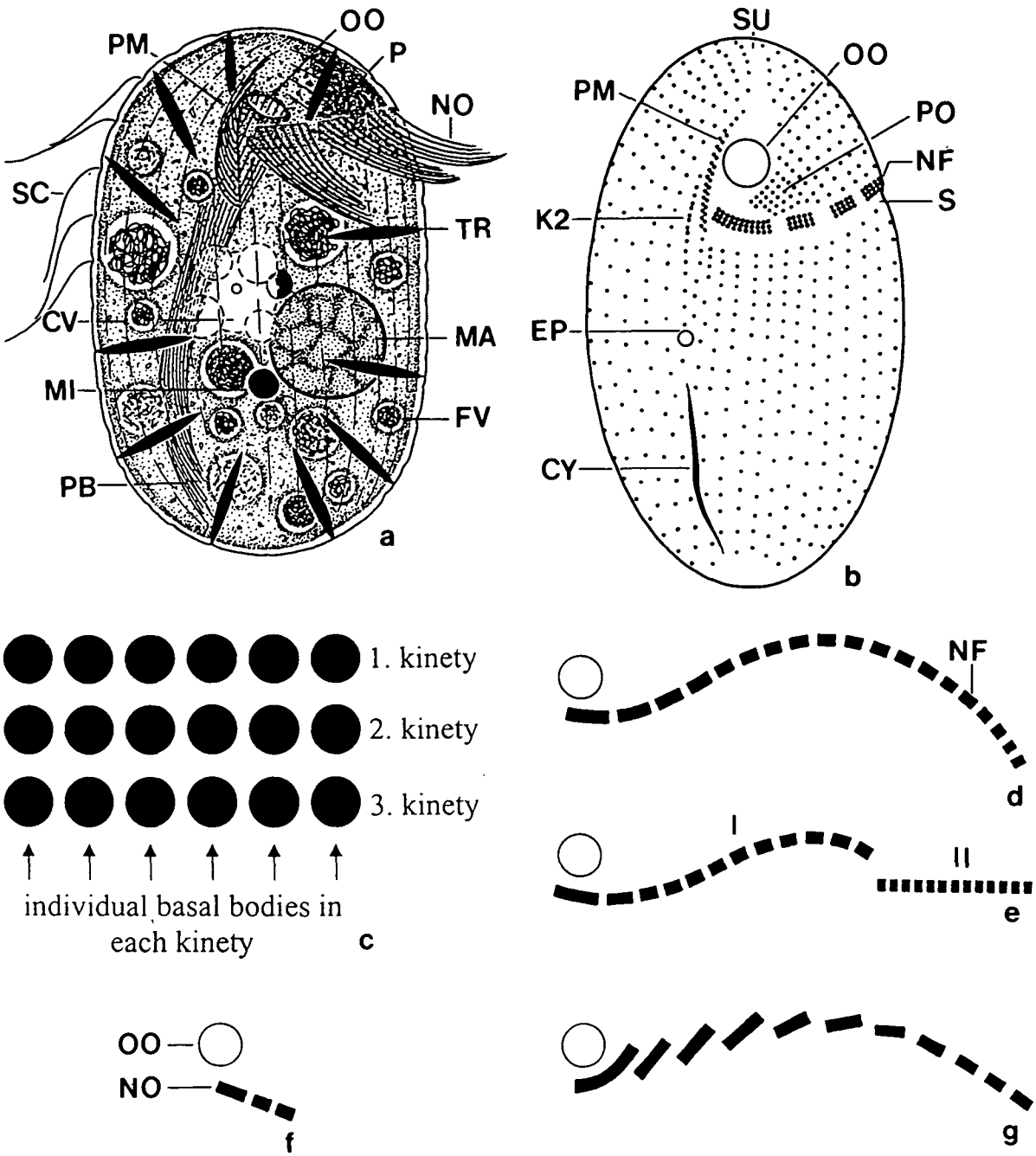


Fig. 94a–g. Family Nassulidae, schemes of representative nassulids (a, b), of a nassulid organelle (c), and for genus distinction by the nassulid frange (d–g; open circle symbolizes oral opening, black rectangles nassulid organelles). **a, b:** Ventral views of specimens from life and after silver impregnation. **c:** The nassulid organelles consist of three kineties. **d:** Genus → *Nassula*. The numerous nassulid organelles form a sigmoidal band and are orientated parallel to the frange axis. **e:** Genus *Obertrumia*. The nassulid frange is bipartite, that is, consists of a curved ventrolateral (I) and a straight dorsal (II) portion. **f:** Genera → *Naxella* and *Rhinakis*. The nassulid frange is directed posteriorly and composed of few organelles, which are arranged parallel to the frange axis. **g:** Genus → *Nassulides*. The nassulid frange consists of numerous organelles, of which the rightmost are orientated obliquely to the frange axis, while the left are parallel. CV – contractile vacuole, CY – cytopyge, EP – excretory pore, FV – food vacuole, K2 – kinety 2, MA – macronucleus, MI – micronucleus, NF – nassulid frange, NO – nassulid organelle, OO – oral opening, P – granule patch, PB – pharyngeal basket, PM – paroral membrane, PO – postoral kineties, S – postorganellar stripe, SC – somatic cilium, SU – preoral suture, TR – trichocyst.

Silver impregnation showed a conspicuous diversity within the genus *Nassula* EHRENBERG, 1834. Thus, FRYD-VERSAVEL et al. (1980) split it into → *Nassula*, *Zosterographus*, → *Naxella*, and → *Rhinakis*. Unfortunately, they did not designate a type species for *Zosterographus* and founded → *Rhinakis* on a nomen nudum species. Therefore, these genera are invalid (FOISSNER 1987a). Nevertheless, both survived in the literature (DEROUX 1994, PATTERSON et al. 1989). Further nomenclatural ambiguities were introduced by DEROUX (1994). Although regarding → *Rhinakis* as valid (citing, however, the authors of the genus incorrectly), he reinstalled it with the combined description of "*Rhinakis faurei* n. g., n. sp.". Our detailed investigations on 18 nassulids showed that the structure of the nassulid frange is the best feature, at least at light microscopic level, to distinguish genera within the family.

The paroral membrane is composed of dikinetids, which are sometimes rather loosely arranged (EISLER 1986, PUYTORAC & NJINE 1980). In the light microscope, it is often difficult to recognize, and thus should not be used to differentiate genera (see → *Rhinakis*). Furthermore, paroral dikinetids generated in the opisthe during ontogenesis are apparently reduced to monokinetids in late dividers of some species (EISLER & BARDELE 1986). These monokinetids are often more closely spaced than those in the anterior portion of kinety 2. As concerns the structure of the nassulid organelles, see GRAIN et al. (1978), EISLER (1986, 1988, 1989), and figures 94a–g.

Species identification and description: As concerns species identification, combined data from live observation (especially extrusomes and pharyngeal basket) and silver-impregnated specimens (especially shape of nassulid frange and number of nassulid organelles and ciliary rows) are indispensable because many nassulids look alike, that is, have a similar size and shape.

Of outstanding importance are the shape, structure, and presence/absence of extrusomes. Except for the microthoracids (HAUSMANN 1978), the fine structure of the nassulid extrusomes is poorly known, and they are considered either as mucocysts (GRAIN et al. 1978) or trichocysts (EISLER 1986). We designate them pragmatically as "trichocysts" because they usually look very similar to hymenostome spindle trichocysts. Furthermore, in several groups/species not only highly refractive, fusiform trichocysts occur, but also inconspicuous, platelet-like mucocysts, which can form a voluminous coat, similar as, e.g., in *Tetrahymena*.

Nassula EHRENBERG, 1834

Improved diagnosis (Fig. 94d): Nassulidae with nassulid frange extending sigmoidally to main body axis. Nassulid organelles numerous and orientated parallel to frange axis.

Type species: *Nassula flava* CLAPARÈDE & LACHMANN, 1859 [subsequent designation by FROMENTEL (1874), see FOISSNER (1987a)].

Obertrumia Foissner & Adam, 1981

Improved diagnosis (Fig. 94e): Nassulidae with bipartite nassulid frange: ventrolateral portion curved, dorsal portion straight. Nassulid organelles numerous and orientated parallel to frange axis.

Type species: *Nassula georgiana* DRAGESCO, 1972 (original designation).

Remarks: Contrary to DRAGESCO & DRAGESCO-KERNÉIS (1986) and DEROUX (1994), we maintain *Obertrumia* with the arguments given by FOISSNER (1987a).

Naxella FRYD-VERSAVEL, IFTODE & DEROUX, 1980

Diagnosis (according to FRYD-VERSAVEL et al. 1980; Fig. 94f): Nassulidae with stomatogenic kineties reduced to the paroral segment.

Type species: *Nassula lateritia* CLAPARÈDE & LACHMANN, 1859 (original designation).

Remarks: FRYD-VERSAVEL et al. (1980) never substantiated this ontogenetic genus definition with detailed data. Thus, the status of the genus is doubtful. The species assigned to *Naxella* by FRYD-VERSAVEL et al. (1980) and FOISSNER & O'DONOGHUE (1990) look rather dissimilar to *Nassula* because they have few (3–4; many in *Nassula*) nassulid organelles, which form a slightly posteriorly extending (anteriorly or perpendicularly in *Nassula*) frange. Furthermore, and possibly of greater importance than the other features mentioned, the distal portion of the pharyngeal basket must be different in *Naxella* and *Nassula* because it looks quite different in silver carbonate impregnations. In *Nassula*, the distal basket end is dome-shaped. In *Naxella*, the basket end is more or less distinctly cone-shaped and composed of heavily impregnated, ellipsoidal structures (seemingly?) connected by a ring-shaped, membranous structure. Clearly, detailed ontogenetic and electron microscopic investigations are needed to establish whether or not *Naxella* is a bona fide genus. For the present, we pragmatically assign those species which have the features discussed above to this genus, that is, few nassulid organelles forming a slightly posteriorly directed frange and a cone-shaped basket end composed of ellipsoidal structures.

Rhinakis DEROUX, 1994

1980 *Rhinakis* nouveau genre FRYD-VERSAVEL, IFTODE & DEROUX, J. Protozool., 27: 79A (abstract 246).

1987 *Rhinakis* FRYD-VERSAVEL, IFTODE & DEROUX, 1980 — FOISSNER, Arch. Protistenk., 133: 223 (nomenclature; genus suppressed because single included species not described).

1994 *Rhinakis* IFTODE, FRYD & DEROUX, 1980 — DEROUX, Traité de Zoologie, 2(2): 594 (incorrect citation of authors of genus).

1994 *Rhinakis* n. g., n. sp. DEROUX, Traité de Zoologie, 2(2): 593, Fig. 195g (reinstallation by combined description of genus and single included species).

Diagnosis (Fig. 94f): Nassulidae with short nassulid frange (3–5 organelles) and without paroral membrane.

Type species: *Rhinakis faurei* DEROUX, 1994 (type by monotypy).

Remarks: The lack of a paroral membrane in *Rhinakis*, as stated by FRYD-VERSAVEL et al. (1980) and DEROUX (1994), is not unlikely because we also found two species, → *N. granata* and → *N. tuberculata*, where no paroral formation is recognizable, not even in excellently prepared specimens (Fig. 348g, i). Furthermore, a reinvestigation of the type material of *N. terricola* FOISSNER, 1989 showed that FOISSNER (1989) over-interpreted his slides, viz., considered the slightly narrowed spacing of the kinetids in the anterior portion of kinety 1 as indication of paroral dikinetids, which are recognizable neither in silver nitrate stains nor in a silver carbonate preparation (Fig. 350b). However, the paroral is inconspicuous in many nassulids, and thus the supposed lack must be proven by electron microscopy before the genus can be recognized. Furthermore, the paroral is partially reduced during late ontogenesis (EISLER & BARDELE 1986).

Nassulides nov. gen.

Diagnosis (Fig. 94g): Nassulid organelles numerous, rightmost ones orientated obliquely to frange axis and overlapping proximally, others arranged parallel to frange axis.

Type species: *Nassula picta* GREEFF, 1888.

Etymology: Composite of *Nassula* (nassa; lat., basket) and *ides* (gr., similar to genus *Nassula*). Masculine gender.

Systematic position and comparison with related genera: *Nassulides* has a nassulid frange which commences underneath the oral opening, extends across the left ventral side, and terminates dorsally. Accordingly, it belongs to the family Nassulidae, as defined above. *Nassulides* is rather similar to *Nassula*, differing solely by the oblique arrangement of the right nassulid organelles. Thus, its generic status might be questioned. On the other hand, nassulids are a species-rich group requiring some organization for practical purposes. The following species have to be combined with *Nassulides*: *N. pictus* (GREEFF, 1888) nov. comb. (basinoym: *Nassula picta*), as redescribed by FOISSNER (1980e, 1989) and FOISSNER et al. (1994); → *N. labiatus* (KAHL, 1933) nov. comb. (basionym: *Nassula labiata*), as redescribed in the present paper and by BORROR (1972b), DRAGESCO & DRAGESCO-KERNÉIS (1986) and SONG & WEI (1998); *N. pratensis* (CZAPIK & JORDAN, 1976b) nov. comb. (basionym: *Nassula pratensis*), as originally described and confirmed by DRAGESCO & DRAGESCO-KERNÉIS (1986); *N. vernalis* (GELEI & SZABADOS, 1950) nov. comb. (basionym: *Nassula vernalis*), as redescribed and neotypified by FOISSNER (1989). Two of these species (→ *N. labiatus, N. pratensis*) were assigned by FRYD-VERSAVEL et al. (1980) to *Zosterographus*, which is, however, invalid because of the lack of a type species (FOISSNER 1987a). Furthermore, FRYD-VERSAVEL et al. (1980) have a different genus concept, with which we do not agree. For instance, they assign *Nassula aurea* and *N. ornata* to the same genus (*Nassula*), although the nassulid frange is quite different.

Nassula longinassa FOISSNER, 1980e (Fig. 95a–f; 263–266, 345a–p; Table 77)

Neotype material: Neotypified from Namibian site (57) population, according to reasons 1, 4, 6 given in chapter 2.4.2.

Improved diagnosis: Size about 30–50 × 20–30 µm in vivo; broadly ellipsoidal. Two types of extrusomes: fusiform, about 7 µm long trichocysts and platelet-like, minute mucocysts. On average 28 ciliary rows and 6 nassulid organelles extending onto dorsal side of cell terminating distinctly underneath level of oral opening. Pharyngeal basket composed of about 13 slightly twisted rods extending to posterior body end. Paroral membrane distinct, composed of about 11 dikinetids.

Description of Namibian population: Size 28–50 × 20–30 µm, usually about 35 × 25 µm in vivo, length:width ratio approximately 1.6:1 in vivo, about 1.4:1 in preparations, and approximately 1.2:1 in precystic cells; specimens from Austrian type population 45–55 µm long. Overall shape broadly ellipsoidal to cylindroidal, with widely rounded ends and shallow postorganellar furrow (Fig. 95a, e; 345 l; Table 77). Macronucleus usually in middle third of cell, about 8 µm across in vivo, with reticular nucleolus. Usually two globular micronuclei adjacent to macronucleus. Contractile vacuole in mid-body, surrounded by small contributory vesicles during diastole; excretory pore in line with paroral membrane. Cytopyge slit underneath excretory pore, extends to near posterior body end, about 6–8 µm long. Resting trichocysts attached almost perpendicularly to cortex, fusiform, about 7 × 0.7–0.8 µm, not very numerous (do not form distinct fringe), but highly conspicuous because large compared to size of cell; extruded trichocysts also fusiform, up to 50 µm long and 1.5 µm wide (Fig. 95a, c, d; 345f, o). Trichocysts more numerous and only 5 µm long in alpine type population. Resting mucocysts hardly recognizable, produce bright, about 1 µm thick cortical layer, released as 1–2 µm-sized, polygonal platelets when methyl green-pyronin is added, soon swelling to a fluffy coat (Fig. 345i, p); become bright, distinct globules about 1–2 µm across in precystic cells (Fig. 345g, h). Cortex slightly punctated by ciliary pits. Cells greenish and/or yellow-brown, as in type population, due to ingested cyanobacteria and citrine to golden patch of granules in left anterior body portion; granules 0.2–1 µm across and also scattered in cytoplasm but sparse and thus not colouring cell. Feeds mainly on coccal cyanobacteria digested in vacuoles 2–5 µm across. Swims rapidly and irregularly.

Somatic cilia about 8 µm long in vivo, arise from shallow cortical pits, loosened in posterior pole area; distances between individual cilia increase from anterior to posterior, especially in second kinety and ciliary rows underneath first nassulid organelle. Ciliary rows longitudinally and equidistantly arranged, except for more closely spaced first (paroral) and second kinety, which end in mid-body; form distinct preoral suture and postorganellar stripe both about 3 µm wide (Fig. 95a, e, f; 263–266, 345a–e, i–l).

Oral opening subapical, elliptical. Pharyngeal basket extends obliquely to dorsal side and posterior end of cell, funnel-shaped, about 4 µm wide and slightly bulbous distally, composed of 10–14 thick, indistinctly twisted rods; annulus and distal microtubular sheath recognizable neither in vivo nor protargol preparations. Nassulid frange slightly sigmoidal, terminates near dorsal margin more or less distinctly above mid-body (Fig. 95e, f; 263–266, 345c, d, k; Table 77). Nassulid organelles composed of three kineties each, decrease in size from right to left, that

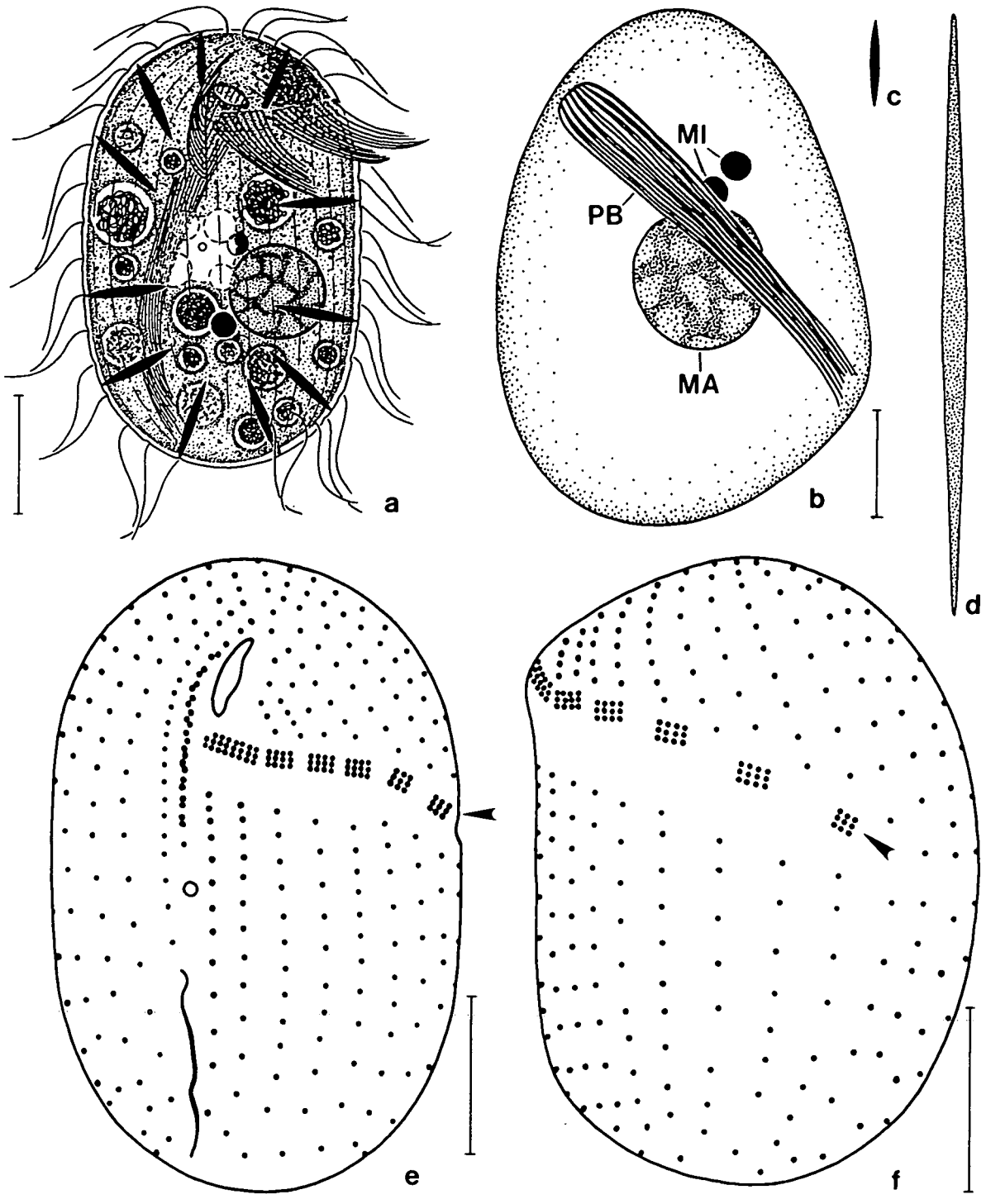


Fig. 95a–f. *Nassula longinassa* from life (a, c, d), after protargol impregnation (b), and silver nitrate impregnation (e, f). **a:** Ventral view of a representative specimen. Note the conspicuous trichocysts and the broadly ellipsoidal body. **b:** Left lateral view showing the nuclear apparatus and the pharyngeal basket extending to rear end. **c, d:** Resting (7 μm) and exploded trichocyst (up to 50 μm), drawn to scale. **e, f:** Ciliary pattern of ventral and left side showing the distinct paroral membrane and the slightly sigmoidal nassulid frange, which terminates near the dorsal margin (arrowheads mark last organelle). MA – macronucleus, MI – micronuclei, PB – pharyngeal basket. Scale bars 10 μm.

is, first organelle with about eight cilia per kinety, last with only two to three; upper rightmost basal bodies of first organelle frequently lacking (Fig. 95e; 345a, d, j, n), other organelles occasionally also incomplete (Fig. 345d). Length of cilia decreases within each organelle from about 10 µm at right to about 7 µm at left end. Paroral membrane rather conspicuous, continuous with first somatic ciliary row, commences at level of oral opening and extends in a flat bow to near excretory pore of contractile vacuole, composed of 8–15 closely spaced, counter-clockwise inclined dikinetids in anterior portion and parallel dikinetids in posterior (Fig. 95e; 263–266, 345a, j).

Occurrence and ecology: FOISSNER (1980e) discovered *Nassula longinassa* in a meltwater pond in the Austrian Central Alps. We found it in highly saline soils of the Etosha Pan (sites 53, 57). Thus, *N. longinassa* seems to be a euryhaline, cosmopolitan species.

Table 77. Morphometric data on *Nassula longinassa*.

Characteristics [a]	Me [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	CHL	33.2	33.0	3.3	0.9	9.9	26.0	38.0	15
Body, width	CHL	23.1	23.0	1.9	0.5	8.4	20.0	25.0	15
Body length:width, ratio	CHL	1.4	1.4	0.1	0.1	9.1	1.3	1.8	15
Anterior body end to macronucleus, distance	CHL	15.5	16.0	3.0	0.8	19.4	11.0	20.0	15
Anterior body end to excretory pore, distance	CHL	17.9	16.0	3.9	1.5	21.8	13.0	24.0	7
Anterior body end to cyrtos, distance	CHL	4.1	4.0	1.0	0.3	24.0	3.0	6.0	15
Anterior body end to last nassulid organelle, distance	CHL	14.5	15.0	1.5	0.4	10.1	11.0	16.0	15
Macronucleus, diameter	CHL	8.2	8.0	1.1	0.3	13.2	6.0	10.0	15
Micronucleus, diameter	CHL	2.9	3.0	–	–	–	2.0	3.0	15
Pharyngeal basket, maximum diameter	CHL	4.1	4.0	–	–	–	4.0	5.0	15
First nassulid organelle, length	CHL	3.9	4.0	0.5	0.1	11.6	3.0	5.0	15
Last nassulid organelle, length	CHL	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15
Paroral membrane, length	CHL	6.7	6.0	1.3	0.3	19.0	5.0	9.0	15
Macronucleus, number	SC	1.0	1.0	0.0	0.0	0.0	1.0	1.0	24
Micronuclei, number [b]	SC	2.0	2.0	–	–	–	1.0	2.0	24
Somatic ciliary rows, number	SC	27.8	28.0	1.2	0.2	4.2	26.0	30.0	24
Kinetids in a dorsal kinety, number	CHL	15.9	16.0	1.7	0.6	10.6	13.0	18.0	7
Nassulid organelles, number	SC	6.4	6.0	0.6	0.1	9.0	6.0	8.0	24

[a] Data based on silver-impregnated, randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Me – methods, Min – minimum, n – number of individuals investigated, SC – silver carbonate impregnation, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Of 24 specimens investigated, only one has a single micronucleus.

Comparison with original description and related species: The original description of *N. longinassa* is entirely based on live observations and thus fairly incomplete. However, the main features mentioned (small size, long pharyngeal basket, conspicuous trichocysts) are also found in the Namibian specimens. Thus, neotypification seems justified. The few differences found, such as the number and length of the trichocysts (see above) and

the diameter of the pharyngeal basket (4–5 vs. 7 µm), are inconspicuous and insufficient to separate the populations. There are several other small nassulids resembling *N. longinassa*: → *Nassula parva*; *Nassula argentula* BIERNACKA, 1963; → *Nassula exigua*; and *Naxella minuta* DRAGESCO & DRAGESCO-KERNÉIS, 1986. However, these species lack trichocysts (at least, none are mentioned in the descriptions) and should thus not be identified (synonymized) with *N. longinassa*.

Nassula parva KAHL, 1928 (Fig. 96a–i; 346c–f; Table 78)

Neotype material: Neotypified from Kenyan population, according to reasons 1, 2, 4, 6 given in chapter 2.4.2.

Improved diagnosis: Size about 50 × 30 µm in vivo; broadly ellipsoidal. Mucocysts minute, platelet-like. On average 22 ciliary rows and 5 nassulid organelles terminating dorsolaterally at level of oral opening. Pharyngeal basket composed of about 16 distinctly twisted rods extending to posterior third of cell. Paroral membrane conspicuous, composed of about 7 dikinetids.

Redescription: Size 40–70 × 25–40 µm in vivo, as calculated from measurements of live specimens and values shown in table 78, assuming a shrinkage of about 10% due to preparation procedures. Overall shape broadly ellipsoidal with shallow furrow underneath nassulid frange; length:width ratio about 1.6:1 both in vivo and after protargol impregnation, 2:1 in specimens without food vacuoles; dorsoventrally flattened up to 2:1 (Fig. 96a, d, f). Macronucleus usually in posterior half of cell, globular to broadly ellipsoidal, with reticular nucleolus. Micronucleus in indentation of macronucleus, lenticular. Contractile vacuole slightly below mid-body, surrounded by small contributory vesicles during diastole; excretory pore between last and penultimate kinety. Cytopyge slit underneath excretory pore, about 10 µm long. Resting mucocysts hardly recognizable, produce bright, about 1 µm thick cortical layer, occasionally released as 1–2 µm-sized, polygonal platelets swelling to a fibrous coat when methyl green-pyronin is added (Fig. 346f). No trichocysts. Cortex punctated by ciliary pits. Cells blue-green or yellow due to cyanobacteria in various stages of digestion and 1–1.5 µm-sized, yellow, bright globules forming distinct patch in left anterior body portion and persisting in specimens with few or no food vacuoles. Feeds mainly on cyanobacteria digested in 3–10 µm-sized food vacuoles becoming yellow during late digestion stages. Moves slowly.

Somatic cilia about 8 µm long in vivo, slightly loosened but not elongated in posterior pole area; distances between individual cilia increase from anterior to posterior, especially in ciliary rows right of oral opening and underneath first nassulid organelle. Ciliary rows meridionally and equidistantly arranged, except for a few closely spaced postoral kineties, form distinct preoral suture and an about 3 µm wide postorganellar stripe (Fig. 96a, b, h, i; 346d; Table 78).

Oral opening subapical. Pharyngeal basket extends obliquely to dorsal side and posterior third of cell, funnel-shaped, in vivo slightly bulbous and about 6 µm wide distally, composed of 12–18 rather thin, strongly twisted rods; distal microtubular sheath distinct in protargol preparations; annulus recognizable neither in vivo nor after protargol impregnation. Nassulid

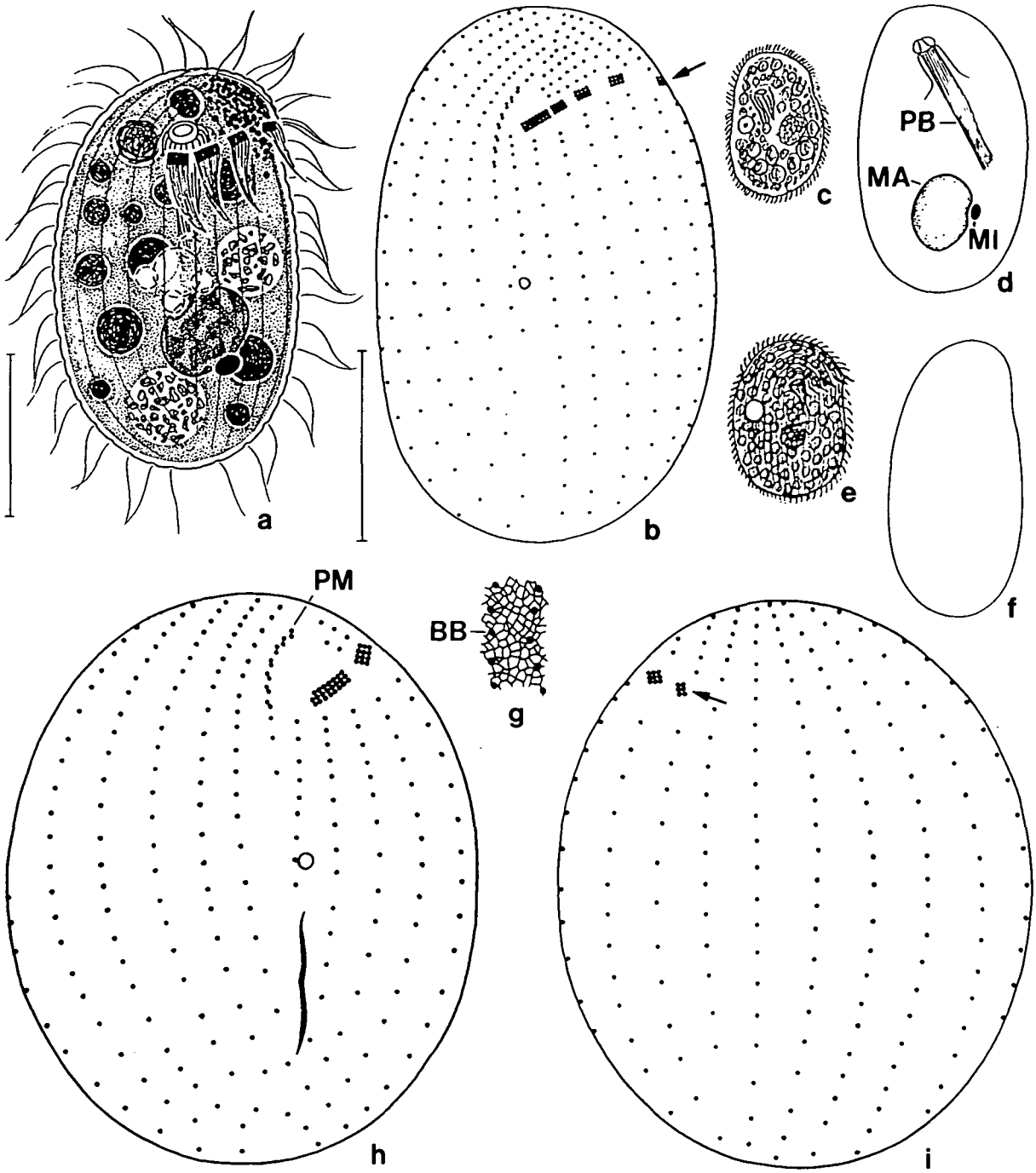


Fig. 96a–i. *Nassula parva*, German type population (c, from KAHL 1928) and Kenyan neotype specimens (a, b, d, f–i) from life (a, c, e, f), after protargol impregnation (b, d), and silver carbonate impregnation (g–i). **a:** Ventral view of a representative, broadly ellipsoidal specimen. **b, h, i:** Ciliary pattern of ventral and dorsal side (h, i show same specimen). The nassulid frange is short and terminates dorsolaterally at level of oral opening (last organelle marked by arrow). The paroral membrane is distinct and consists of clockwise inclined dikinetids. **c:** Ventral view of type specimen, 60 × 40 µm. **d:** Ventrolateral view showing nuclear apparatus in posterior half of cell. The pharyngeal basket is composed of rather thin, distinctly twisted rods and a distal microtubular sheath. **e:** *Nassula* sp. from a Romanian lake, length 55–65 µm (from VUXANOVICI 1962a). **f:** Undernourished specimens are ellipsoidal. **g:** The silverline system consists of small polygons. BB – basal body, MA – macronucleus, MI – micronucleus, PB – pharyngeal basket. Scale bars 20 µm.

frange commences mid-ventrally and extends slightly sigmoidally to left side, terminating at level of oral opening (Fig. 96b, h, i; 346c–e). Nassulid organelles composed of three kineties each, decrease in size from right to left, that is, first organelle with about 6–8 cilia per kinety, last with 2–3; upper rightmost basal body of first organelle frequently lacking. Paroral membrane conspicuous, continuous with first somatic kinety, extends in a flat bow at right side of oral opening, composed of about 7 clockwise inclined dikinetids recognizable both in protargol and silver carbonate-impregnated specimens (Fig. 96b, h; 346c–e; Table 78).

Silverline system as in *Parafurgasonia*, that is, tightly and irregularly meshed producing about five polygons between each two ciliary rows (Fig. 96g).

Occurrence and ecology: KAHL (1928) discovered *Nassula parva* in a possibly slightly saline pond of northern Germany. We found it in slightly to strongly saline materials from Kenya and Namibia (sites 62, 70). The neotype is from the margin of a geyser in the littoral of Lake Baringo in Kenya (01°N 36°E). The grass around the geyser is densely colonized by brownish algae, and the soil is highly saline. The sample consisted mainly of such grass and some adhering soil particles. The ciliate community developed comprised about 17, mainly edaphic species. In Namibia, *N. parva* occurred in slightly to highly saline soils, suggesting that it is a halophile cosmopolitan.

Table 78. Morphometric data on *Nassula parva* (NP) and *Nassula exigua* (NE).

Characteristics [a]	Species	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	NP	PA	48.2	48.0	7.6	2.1	15.8	35.0	64.0	13
	NE	CHL	33.1	33.0	5.1	1.3	15.5	26.0	44.0	15
Body, width	NP	PA	30.5	29.0	4.9	1.4	16.0	24.0	40.0	13
	NE	CHL	22.6	21.0	4.8	1.2	21.1	18.0	33.0	15
Body length:width, ratio	NP	PA	1.6	1.6	0.1	0.1	6.0	1.4	1.7	13
	NE	CHL	1.5	1.5	0.1	0.1	6.6	1.3	1.7	15
Anterior body end to macronucleus, distance	NP	PA	26.2	27.0	3.6	1.0	13.7	17.0	31.0	13
	NE	CHL	16.2	16.0	4.4	1.1	27.1	8.0	25.0	15
Anterior body end to excretory pore, distance	NP	PA	25.3	25.0	3.0	0.8	11.8	20.0	29.0	13
	NE	preparations too mediocre for measurements								
Anterior body end to cyrtos, distance	NP	PA	6.4	6.0	0.9	0.2	13.6	5.0	8.0	13
	NE	CHL	3.8	4.0	0.8	0.2	20.4	3.0	6.0	15
Anterior body end to last nassulid organelle, distance	NP	PA	7.8	7.0	1.8	0.6	23.3	6.0	11.0	10
	NE	CHL	8.1	8.0	2.0	0.5	24.6	5.0	12.0	15
Macronucleus, length	NP	PA	12.0	13.0	1.4	0.4	11.3	10.0	14.0	13
	NE	CHL	8.3	9.0	1.0	0.3	12.6	6.0	10.0	15
Macronucleus, width	NP	PA	9.2	10.0	1.3	0.4	14.1	7.0	11.0	13
	NE	CHL	8.0	8.0	1.0	0.3	12.5	6.0	9.0	15
Micronucleus, length	NP	PA	3.1	3.0	–	–	–	3.0	4.0	13
	NE	CHL	1.3	1.0	–	–	–	1.0	2.0	15
Micronucleus, width	NP	PA	2.5	2.0	–	–	–	2.0	3.0	13
	NE	CHL	1.3	1.0	–	–	–	1.0	2.0	15
Pharyngeal basket, length	NP	PA	20.8	21.0	1.4	0.4	6.6	18.0	22.0	13
	NE	preparations too mediocre for measurements								
Pharyngeal basket, maximum	NP	PA	4.7	5.0	0.6	0.2	13.4	4.0	6.0	13

(continued)

Characteristics [a]	Species	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
diameter	NE	CHL	4.0	4.0	0.4	0.1	9.4	3.0	5.0	15
First nassulid organelle, length	NP		preparations too mediocre for measurements							
	NE	CHL	3.7	4.0	0.6	0.2	16.8	3.0	5.0	15
Last nassulid organelle, length	NP		preparations too mediocre for measurements							
	NE	CHL	1.9	2.0	–	–	–	1.0	2.0	15
Macronucleus, number	NP	SC	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13
	NE	CHL	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Micronuclei, number [b]	NP	SC	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13
	NE	CHL	2.1	2.0	–	–	–	2.0	3.0	15
Somatic ciliary rows, number	NP	SC	22.1	22.0	0.9	0.3	4.1	21.0	23.0	7
	NE	CHL	21.8	22.0	2.9	1.3	13.1	17.0	24.0	5
Pharyngeal basket, number of rods	NP	PA	15.2	16.0	1.9	0.5	12.6	12.0	18.0	13
	NE	CHL	10.1	10.0	1.3	0.3	13.3	8.0	12.0	15
Nassulid organelles, number	NP	SC	4.8	5.0	–	–	–	4.0	5.0	13
	NE	CHL	3.9	4.0	–	–	–	3.0	4.0	15

[a] Data based on silver-impregnated, randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, PA – protargol impregnation (FOISSNER's method), SC – silver carbonate impregnation, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Of 15 *Nassula exigua* specimens investigated, one has 3 micronuclei.

Comparison with original description and related species: Our population matches the rather incomplete original description (Fig. 96c) in body shape, body size (60 × 40 µm), lack of trichocysts (at least none are mentioned), and habitat (saline pond). There are, however, several other small, trichocyst-less nassulids: → *Nassula exigua* KAHL, 1931 (only 35 µm long and only 10 pharyngeal rods, as redescribed below), *N. argentula* BIERNACKA, 1963 (a junior synonym of *N. exigua*, see below), and *N. pusilla* KAHL, 1931 (about 40 pharyngeal rods). Our specimens also resemble *Nassula* sp. found by VUXANOVICI (1962a) in a Romanian lake. Unfortunately, neither KAHL (1928, 1931) nor VUXANOVICI (1962) give any information about the frange and number of pharyngeal rods and ciliary rows; thus, any identification is more or less arbitrarily and neotypification is required. *Nassula tumida* MASKELL, 1887, as redescribed by PUYTORAC & NJINE (1980), differs from *N. parva* greatly in body size (90–100 × 55–60 µm vs. 35–65 × 25–40 µm) and number of nassulid organelles (12–13 vs. 4–5) and ciliary rows (55–60 vs. 21–23); thus, they are not synonymous, as supposed by KAHL (1931) and DINGFELDER (1962).

The general appearance of *N. parva* highly resembles a miniaturized *Nassulides pictus*. In silver preparations, both are easily distinguished by the genus diagnostics, that is, the arrangement of the nassulid organelles; in vivo, they can be distinguished by body size (< 70 µm vs. > 70 µm) and the number of ciliary rows (< 25 vs. > 35), pharyngeal rods (≤ 18 vs. about 24), and nassulid organelles (4–5 vs. 7–8). The same features basically separate *N. parva* from species of the *N. terricola*-complex (→ *N. tuberculata*, *N. terricola*, → *N. granata*).

Nassula exigua KAHL, 1931 (Fig. 97a–g; 346a, b; Table 78)

1963 *Nassula argentula* BIERNACKA, Polskie Archwm Hydrobiol., 11: 38 (new synonym).

Neotype material: Neotypified from Venezuelan population, according to reasons 1–4, 6 given in chapter 2.4.2.

Synonymy: *Nassula argentula* was superficially described and discussed by BIERNACKA (1963; Fig. 97f). The characteristics given, especially the minute size (less than 35 µm) match those of *N. exigua*, except for the habitat (brackish coastal water vs. terrestrial mosses). We suggest synonymy at the present state of knowledge and because we found a *Nassula* which highly resembles KAHL'S *N. exigua* in an inland salt pan.

Improved diagnosis: Size about 35 × 20 µm in vivo; broadly ellipsoidal. Mucocysts minute, platelet-like. On average 22 ciliary rows and 4 nassulid organelles extending slightly sigmoidally to left body margin terminating near level of oral opening. Pharyngeal basket composed of about 10 straight rods extending to posterior third of cell. Paroral membrane conspicuous, composed of about 8 dikinetids.

Redescription: Size 27–45 × 15–30 µm in vivo, as calculated from measurements of live specimens and values shown in table 78, assuming a shrinkage of about 5% due to the preparation procedures. Overall shape ellipsoidal to broadly ellipsoidal, with shallow furrow underneath nassulid frange; length: width ratio about 1.8:1 in vivo and 1.5:1 in silver nitrate preparations, slightly flattened dorsoventrally (Fig. 97a; 346a). Macronucleus frequently in posterior half of cell, globular. Usually two globular micronuclei attached to macronucleus. Contractile vacuole slightly above mid-body, surrounded by small contributory vesicles during diastole; excretory pore distinct in vivo but not recognizable in silver nitrate preparations. Cytopyge slit in line with paroral membrane, about 8 µm long, rarely recognizable in silver nitrate impregnations. Resting mucocysts hardly recognizable, produce bright, about 1 µm thick cortical layer, released as 2–3 µm-sized, polygonal platelets swelling to a thin coat when methyl green-pyronin is added (Fig. 346b). No trichocysts. Cortex punctated by ciliary pits. Cells greenish or yellowish due to cyanobacteria in various stages of digestion and yellow, bright, minute globules forming patch in left anterior body portion (Fig. 346a). Feeds on cyanobacteria digested in vacuoles becoming yellow during late digestion stages. Swims and glides rather rapidly.

Somatic cilia about 7 µm long in vivo, except for 10 µm long and loosened cilia in posterior pole area; distances between individual cilia increase from anterior to posterior, especially in ciliary rows right of oral opening and underneath first nassulid organelle. Ciliary rows meridionally and equidistantly arranged, except for a few closely spaced postoral kineties, form distinct preoral suture and a 2–3 µm wide postorganellar stripe. Second kinety frequently with some clockwise inclined dikinetids at level of paroral membrane (Fig. 97a, c, g).

Oral opening subapical. Pharyngeal basket extends obliquely to dorsal side and posterior third of cell, funnel-shaped, composed of about 10 rather thick, straight rods; basket annulus and microtubular sheath recognizable neither in vivo nor silver nitrate preparations. Nassulid frange extends slightly sigmoidally to left body margin terminating near level of oral opening

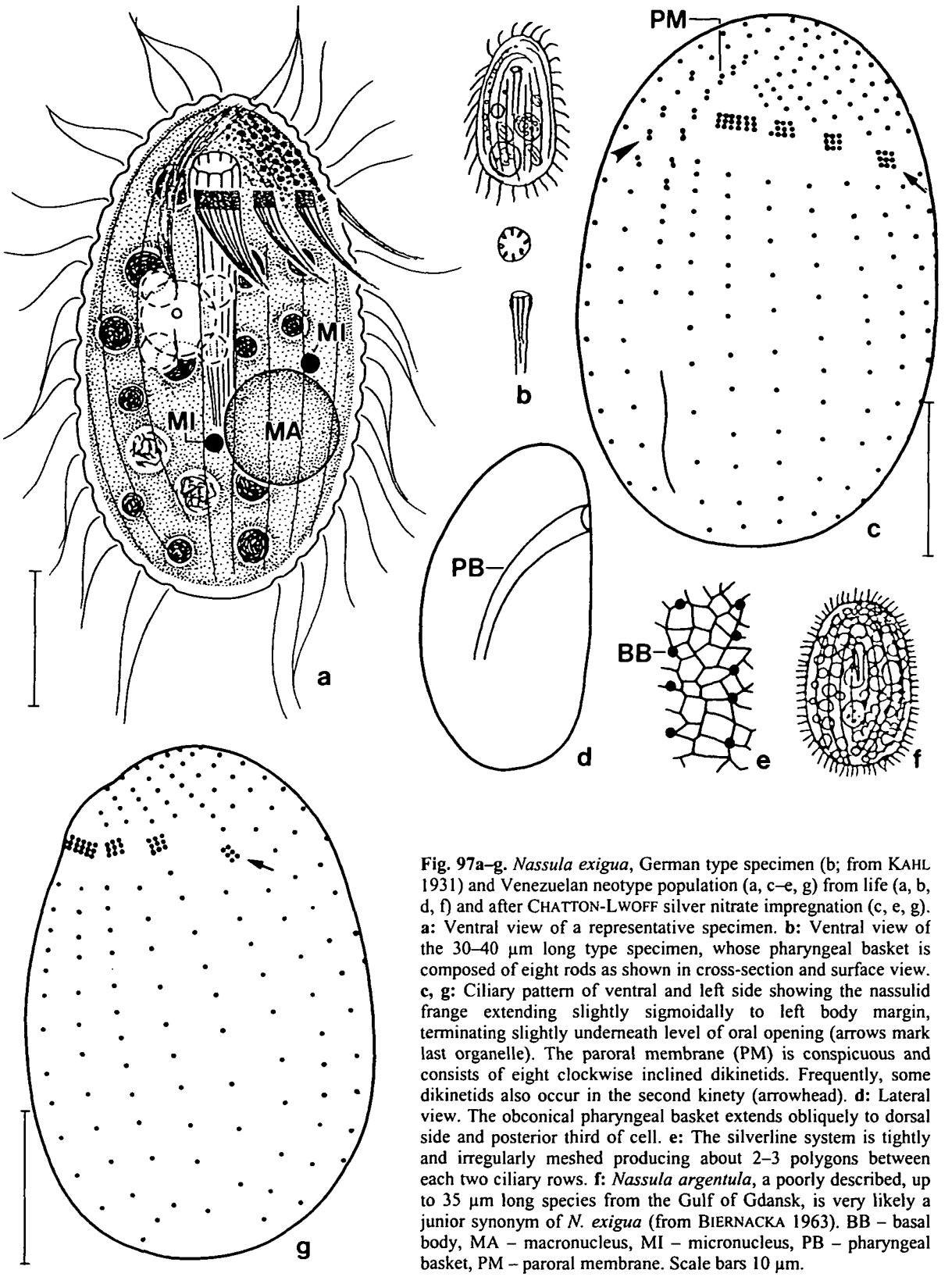


Fig. 97a–g. *Nassula exigua*, German type specimen (b; from KAHL 1931) and Venezuelan neotype population (a, c–e, g) from life (a, b, d, f) and after CHATTON-LWOFF silver nitrate impregnation (c, e, g). **a:** Ventral view of a representative specimen. **b:** Ventral view of the 30–40 µm long type specimen, whose pharyngeal basket is composed of eight rods as shown in cross-section and surface view. **c, g:** Ciliary pattern of ventral and left side showing the nassulid frange extending slightly sigmoidally to left body margin, terminating slightly underneath level of oral opening (arrows mark last organelle). The paroral membrane (PM) is conspicuous and consists of eight clockwise inclined dikinetids. Frequently, some dikinetids also occur in the second kinety (arrowhead). **d:** Lateral view. The obconical pharyngeal basket extends obliquely to dorsal side and posterior third of cell. **e:** The silverline system is tightly and irregularly meshed producing about 2–3 polygons between each two ciliary rows. **f:** *Nassula argentula*, a poorly described, up to 35 µm long species from the Gulf of Gdansk, is very likely a junior synonym of *N. exigua* (from BIERNACKA 1963). BB – basal body, MA – macronucleus, MI – micronucleus, PB – pharyngeal basket, PM – paroral membrane. Scale bars 10 µm.

(Fig. 97c, g). Nassulid organelles conspicuous even in vivo, composed of three kineties each, decrease in size from right to left, that is, first organelle with about 6 cilia per kinety, last with 2–3; upper rightmost basal bodies occasionally lacking. Paroral membrane recognizable even in vivo because large compared to body size, continuous with first kinety, extends in flat bow at right side of oral opening, composed of about eight clockwise inclined, ciliated dikinetids (Fig. 97c and in vivo observ.).

Silverline system as in *Parafurgasonia*, that is, tightly and irregularly meshed producing about two to three polygons between each two ciliary rows (Fig. 97e).

Occurrence and ecology: KAHL (1931b) discovered *N. exigua* in mosses from two sites of Germany and a site in Wisconsin, USA. Later, the proposed synonym *N. argentula* was recorded from coastal waters of the Gulf of Gdansk at salinities of 6.5–7.5‰ (BIERNACKA 1963). We found *N. exigua* in the Morrocoy National Park, that is, in a soil sample from a small salt pan about 500 m inshore near the town of Morrocoy, Venezuela (10°N 68°W). The sample contained brownish, circumneutral (pH 7.3), highly saline soil, litter and roots from halophytes, and some greenish salt crusts from the pan surface. Accordingly, *N. exigua* is a eurytopic and euryhaline cosmopolitan.

Comparison with original description and related species: The original description of *N. exigua* is entirely based on live observations. Thus, it is fairly incomplete and lacks, for instance, information about the nassulid frange. However, other main diagnostics, such as the small size (30–40 µm), body shape, number of pharyngeal rods (8), and lack of trichocysts match the Venezuelan specimens. Only the colour (colourless vs. green-yellow) and habitat (mosses vs. highly saline soil) are different. Colour is a weak feature depending on food organisms (bacilli according to KAHL 1931b vs. cyanobacteria) and the life cycle. The habitat salinity is a more serious difference. However, some (many?) nassulids are euryhaline, for instance → *Nassulides labiatus*. Further, the proposed junior synonym, *Nassula argentula* BIERNACKA, 1963 was discovered in brackish coastal water. Thus and because of the meagre original description, it seems justified to consider the Venezuelan population as a neotype.

There are several small nassulids, which resemble *N. exigua*: *Nassula minima* MINKEWITSCH, 1899 (two contractile vacuoles), *N. pusilla* KAHL, 1931b (about 40 pharyngeal rods), → *N. longinassa* FOISSNER, 1980e (trichocysts and 6–8 nassulid organelles, as redescribed above), → *Nassula lucida* REUTER, 1961 (trichocysts and 2 nassulid organelles, as redescribed below), and *Naxella minuta* DRAGESCO & DRAGESCO-KERNÉIS, 1986 (40 ciliary rows and 5–8 nassulid organelles). Furthermore, *N. exigua* is rather difficult to distinguish from → *Nassula parva*, as redescribed above: body size (in vivo: 27–45 × 15–30 µm vs. 40–70 × 25–40 µm) as well as the number of micronuclei (2–3 vs. 1), pharyngeal rods (8–12 vs. 12–18), and nassulid organelles (3–4 vs. 4–5) are different, but not to an extent making species status indisputable. Thus, further populations should be studied, especially as concerns the number of micronuclei, which might be a main and easy-to-recognize feature for separating these minute species.

The generic assignment of our population is also questionable, that is, possibly it belongs to *Naxella*. However, in the absence of detailed data on the pharyngeal basket, we prefer to maintain the species in *Nassula*.

Nassula dragescoi nov. spec. (Fig. 98a–i; 347a–r; Table 79)

Diagnosis: Size about 80 × 40 µm in vivo; ellipsoidal. Two types of extrusomes: fusiform, 3–5 µm long trichocysts and platelet-like, minute mucocysts. On average 61 ciliary rows and 10 nassulid organelles very widely spaced in left half of frange, which thus ends on right side of cell and leaves many ciliary rows uninterrupted between the individual organelles. Pharyngeal basket composed of 20–30 twisted rods extending to posterior third of cell. Paroral membrane indistinct.

Type location: Highly saline soil from Etosha Pan, Namibia, 19°10'S 15°55'E (site 57 in figures 2, 3 and chapter 2.1.2).

Dedication: We dedicate this new species to Prof. Dr. Jean DRAGESCO, who significantly contributed to the knowledge of limnetic ciliates from Africa.

Description: Size 65–95 × 35–55 µm in vivo, as calculated from measurements of live specimens and values shown in table 79, assuming a shrinkage of about 5% due to the preparation procedures. Overall shape ellipsoidal, length:width ratio about 2:1, dorsoventrally flattened up to 2:1, ventral side almost flat, dorsal more or less distinctly convex (Fig. 98a, f, g). Macronucleus usually in middle third of cell, broadly ellipsoidal, with reticular nucleolus. Micronuclei usually attached to macronucleus, globular. Contractile vacuole near mid-body, surrounded by small contributory vesicles during diastole; excretory pore in line with paroral membrane. Cytopyge slit in line with excretory pore, near posterior body end, about 13 µm long. Resting trichocysts attached almost perpendicularly to cortex, numerous and thus forming distinct fringe, fusiform, about 5 × 0.6 µm in specimens from Namibian site (56) and Benin, 3–4 µm in specimens from Namibian site (59). Resting mucocysts hardly recognizable, produce bright, about 1 µm thick cortical layer, released as 1–2 µm-sized, polygonal platelets occasionally swelling to a voluminous, fibrous coat when methyl green-pyronin is added (Fig. 347e, f, h). Cortex punctated by ciliary pits; cortical units usually hexagonal to indistinctly rectangular, each containing a kinetid (Fig. 347g, k, l). Cells blue-green due to ingested cyanobacteria; cytoplasm colourless, but with numerous lipid droplets and conspicuous citrine patch of about 1 µm-sized granules in left anterior body portion. Feeds mainly on cyanobacteria (*Oscillatoria*) digested in 4–10 µm-sized food vacuoles becoming golden during late digestion stages. Movement without peculiarities.

Ciliature loosened in posterior pole area and underneath paroral membrane; distances between individual cilia increase from anterior to posterior, especially in ciliary rows right of oral opening and underneath first nassulid organelle. Ciliary rows meridionally and equidistantly arranged, except for more closely spaced postoral kineties and first (paroral) and second kinety, which usually end near the nassulid frange, respectively, near mid-body; form indistinct preoral suture; occasionally shortened anteriorly and/or posteriorly and often more or less distinctly interrupted on left and dorsal side, where the nassulid frange extends. Postorganellar stripe distinct only on ventral side because most kineties continuous on left and dorsal side due to the wide spacing of the nassulid organelles (Fig. 98h, i; 347k, l, m, q; Table 79).

Oral opening subapical. Pharyngeal basket extends obliquely to dorsal side and posterior third of cell, funnel-shaped, about 11 µm wide in vivo and slightly bulbous distally, composed of

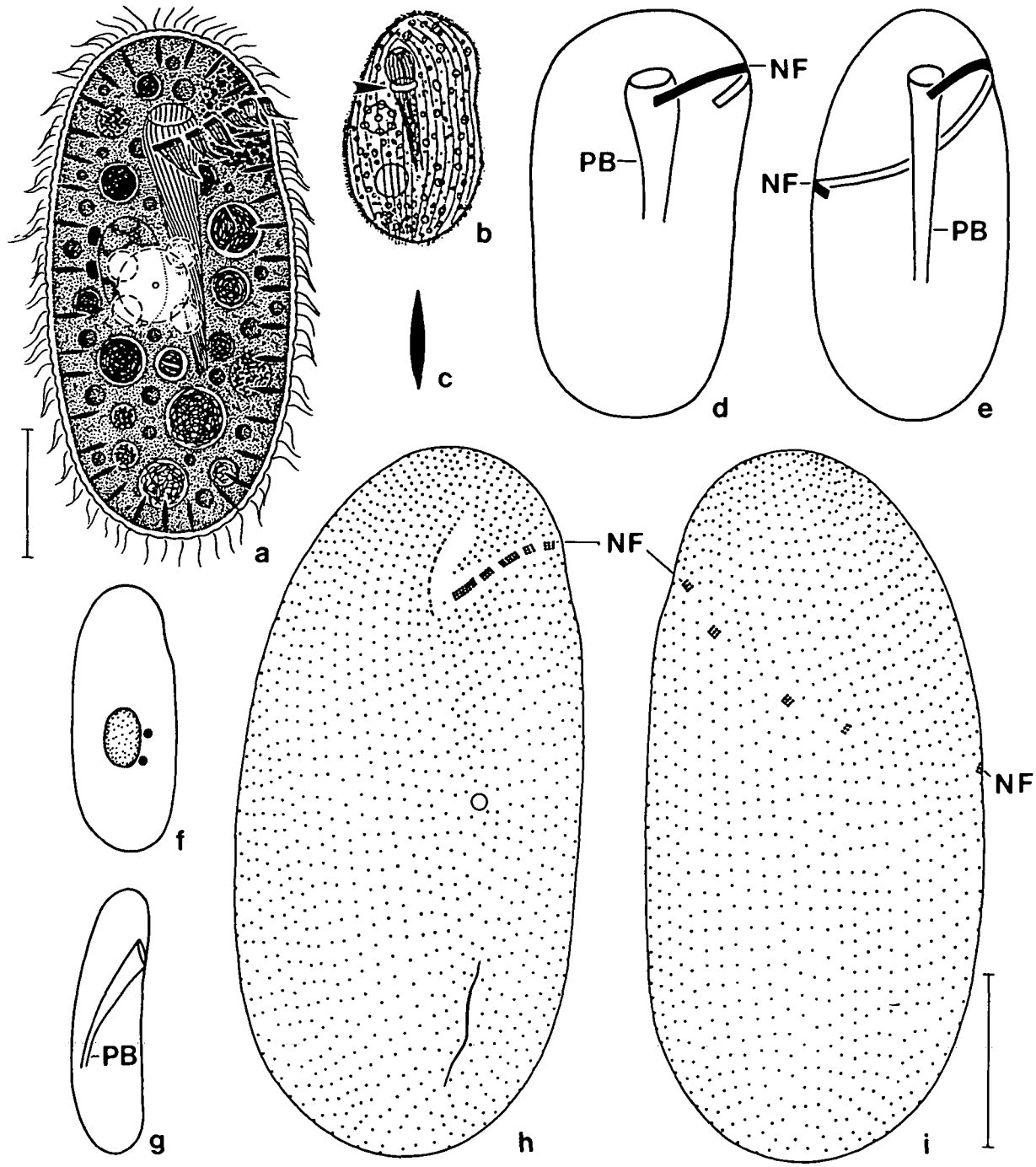


Fig. 98a–i. *Nassula dragescoi* from Namibian (a, e, h, i) and Benin (c, f, g) population and similar species (b, d) from life (a–c, f, g) and after silver nitrate impregnation (d, e, h, i). **a:** Ventral view of a representative specimen showing the fringe of trichocysts and the pharyngeal basket composed of twisted rods. **b:** *Nassula gutturata* GAJEVSKAJA, 1927, about 100 × 70 µm, has a conspicuous basket annulus (arrowhead). **c:** Resting trichocysts are 3–5 µm long. **d, e:** *Nassula citrea* KAHL, 1931, as redescribed by EISLER & BARDELE (d), and *N. dragescoi* (e) differ mainly in the length of the nassulid frange. **f, g:** Ventral and lateral view showing ellipsoidal body shape, dorsoventral flattening, and nuclear apparatus. **h, i:** Ciliary pattern of ventral and dorsal side. Most ciliary rows are continuous between the widely spaced nassulid organelles on left, dorsal, and right side; the postorganellar stripe is thus indistinct. The paroral membrane is rather inconspicuous because composed of *longitudinally* arranged dikinetids. NF – nassulid frange, PB – pharyngeal basket. Scale bars 20 µm.

20–30 rather thin, twisted rods forming a tortuous bundle in posterior third in protargol preparations; distal microtubular sheath very conspicuous after protargol impregnation; annulus recognizable neither in vivo nor silver slides (Fig. 347a–c, i, p). Nassulid frange sigmoidal and exceptionally long due to the wide spacing of the organelles in left (distal) half, commences mid-ventrally and extends obliquely across dorsal surface terminating slightly above mid-body on right side of cell; thus, both ends of frange visible when cell is viewed ventrally (Fig. 98e; 347j, q; Table 79)! Nassulid organelles decrease in size from right to left, composed of three kineties each, of which apparently only two bear cilia decreasing in length from right to left within each organelle (Fig. 347o; Table 79). Paroral membrane rather inconspicuous because composed of 5–10 *longitudinally* arranged dikinetids, continuous with first somatic ciliary row, commences at level of oral opening and extends in a flat bow to the nassulid frange (Fig. 98h; 347m).

Occurrence and ecology: Found in moderate numbers at the highly saline Namibian sites (56–60) and in a non-saline soil sample taken by Prof. Dr. Jean DRAGESCO at the Campus of Benin University, Abomay. Thus, *N. dragescoi* is euryhaline.

Table 79. Morphometric data on *Nassula dragescoi*.

Characteristics [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	CHL	76.5	78.0	8.9	2.6	11.7	59.0	89.0	12
Body, width in ventral view	CHL	38.7	39.0	4.2	1.2	10.8	34.0	50.0	12
Body length:width, ratio	CHL	2.0	2.0	0.2	0.1	8.0	1.7	2.2	12
Anterior body end to macronucleus, distance	CHL	36.5	39.0	9.7	2.8	26.7	16.0	54.0	12
Anterior body end to excretory pore, distance	CHL	39.1	40.0	4.5	1.3	11.6	26.0	44.0	12
Anterior body end to cyrtos, distance	CHL	11.7	11.0	1.5	0.4	12.8	10.0	15.0	12
Anterior body end to last nassulid organelle, distance	CHL	28.8	29.5	4.5	1.3	15.6	23.0	36.0	12
Macronucleus, length	PA	16.7	16.0	2.3	0.7	13.6	13.0	20.0	12
Macronucleus, width	PA	10.8	10.0	1.4	0.4	13.2	9.0	14.0	12
Micronucleus, length	PA	3.0	3.0	0.0	0.0	0.0	3.0	3.0	12
Micronucleus, width	PA	2.5	3.0	0.9	0.3	36.2	1.0	3.0	12
Pharyngeal basket, maximum diameter	CHL	8.1	9.0	1.3	0.4	16.2	6.0	9.0	12
First nassulid organelle, length	CHL	3.8	4.0	–	–	–	3.0	4.0	12
Last nassulid organelle, length	CHL	1.9	2.0	0.7	0.2	34.9	1.0	3.0	12
Macronucleus, number	SC	1.0	1.0	0.0	0.0	0.0	1.0	1.0	12
Micronuclei, number [b]	SC	2.2	2.0	–	–	–	2.0	3.0	12
Somatic ciliary rows, number	SC	61.3	61.0	5.4	1.6	8.8	51.0	69.0	12
Kinetids in a dorsal kinety, number	SC	39.3	40.0	4.4	1.3	11.1	33.0	47.0	12
Nassulid organelles, number [c]	SC	10.3	10.0	–	–	–	10.0	11.0	12

[a] Data based on silver-impregnated, randomly selected specimens from non-flooded Petri dish cultures of Namibian sites (57) and (58). Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, PA – protargol impregnation (FOISSNER's method), SC – silver carbonate impregnation, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Of 12 specimens investigated, only two have 3 micronuclei.

[c] Of 12 specimens investigated, only three have 11 nassulid organelles.

Generic classification and comparison with related species: *Nassula dragescoi* has two unique features: (i) the nassulid frange is, due to the wide spacing of the organelles in its left half, so long that both ends are visible when the cell is viewed ventrally (Fig. 98e; 347q); (ii) the postorganellar stripe is distinct only on the ventral side and thus many uninterrupted ciliary rows extend between the widely spaced nassulid organelles on the left, dorsal, and right side (Fig. 98h, i; 347k, l). Accordingly, *N. dragescoi* could even be considered as a representative of a new genus. However, *Nassula terricola* FOISSNER, 1989, → *N. granata,* and → *N. tuberculata* show transitions of these features. Thus, generic separation seems inappropriate at the present state of knowledge.

The diagnosis and description summarize observations from six populations (five from Namibia, one from Benin; see "occurrence and ecology"), which were studied with varying precision during a period of one month. All populations were identical in the main features, such as trichocysts and number and arrangement of the nassulid organelles.

Nassula dragescoi resembles *Nassula citrea* KAHL, 1931, as redescribed by EISLER & BARDELE (1986), in body shape, body size (80–120 × 40–50 µm), trichocysts, number of ciliary rows (55), and the citrine granule patch in the left anterior body end. However, *N. citrea* has only 4–7 nassulid organelles and the frange terminates on the left body side because the organelles are much more closely spaced than in *N. dragescoi* (Fig. 98d, e). Furthermore, the number of pharyngeal rods is rather different (20–30 vs. 34–38). *Nassula gutturata* GAJEVSKAJA, 1927, a species from the littoral of Lake Baikal, is similar to *N. dragescoi* in body size and trichocysts, but has a very distinct basket annulus (Fig. 98b), which is very indistinct or even lacking in *N. dragescoi* (Fig. 98a; 347c, i, p). Unfortunately, a more detailed comparison is impossible because GAJEVSKAJA (1927) did not provide any information about the nassulid frange.

Nassula granata nov. spec. (Fig. 99a–p; 276–269, 348a–j; Table 80)

Diagnosis: Size about 90 × 35 µm in vivo. Shellcase-shaped in ventral, ovoidal in lateral view, lanceolate when swimming for a while. Mucocysts minute, platelet-like. On average 47 ciliary rows and 8 nassulid organelles forming slightly sigmoidal frange terminating mid-dorsally at or slightly above level of oral opening. Pharyngeal basket composed of about 27 almost straight rods extending to posterior third of cell. Type I resting cysts.

Type location: Highly saline soil from Etosha National Park, Namibia, 18°45'S 16°45'E (site 69 in figures 2, 3 and chapter 2.1.2).

Etymology: The Latin noun *granata* refers to the peculiar, shellcase-like shape.

Description: Size 75–100 × 30–45 µm in vivo, as calculated from measurements of live specimens and values shown in table 80, assuming a shrinkage of 10–20% due to preparation procedures; length:width ratio about 2.5:1 in vivo, 2.1:1 in preparations, and up to 4:1 in hyaline cells without food vacuoles (Fig. 99h). Shellcase-like in ventral and dorsal view, that is, cylindroidal with evenly rounded posterior and broadly conical anterior end; ovoidal when viewed laterally (Fig. 99a, d, e, h); specimens swimming for some time become lanceolate, highly resembling *Paraenchelys* spp. (Fig. 99f, g). Macronucleus usually in middle third of

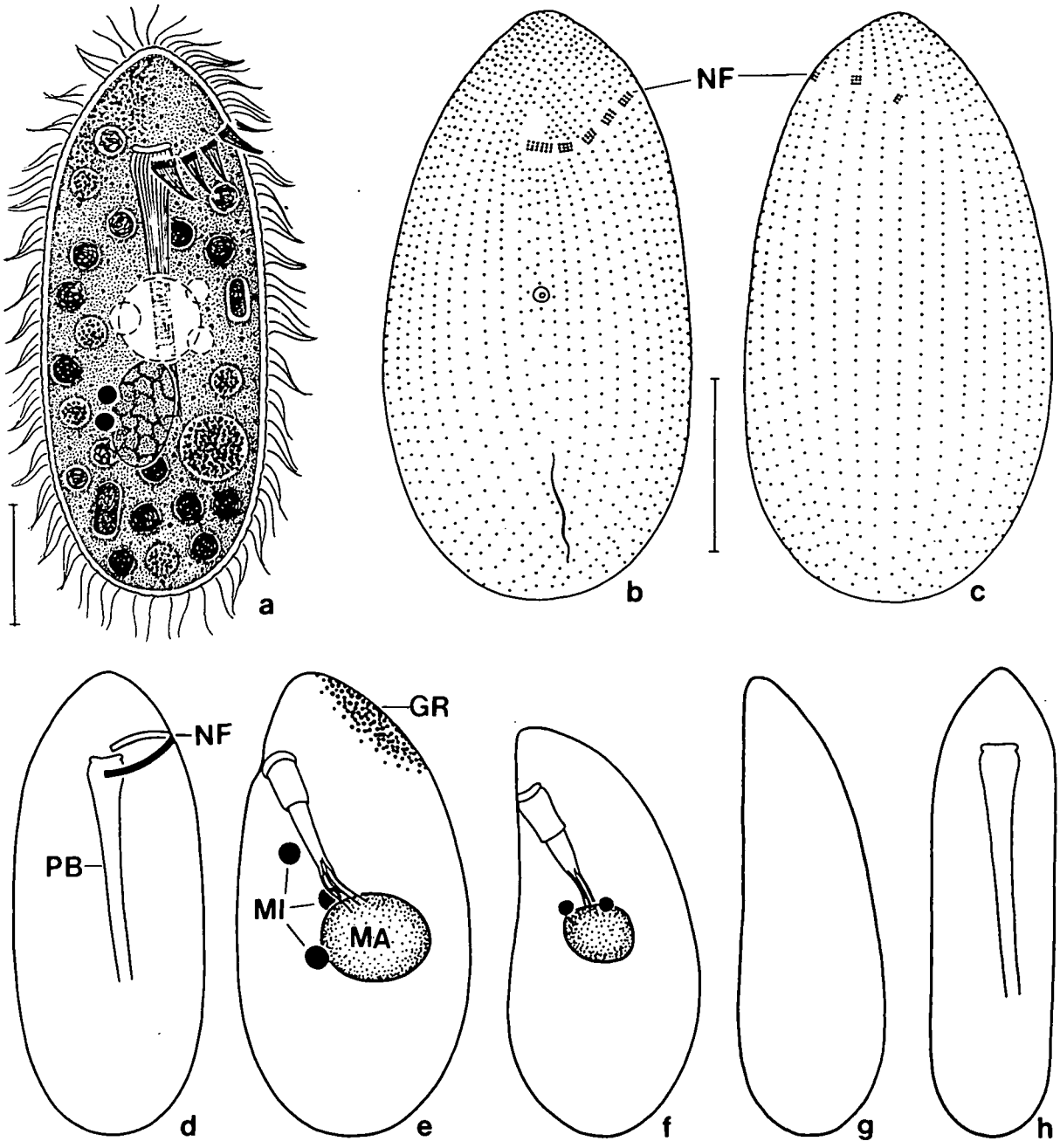


Fig. 99a–h. *Nassula granata* from life (a, d, g, h), after silver nitrate impregnation (b, c), and protargol impregnation (e, f). **a, d:** Ventral view [schematically in (d)] of a representative specimen showing the peculiar, shellcase-like shape (cylindroidal with broadly conical anterior end) and the nassulid frange which extends almost parallel to the perimeter of the cell. The specimen is packed with food vacuoles containing *Oscillatoria* remnants. **b, c:** Ciliary pattern of ventral and dorsal side of same specimen showing the special course of the nassulid frange, which commences mid-ventrally and extends, at level of oral opening, slightly sigmoidally to mid-dorsal side. **e–g:** Left lateral views of a creeping (e) and of swimming (f, g) specimens, which are lanceolate highly resembling *Paraenchelys* spp. Both shapes were also seen in live specimens (g). **h:** Hyaline, slender specimen without food vacuoles. GR – patch of orange granules, MA – macronucleus, MI – micronuclei, NF – nassulid frange, PB – pharyngeal basket. Scale bars 20 μm.

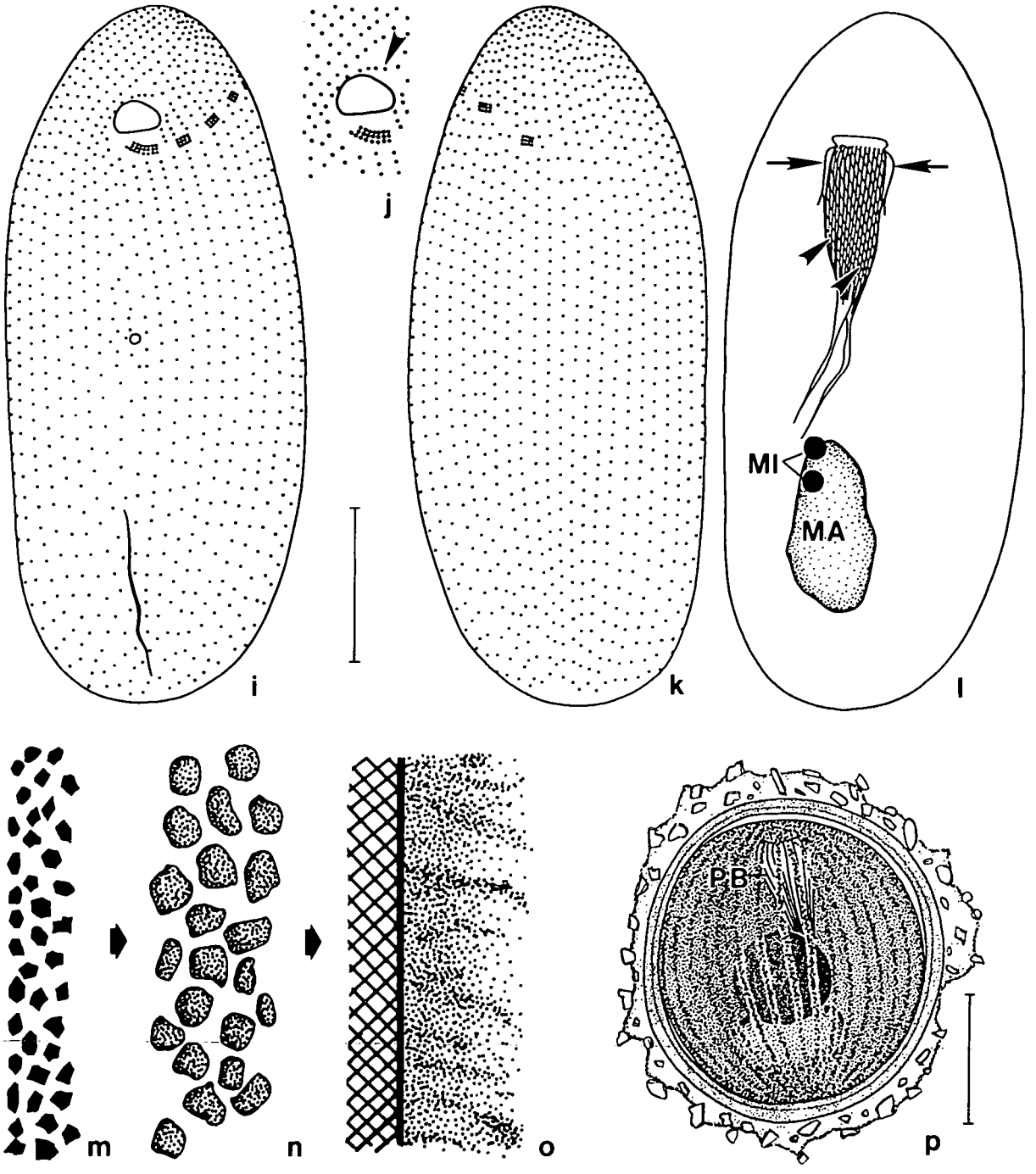


Fig. 99i–p. *Nassula granata* after protargol impregnation (i–l), methyl green-pyronin staining (m–o), and from life (p). **i–l:** Ciliary pattern of ventral (i) and dorsal (k) side, oral region at higher magnification (j), and optical section (l) of same specimen. The pharyngeal basket consists of the distal microtubular sheath (l; arrows), the crests (arrowheads), and the rods, which form a tortuous bundle in the posterior third. No paroral dikinetids are recognizable (i, j; arrowhead), although the specimen is excellently impregnated. **m–o:** Mucocysts are released as 1 µm-sized, polygonal platelets (m) and swell to a rather thin, fluffy coat (n, o) when methyl green-pyronin is added. **p:** The globular resting cysts are orange due to countless golden granules forming stripes in the cell periphery. The wall is smooth and covered with a mucous layer to which clay particles and organic debris adhere. The pharyngeal basket is maintained and a vacuole with food remnants (asterisk) is in the centre of the cyst. MA – macronucleus, MI – micronuclei, PB – pharyngeal basket. Scale bars 20 µm.

cell, ellipsoidal to broadly ellipsoidal, with reticular nucleolus. Micronuclei near or attached to macronucleus, about 3 µm across in vivo. Contractile vacuole slightly above mid-body, surrounded by small contributory vesicles during diastole; excretory pore almost in line with paroral membrane. Cytopyge slit in line with excretory pore, near posterior body end, about 15 µm long. Resting mucocysts hardly recognizable, produce bright, about 1 µm thick cortical layer, released as 1–2 µm-sized, polygonal platelets swelling to a thin, fluffy coat when methyl green-pyronin is added (Fig. 99m–o; 348c, d). No trichocysts. Cortex slightly punctated by ciliary pits. Cells greenish and/or golden due to ingested cyanobacteria and 0.2–1 µm-sized, greasily shining granules scattered in the cytoplasm and accumulated subapically on dorsal side forming distinct, golden patch; cells without food vacuoles light yellow-orange. Food vacuoles 5–11 µm across, contain cyanobacteria (*Oscillatoria*) partially turning into golden granules, similar to those forming the dorsal patch, during late digestion stages. Usually creeping between organic debris and *Oscillatoria* filaments, like many congeners; when swimming for a while, it assumes the lanceolate "swimming shape" described above, possibly due to environmental changes during observation.

Somatic cilia about 8 µm long in vivo, loosened in posterior pole area and underneath first nassulid organelle; distances between individual cilia increase from anterior to posterior, especially in ciliary rows right of oral opening. Ciliary rows meridionally and equidistantly arranged, except for more closely spaced postoral kineties and first (paroral) and second kinety, which usually end near the cytopyge. Preoral suture and postorganellar stripe indistinct because kineties abut tightly preorally and extend close to the nassulid frange; however, continuous ciliary rows, as in → *N. dragescoi*, rarely occur (Fig. 99a–c, k, l; 267–269, 348g–i; Table 80).

Oral opening subapical. Pharyngeal basket extends obliquely to dorsal side and posterior third of cell, funnel-shaped, about 9 µm wide in vivo and slightly bulbous distally, composed of about 27 rather thin, almost straight rods forming tortuous bundle in posterior third of protargol-impregnated specimens; crests and distal microtubular sheath conspicuous only in silver slides; annulus recognizable neither in vivo nor silver preparations (Fig. 99a, d–e, f, l; 267–269, 348a, b, f). Nassulid frange slightly sigmoidal, invariably terminating mid-dorsally at level, or even slightly anteriorly of oral opening. Nassulid organelles composed of three kineties each, decrease in size from right to left, bear about 8 µm long cilia; upper leftmost basal body occasionally lacking (Fig. 99a–c; 348g, h; Table 80). Paroral membrane (dikinetids) recognizable neither in silver carbonate preparations (Fig. 348i) nor the excellently protargol-impregnated cell shown in figures 348i, j; basal bodies, however, slightly more closely spaced at anterior end of kinety 1 than of kinety 2.

Resting cysts globular, about 50 µm across in vivo, orange due to citrine cytoplasm and innumerable golden granules forming stripes in cell periphery; in cyst centre a large (about 17 µm across), yellow-brown vacuole with food remnants, usually even present in older cysts. Wall smooth and colourless, frequently indistinctly bilaminar, about 3 µm thick, covered with a mucous layer to which clay particles and organic debris adhere. Pharyngeal basket maintained (Fig. 99p; 348j).

Occurrence and ecology: To date found only in slightly (0.5‰) to highly saline soils of the Etosha Pan region (sites 54, 64, 67, 69).

Comparison with related species: The diagnosis and description summarize observations from populations of Namibian sites (67) and (69) studied during a period of one

month. Both populations are identical in the main features, such as shellcase-like body shape, lack of trichocysts, number of nassulid organelles, and structure of pharyngeal basket.

Nassula granata is rather close to a trichocyst-less, **unnamed** variety of *N. citrea* found by KAHL (1931) in a saline habitat of northern Germany. We consider the redescription of *N. citrea* by EISLER & BARDELE (1986) as authoritative because it matches the trichocyst-bearing *N. citrea* variety described by KAHL (1931). *Nassula granata* is easily distinguished from *N. citrea* by the lack of trichocysts, the length of the nassulid frange (terminating mid-dorsally vs. at left body side), and the number of pharyngeal rods (25–29 vs. 34–38). *Nassula terricola* FOISSNER, 1989 differs from *N. granata* mainly in the resting cyst (ectocyst faceted vs. smooth), while the active states are similar in body size, course of the nassulid frange, indistinctness of the postorganellar stripe, and number of ciliary rows. Minor distinguishing features are: body shape (broadly ellipsoidal vs. shellcase-like), length:width ratio (about 1.7:1 vs. 2.5:1 in vivo), macronucleus shape (globular vs. ellipsoidal to broadly ellipsoidal), the granule patch (lacking vs. present), and the number of micronuclei (1 vs. 2–3), pharyngeal rods (about 20 vs. 25–29), and nassulid organelles (9–13 vs. 5–9). Our species is also different from *Nassula tumida* MASKELL, 1887, as redescribed by PUYTORAC & NJINE (1980; see FOISSNER 1989 for a detailed discussion of this population), especially in several morphometric features and in that the nassulid frange terminates at oral opening level.

Table 80. Morphometric data on one population of *Nassula granata* and two populations of *N. tuberculata*: NG – *N. granata*, NP – *N. tuberculata* from Portugal, NS – *N. tuberculata* from Saudi Arabia.

Characteristics [a]	Pop [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	NG	CHL	72.0	71.0	5.7	1.5	7.9	63.0	80.0	15
	NP	CHL	73.1	73.0	7.3	1.9	10.0	65.0	85.0	15
Body, width in ventral view	NG	CHL	34.1	34.0	2.3	0.6	6.6	30.0	40.0	15
	NP	CHL	44.2	46.0	5.4	1.4	12.2	34.0	53.0	15
Body length:width, ratio	NG	CHL	2.1	2.1	0.2	0.1	9.5	1.9	2.6	15
	NP	CHL	1.7	1.7	0.2	0.1	11.7	1.3	2.0	15
Anterior body end to macronucleus, distance	NG	CHL	31.1	31.0	5.8	1.5	18.6	23.0	41.0	15
	NP	CHL	35.6	35.0	8.3	2.1	23.3	21.0	54.0	15
Anterior body end to excretory pore, distance	NG	CHL	33.6	33.0	3.2	0.8	9.4	28.0	39.0	15
	NP	CHL	35.3	35.0	3.1	0.8	8.9	29.0	40.0	15
Anterior body end to cyrtos, distance	NG	CHL	12.1	13.0	1.9	0.5	15.5	9.0	16.0	15
	NP	CHL	12.6	14.0	2.0	0.5	15.8	9.0	15.0	15
Anterior body end to last nassulid organelle, distance	NG	CHL	11.7	11.0	3.0	0.8	25.5	5.0	18.0	15
	NP	CHL	13.3	14.0	1.8	0.5	13.2	9.0	16.0	15
Macronucleus, length	NG	PA	15.7	15.0	2.4	0.6	15.0	11.0	20.0	15
	NP	CHL	15.7	15.0	2.3	0.6	14.6	11.0	20.0	15
	NS	SC	26.3	26.0	4.1	1.3	15.7	20.0	35.0	10
Macronucleus, width	NG	PA	11.5	11.0	1.5	0.4	13.1	10.0	14.0	15
	NP	CHL	9.2	9.0	1.1	0.3	12.5	8.0	12.0	15
	NS	SC	17.0	17.0	2.6	0.8	15.4	12.0	20.0	10
Micronucleus, largest diameter	NG	PA	2.7	3.0	–	–	–	2.0	3.0	15
	NP	CHL	3.0	3.0	0.4	0.1	12.6	2.0	4.0	15

(continued)

Characteristics [a]	Pop [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Pharyngeal basket, maximum	NG	PA	5.4	5.0	–	–	–	5.0	6.0	15
diameter	NP	CHL	7.2	7.0	1.2	0.3	16.8	6.0	9.0	15
First nassulid organelle, length	NG	CHL	4.1	4.0	0.8	0.2	19.6	3.0	5.0	15
	NP	CHL	4.0	4.0	0.8	0.2	21.1	3.0	6.0	15
Last nassulid organelle, length	NG	CHL	1.5	2.0	–	–	–	1.0	2.0	15
	NP	CHL	2.6	3.0	0.7	0.2	28.3	1.0	4.0	15
Macronucleus, number	NG	PA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	NP	CHL	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	NS	SC	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10
Micronuclei, number [b]	NG	PA	2.2	2.0	–	–	–	2.0	3.0	15
	NP	CHL	2.7	2.0	0.8	0.2	30.6	2.0	4.0	15
	NS	SC	1.9	2.0	0.6	0.2	29.9	1.0	3.0	10
Somatic ciliary rows, number	NG	SC	47.0	47.0	1.7	0.4	3.7	44.0	52.0	22
	NP	CHL	43.9	42.0	7.7	2.0	17.4	36.0	61.0	15
	NS	SC	41.2	41.5	4.0	1.3	9.7	31.0	45.0	10
Kinetids in a dorsal kinety, number	NG	SC	49.5	52.0	3.8	1.0	7.7	43.0	54.0	15
	NP	CHL	36.9	36.0	4.7	1.2	12.6	29.0	45.0	15
	NS	SC	48.1	46.5	5.2	1.7	10.9	42.0	60.0	10
Pharyngeal basket, number of rods	NG	SC	26.6	27.0	1.7	0.8	6.3	25.0	29.0	5
	NP	CHL	23.6	24.0	2.0	0.5	8.6	20.0	26.0	15
	NS	SC	24.6	25.0	1.1	0.3	4.4	23.0	26.0	10
Nassulid organelles, number	NG	SC	7.5	7.5	1.0	0.2	12.8	5.0	9.0	22
	NP	CHL	7.2	7.0	1.0	0.3	14.1	6.0	9.0	15
	NS	SC	7.7	8.0	1.1	0.3	13.8	6.0	10.0	10
Resting cysts, length	NS	IV	44.9	45.0	2.0	0.7	4.5	42.0	48.0	9
Resting cysts, width	NS	IV	43.6	44.0	2.9	1.0	6.6	39.0	48.0	9

[a] Data based on well-fed, silver-impregnated and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, IV – in vivo, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, PA – protargol impregnation (FOISSNER's method), Pop – population, SC – silver carbonate impregnation, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Of 15 *Nassula granata* specimens investigated, three have 3 micronuclei.

Generic classification: *Nassula granata* has a special course of the nassulid frange, which extends almost parallel to the body perimeter, terminating at level, or even slightly anteriorly of the pharyngeal basket opening. In most other thoroughly studied *Nassula* s. str. species the nassulid frange invariably extends more or less distinctly rearwards: → *Nassula longinassa*, → *N. dragescoi*, → *N. etoschensis*, *N. rotunda* (FOISSNER 1980e), *N. ornata* (FOISSNER et al. 1994), and *N. citrea* (EISLER & BARDELE 1986; less distinct because frange is short). Only in *N. terricola* extends the nassulid frange as in *N. granata* (FOISSNER 1989). However, the special course of the frange in *N. terricola* is not as evident as in *N. granata* because the species is broader and the frange does not extend onto the dorsal side. Both species agree also in the indistinctness of the postorganellar stripe. There is, however, a "strong" difference between *N. terricola* and *N. granata*, namely, the presence/absence of paroral dikinetids. However, a reinvestigation of the type material of *N. terricola* showed that

FOISSNER (1989) over-interpreted his slides, viz., considered the slightly narrowed spacing of the kinetids in the anterior portion of kinety 1 as indication of paroral dikinetids. Such dikinetids are recognizable neither in the silver nitrate stains nor in a silver carbonate preparation (Fig. 350a). Actually, *N. terricola* and *N. granata* are identical in the inconspicuousness or lack of paroral dikinetids (cp. figure 350b with 348i). They might be the core of a distinct genus, possibly *Rhinakis* (see introduction to family). However, generic separation would probably be too progressive at the present state of knowledge, and is weakened by the different resting cysts in *N. terricola* and *N. granata* (see above and → *Nassulides labiatus*). As concerns *Rhinakis*, the number and course of the nassulid organelles are rather different in *R. faurei*, *N. terricola*, and *N. granata*.

Nassula tuberculata nov. spec. (Fig. 100a–o; 349a–u, 350a, b; Tables 80, 81)

1996 *Nassula picta* GREEFF, 1888 – FOISSNER, Acta Protozool., 35: 100 (misidentification).

Diagnosis: Size about 80 × 40 µm in vivo; ellipsoidal. Mucocysts minute, platelet-like. On average 41 ciliary rows and 8 nassulid organelles forming sigmoidal frange terminating mid-dorsally at or slightly underneath level of oral opening. Pharyngeal basket composed of about 25 slightly twisted rods extending to posterior third of cell. Type IV resting cysts.

Type location: Highly saline, cultivated soil from the Al-Hassa Oasis, Saudi Arabia, 25°30'N 49°40'E.

Etymology: The Latin adjective *tuberculata* refers to the tubercular wall of the resting cyst.

Description: Active specimens from Saudi Arabia, Portugal, and Antarctica were investigated. However, the diagnosis comprises only the Saudi Arabian population, in which the resting cysts were studied, too. In the description, data are separated only when appropriate. No permanent preparations are available from the Saudi Arabian population. Thus, we declare figures 349a–u as type material. CHATTON-LWOFF silver nitrate-impregnated voucher slides from the Portuguese material have been deposited (Table 1).

Size in vivo 70–100 × 30–50 µm in Saudi Arabian specimens, 60–80 × 30–40 µm in well-fed Portuguese cells, only 40 µm in undernourished Portuguese cells, and about 70 × 23 µm in Antarctic specimens; length:width ratio usually 2.2-2.3:1 in vivo, about 1.7:1 in silver nitrate-impregnated Portuguese specimens. Overall shape slenderly (3:1) to broadly (1.8:1) ellipsoidal, occasionally slightly ovoidal, usually more or less distinctly reniform and flattened up to 1.5:1 when viewed ventrolaterally or laterally (Fig. 100a–e; 349f, g; Tables 80, 81). Macronucleus usually in middle third of cell, ellipsoidal to broadly ellipsoidal, about 25 × 15 µm in vivo, finely granulated in Saudi Arabian specimens, with distinct, lobed nucleoli in cells from Antarctica. Micronuclei attached to macronucleus, ellipsoidal to globular, about 3 × 2.5 µm in vivo. Contractile vacuole slightly above mid-body, surrounded by small contributory vesicles during diastole; excretory pore in line with or slightly left of first kinety. Cytopyge slit in line with excretory pore, near posterior body end, about 16 µm long. No trichocysts, but mucocysts present in all populations investigated, produce bright, about 1 µm thick cortex; just

released mucocysts globular in the scanning electron microscope, platelet-like and swelling to a more or less voluminous coat after addition of methyl green-pyronin (Fig. 349e, i). Cortex punctated by ciliary pits and conspicuously pustulated in the scanning electron microscope, possibly due to exploding mucocysts or preparation artifacts. Cells greenish or yellowish due to cyanobacteria in various stages of digestion and citrine to ochre cytoplasmic granules 0.2–1 µm across; Portuguese specimens with diffuse, yellowish plasm colouration. Cytoplasmic granules accumulated in left anterior portion of cell forming yellow to ochre patch, especially conspicuous in hungry cells. Food vacuoles 3–15 µm across, contain filamentous cyanobacteria (*Oscillatoria*), whose crystalline, orange remnants turn into yellow to golden granules, similar to those forming the subapical patch, in the egestion vacuoles (Fig. 100g–i). Swims rather rapidly by rotation about main body axis.

Somatic cilia about 8 µm long in vivo, except for slightly elongated and loosened cilia in posterior pole area; distances between individual cilia increase from anterior to posterior, especially in ciliary rows right of oral opening and underneath first nassulid organelle. Ciliary rows meridionally and equidistantly arranged, except for more closely spaced postoral kineties and first and second kinety. Preoral suture and postorganellar stripe indistinct because kineties abut tightly preorally and extend close to the nassulid frange; continuous ciliary rows, as in → *N. dragescoi*, occur only between the last two to three frange organelles. Second kinety occasionally interrupted at level of oral opening or shortened posteriorly (Fig. 100 l, m; 349a–c; Tables 80, 81).

Oral opening subapical. Pharyngeal basket extends obliquely to dorsal side and posterior third of cell, funnel-shaped, distinctly bulbous and about 10 µm wide distally in vivo, composed of approximately 25 rather thin, about 40 µm long and slightly twisted rods; distal microtubular sheath distinct only in silver nitrate preparations; annulus recognizable neither in vivo nor silver preparations (Fig. 100a, k–o; 349a–d). Nassulid frange sigmoidal, terminates mid-dorsally at or slightly below level of oral opening, usually composed of 8 organelles in Saudi Arabian, 7 in Portuguese, and 5 in Antarctic specimens. Nassulid organelles composed of three kineties each, decrease in size from right to left, that is, first organelle with 7–12 basal bodies per kinety, last with 2–4. Length of cilia increases within each organelle from right to left; longest cilia about 15 µm, that is, almost twice the length of ordinary somatic cilia (Fig. 100 l–n; 349a, b, f, h, j; Table 80). Paroral membrane (dikinetids) not recognizable in silver nitrate and silver carbonate preparations; basal bodies, however, slightly more closely spaced at anterior end of kinety 1 than kinety 2 (Fig. 100 l, o; 349a, c).

Resting cysts globular, 45 × 44 µm on average in vivo, light citrine due to countless 1–3 µm-sized, yellowish fat globules occasionally forming distinct subcortical stripes (Fig. 100j; 349 l–u; Table 80). Wall colourless and tubercular, 1–2 µm thick and rigid, very likely trilaminar, covered by an about 10 µm thick, mucilaginous layer having some bacteria attached. Tubercles above longitudinal and equidistant rows of bright dots (possibly basal bodies of ciliary rows), 1–2 µm high, contain 2–3 granules or blunt rods 0.5–2 µm in size. Cytoplasm packed with yellowish fat globules mentioned above and a conspicuous vacuole about 12 µm across with food remnants and yellow granules. Macronucleus ellipsoidal. Pharyngeal basket maintained.

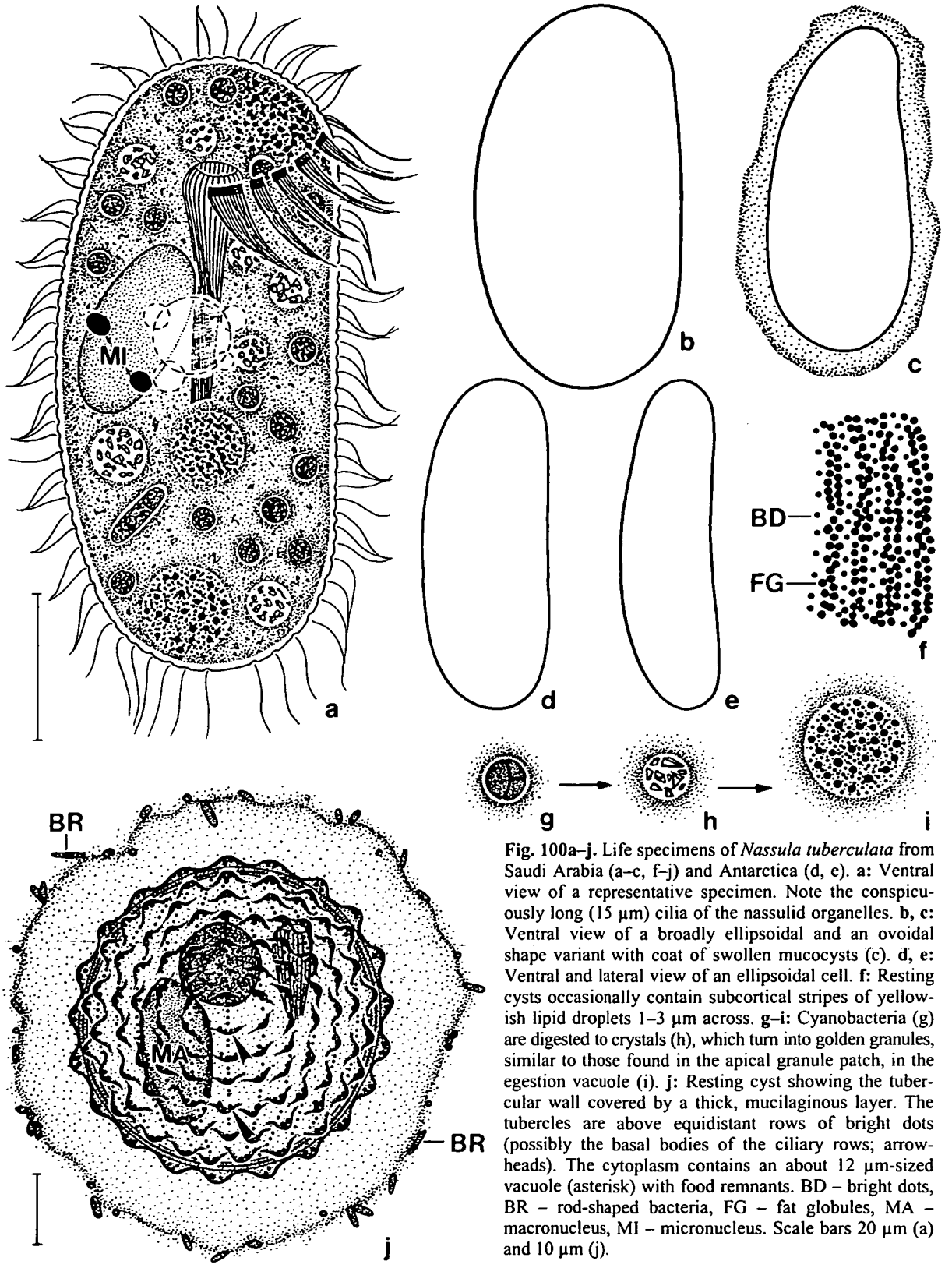


Fig. 100a–j. Life specimens of *Nassula tuberculata* from Saudi Arabia (a–c, f–j) and Antarctica (d, e). **a:** Ventral view of a representative specimen. Note the conspicuously long (15 µm) cilia of the nassulid organelles. **b, c:** Ventral view of a broadly ellipsoidal and an ovoidal shape variant with coat of swollen mucocysts (c). **d, e:** Ventral and lateral view of an ellipsoidal cell. **f:** Resting cysts occasionally contain subcortical stripes of yellowish lipid droplets 1–3 µm across. **g–i:** Cyanobacteria (g) are digested to crystals (h), which turn into golden granules, similar to those found in the apical granule patch, in the egestion vacuole (i). **j:** Resting cyst showing the tubercular wall covered by a thick, mucilaginous layer. The tubercles are above equidistant rows of bright dots (possibly the basal bodies of the ciliary rows; arrowheads). The cytoplasm contains an about 12 µm-sized vacuole (asterisk) with food remnants. BD – bright dots, BR – rod-shaped bacteria, FG – fat globules, MA – macronucleus, MI – micronucleus. Scale bars 20 µm (a) and 10 µm (j).

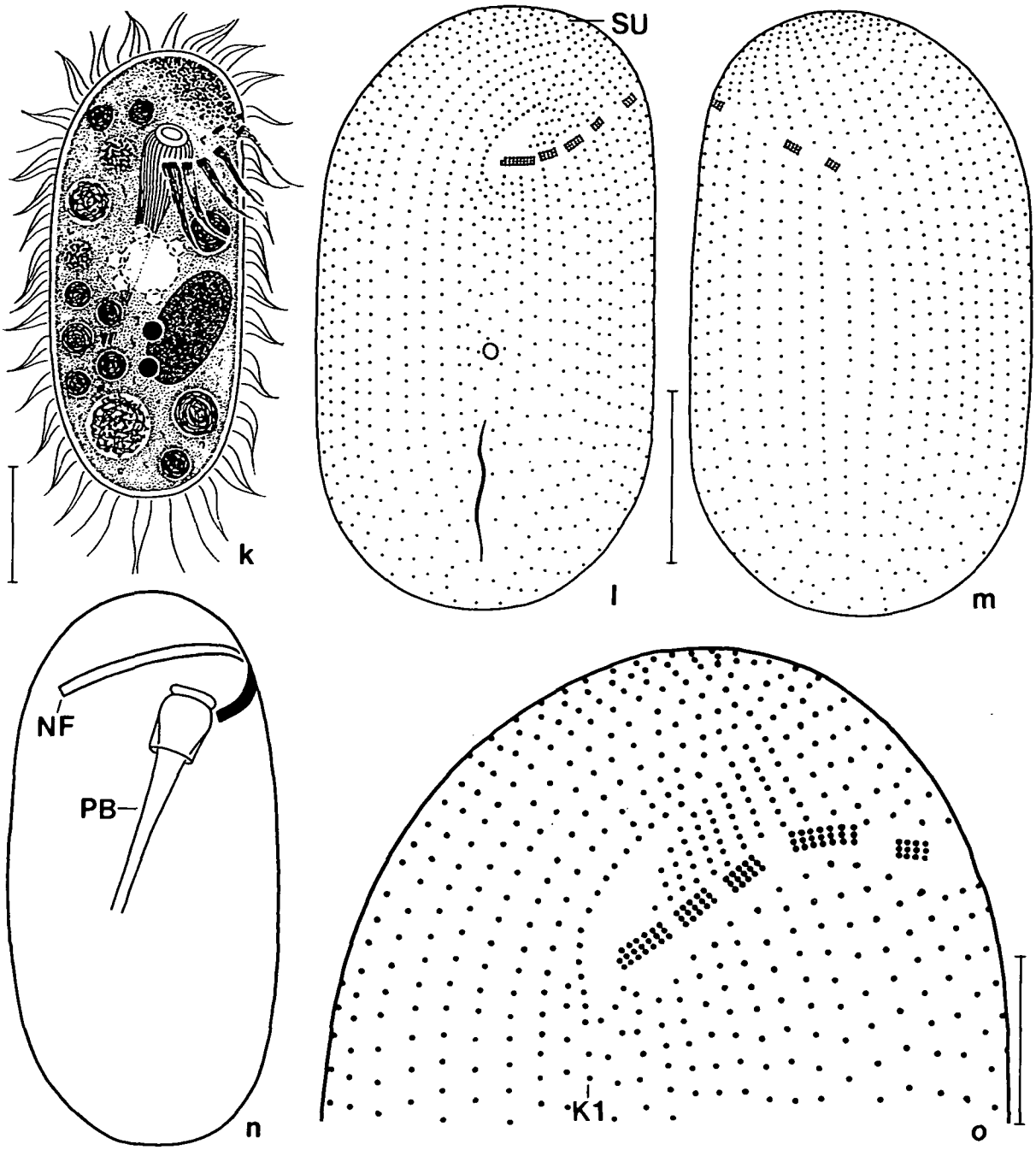


Fig. 100k–o. *Nassula tuberculata*, Portuguese specimens from life (k) and after silver nitrate impregnation (l–o). **k:** Ventral view of a representative specimen. As in the Saudi Arabian type population, the cilia of the nassulid organelles are conspicuously long (about 15 µm) and citrine granules form a distinct patch in the left anterior body portion. The macronucleus is ellipsoidal and has two to four micronuclei attached. **l, m, o:** Ciliary pattern of ventral and dorsal side of same specimen and anterior ventral portion of another cell. The postorganellar stripe and the preoral suture are indistinct because the ciliary rows abut tightly. A paroral membrane (dikinetids) is not recognizable, although the kinetids are slightly more closely spaced in kinety 1 than kinety 2. **n:** The nassulid frange extends almost parallel to the perimeter of the cell and terminates mid-dorsally at or slightly underneath level of oral opening. K1 – kinety 1, NF – nassulid frange, PB – pharyngeal basket, SU – preoral suture. Scale bars 20 µm (k–m) and 10 µm (o).

Occurrence and ecology: To date found at type location, where it was rather abundant; in a saline soil from Portugal; and in mixed terrestrial and limnetic material (pH 4.0–5.2) from Ross Island, Antarctica, where the population was misidentified as *Nassula picta* by FOISSNER (1996a; site 47). The slightly acidic (pH 6.0) sample from Saudi Arabia was a mixture of litter (mainly from legumes planted for desalinization) and highly saline (8‰), yellowish sand with many roots and patches of iron concretions. The Portuguese site was saline grassland about 200 m inshore and behind a coastal dune in the surroundings of Armação de Pêra, a small town at the Algarve coast (37°N 08°W). This sample (pH 8.4) consisted of the upper (0–3 cm) soil layer of a dry, flat pool with a white salt crust and of dry algal crusts between halophytes. Obviously, *N. tuberculata* is a cosmopolitan species occurring within a wide range of salinity and pH.

Comparison of populations and with related species: The Saudi Arabian, Portuguese, and Antarctic population match in the main features, namely, the shape of the nassulid frange; the number of ciliary rows, pharyngeal rods, and nassulid organelles; the coloured granule patch; the lack of trichocysts; and the indistinctness of the postorganellar stripe. The Saudi Arabian specimens are slightly larger than those from Portugal and Antarctica (70–100 µm vs. 60–80 µm) and have more kinetids in a dorsal ciliary row (about 48 vs. 37 and 44). These differences are insignificant and thus conspecificity is beyond reasonable doubt, although the most important feature, that is, the structure of the resting cyst wall, could not be compared.

Table 81. Comparison of main morphometrics of *Nassula tuberculata*, *N. terricola* (from FOISSNER 1989), and → *N. granata*.

Characteristics [a]	*N. tuberculata*			*N. terricola*	*N. granata*
	Saudi Arabia	Portugal	Antarctica	Austria	Namibia
Body, length in vivo	70–100	60–80	70	90–130	75–100
Body length:width, ratio in vivo	1.8–2.7:1 ($\bar{x}$ = 2.2:1)	2.3:1	3.0:1	1.7:1	2.5:1
Macronucleus, shape	ellipsoidal	ellipsoidal	ellipsoidal	globular	ellipsoidal
Micronuclei, number	1–3 ($\bar{x}$ = 2)	2–4 ($\bar{x}$ = 3)	2	1	2–3 ($\bar{x}$ = 2)
Granule patch	left side	left side	left side	lacking	dorsal side
Ciliary rows, number	31–45 ($\bar{x}$ = 41)	36–61 ($\bar{x}$ = 44)	38–42 ($\bar{x}$ = 41)	48–55 ($\bar{x}$ = 53)	44–52 ($\bar{x}$ = 47)
Kinetids in a ciliary row, number	42–60 ($\bar{x}$ = 48)	29–45 ($\bar{x}$ = 37)	?	45–56 ($\bar{x}$ = 51)	43–54 ($\bar{x}$ = 50)
Pharyngeal rods, number	23–26 ($\bar{x}$ = 25)	20–26 ($\bar{x}$ = 24)	20–24	~ 20	25–29 ($\bar{x}$ = 27)
Nassulid organelles, number	6–10 ($\bar{x}$ = 8)	6–9 ($\bar{x}$ = 7)	5	9–13 ($\bar{x}$ = 11)	5–9 ($\bar{x}$ = 8)
Length of frange cilia	15	15	?	?	8
Resting cysts, type [b]	type IV	?	?	type III	type I

[a] Measurements in µm.

[b] See *Nassulides labiatus* for explanation.

Nassula tuberculata, → *N. granata*, and *N. terricola* are almost indistinguishable by conventional morphological characteristics (Table 81), especially when the rather pronounced variability is taken into account. Thus, reliable identification needs the resting cysts, whose wall structure is conspicuously different: tubercular in *N. tuberculata*, smooth in → *N. granata* (Fig. 348j), and with distinct ridges in *N. terricola* (re-checked in the type slides, which contain many cysts clearly showing that they are different from those of *N. tuberculata*).

Admittedly, the alpha-taxonomical value of resting cysts is poorly known. The data available indicate that they are often not species but only genus or family-specific. On the other hand, FOISSNER (1993c) represented an excellent example of resting cyst wall differences in *Colpoda cucullus* and *C. flavicans*, two species as similar in conventional morphological features as *Nassula tuberculata*, → *N. granata*, and *N. terricola*. A further example is provided by various *Stylonychia* species (FOISSNER & BERGER 1999). Thus, we feel justified in separating these three *Nassula* populations at species level by the cyst wall structure. Alternatively, they can be considered as sibling species of a "*Nassula terricola*-complex".

Nassula etoschensis nov. spec. (Fig. 101a–j; 350c–g; Table 82)

Diagnosis: Size about 100 × 65 µm in vivo; broadly ellipsoidal. Two types of extrusomes: fusiform, about 5 µm long trichocysts and platelet-like, minute mucocysts. On average 84 ciliary rows. Nassulid frange sigmoidal, terminating near anterior quarter of left body margin, composed of on average 6 organelles closely spaced in right and widely in left half of frange. Pharyngeal basket composed of about 18 straight, widely spaced rods extending to mid-body. Paroral membrane conspicuous, composed of about 10 dikinetids.

Type location: Highly saline soil from margin of Etosha Pan, Namibia, 18°50'S 16°30'E (site 67 in figures 2, 3 and chapter 2.1.2).

Etymology: Named after the area discovered.

Description: Size 80–120 × 50–75 µm in vivo, as calculated from measurements of live specimens and values shown in table 82, assuming a shrinkage of about 10–20% due to the preparation procedures. Overall shape broadly ellipsoidal, rarely obovoidal, with shallow furrow underneath nassulid frange; length:width ratio about 1.5:1 both in vivo and after silver nitrate impregnation (Fig. 101a, h). Macronucleus usually in middle third of cell, about 30 × 25 µm in vivo, surrounded by a distinct membrane, with reticular nucleolus. Up to 6 globular micronuclei near or attached to macronucleus; exact number difficult to count because of many similarly sized and impregnated cytoplasmic inclusions. Contractile vacuole slightly above mid-body, surrounded by small contributory vesicles during diastole; excretory pore usually in line with kinety 2. Cytopyge slit in line with excretory pore, near posterior body end, about 21 µm long. Resting trichocysts attached almost perpendicularly to cortex, rather sparse and thus not forming distinct fringe, fusiform, about 5 × 0.7–1 µm; exploded trichocysts rod-shaped and slightly curved, up to 25 × 0.5 µm (Fig. 101i, j; 350e). Resting mucocysts hardly recognizable, produce bright, about 1 µm thick cortical layer, released as 1–2 µm-sized, polygonal platelets when methyl green-pyronin is added. Cells greenish and/or orange due to ingested cyanobacteria and inconspicuous patch of orange granules (indeed,

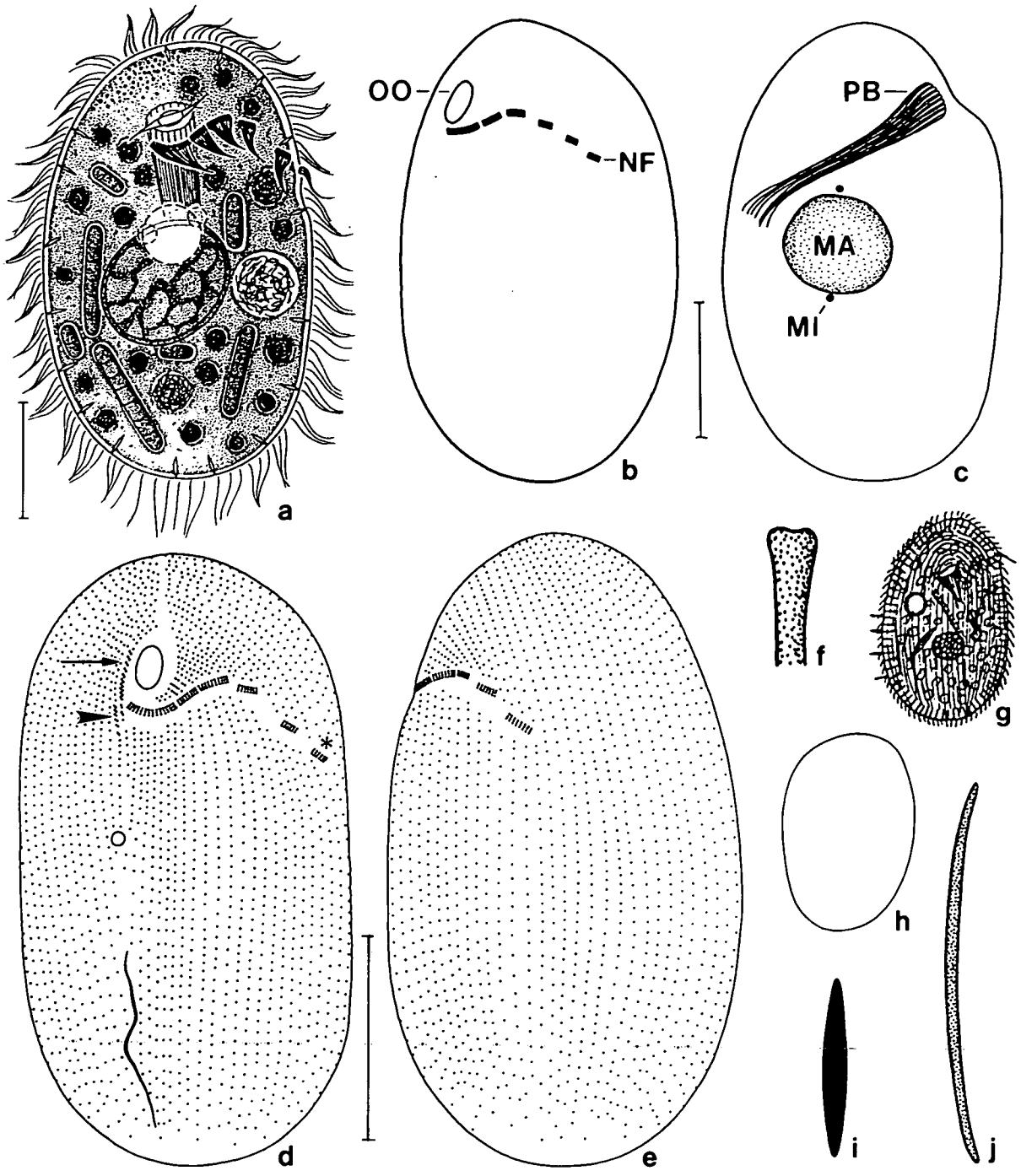


Fig. 101a–j. *Nassula etoschensis* (a–f, h–j) and similar species (g) from life (a, f–j), after silver nitrate impregnation (b, d, e), and protargol impregnation (c). **a:** Ventral view of a representative specimen. Note sparse trichocysts. **b:** Ventrolateral view showing arrangement of nassulid frange. **c:** Right lateral view showing pharyngeal basket composed of straight rods. **d, e:** Ciliary pattern of ventral and left side. The nassulid frange extends sigmoidally to the left body side, terminating slightly below anterior quarter of cell with last organelle marked by an asterisk. The organelles are more closely spaced in the right than the left half of the frange. Note clockwise inclined dikinetids of paroral membrane (arrow) and kinety 2 (arrowhead). **f:** Anterior portion of a pharyngeal rod. **g:** *Nassula picta* (?), length 80 µm (from VUXANOVICI 1962a). **h:** Obovoidal shape variant. **i, j:** Resting (5 µm long) and exploded (up to 25 µm long) trichocyst. MA – macronucleus, MI – micronucleus, NF – nassulid frange, OO – oral opening, PB – pharyngeal basket. Scale bars 30 µm.

0.2–1 µm-sized lipid droplets) subapically on dorsal side; cells without food vacuoles golden. Feeds mainly on filamentous cyanobacteria digested in 4–20 µm-sized food vacuoles changing from blue-green to orange during late digestion stages. Movement without peculiarities.

Somatic cilia about 10 µm long in vivo, slightly elongated and distinctly loosened in posterior pole area; distances between individual cilia increase from anterior to posterior, especially in ciliary rows right of oral opening and underneath first nassulid organelle. Ciliary rows meridionally and equidistantly arranged, except for more closely spaced kineties right and left of oral opening and underneath first nassulid organelle, form distinct preoral suture and postorganellar stripe both about 2–3 µm wide; kinety 2 occasionally shortened anteriorly terminating at level of mid-oral opening with clockwise inclined dikinetids at level of postorganellar stripe (Fig. 101d, e; Table 82).

Oral opening subapical, membranous and fusiform. Pharyngeal basket extends obliquely to dorsal side and mid-body, funnel-shaped, about 10 µm wide in vivo and **not** bulbous distally, composed of approximately 18 thick, straight, and comparatively widely spaced rods with shallow indentation anteriorly; distal microtubular sheath and annulus recognizable neither in vivo nor silver slides (Fig. 101a, c, f; 350b–d). Nassulid frange commences mid-ventrally and extends sigmoidally across ventral side terminating slightly below anterior quarter of left body margin; usually composed of 6 organelles closely spaced and sigmoidally arranged in right half of frange, widely spaced and step-like in left. Nassulid organelles composed of three kineties each; first organelle long (composed of about 20 basal bodies) and curved, others short (composed of 3–9 basal bodies) and straight (Fig. 101b, d, e; Table 82). Paroral membrane conspicuous in silver nitrate and protargol preparations, continuous with first ciliary row, commences at level of mid-oral opening and extends in a flat bow to post-organellar stripe, composed of about 10 clockwise inclined dikinetids (Fig. 101d).

Occurrence and ecology: To date found only in highly saline soils of the Etosha Pan region (sites 54, 65, 67).

Comparison with related species: Several nassulids resemble *N. etoschensis*, especially *N. citrea* and *Nassulides pictus*. *Nassula citrea* KAHL, 1931, as redescribed by EISLER & BARDELE (1986), matches *N. etoschensis* in body size, trichocysts, and number of nassulid organelles (4–7); both, however, differ markedly in the length:width ratio (about 2.2:1 vs. 1.5:1) and the number of ciliary rows (55 vs. 72–92) and pharyngeal rods (34–38 vs. 15–19). Furthermore, the nassulid frange of *N. citrea* is composed of almost equidistantly spaced organelles and has a different course, that is, extends almost straight or in a flat bow to the left body side.

At first glance, *N. etoschensis* resembles *Nassulides pictus* because of the similar size and shape. However, they can be easily separated, even in vivo, by the trichocysts (lacking in *N. pictus* according to the authoritative redescriptions by FOISSNER 1980e, 1989 and FOISSNER et al. 1994) and the pharyngeal basket (composed of about 18 straight and widely spaced rods vs. about 24 twisted, closely spaced rods). Furthermore, *pictus* belongs to the genus *Nassulides* (see introduction to family). KAHL (1931) and VUXANOVICI (1962a) briefly mentioned trichocyst-bearing populations of *N. pictus*. VUXANOVICI's specimens (Fig. 101g) are similar to *N. etoschensis* in body shape, body size (about 80 µm), and number of pharyngeal rods (12–14), but differ rather distinctly in the number of ciliary rows (about 28–30 vs. 36–46 on one side of cell). Unfortunately, a more detailed comparison is impossible

because VUXANOVICI (1962a) did not provide any information about the nassulid frange. *Nassula gutturata* GAJEVSKAJA, 1927, a species from the littoral of Lake Baikal, differs from *N. etoschensis* mainly in the very distinct basket annulus, which is inconspicuous or even lacking in *N. etoschensis* (cp. figure 99b with figures 101c and 350d).

Table 82. Morphometric data on *Nassula etoschensis*.

Characteristics [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	CHL	89.5	89.0	8.1	2.1	9.0	73.0	106.0	15
Body, width	CHL	57.0	58.0	7.4	1.9	13.1	43.0	68.0	15
Body length:width, ratio	CHL	1.6	1.5	0.1	0.0	7.5	1.4	1.8	15
Anterior body end to macronucleus, distance	CHL	35.2	36.0	5.5	1.4	15.5	26.0	44.0	15
Anterior body end to excretory pore, distance	CHL	38.1	39.0	4.1	1.1	10.8	31.0	45.0	15
Anterior body end to cyrtos, distance	CHL	12.1	13.0	2.1	0.5	17.0	9.0	15.0	15
Anterior body end to last nassulid organelle, distance	CHL	24.8	25.0	3.1	0.8	12.7	19.0	30.0	15
Macronucleus, length	PA	26.3	26.0	3.9	1.0	14.8	20.0	33.0	15
Macronucleus, width	PA	22.7	21.0	4.5	1.2	19.6	15.0	33.0	15
Micronuclei, diameter	PA	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
Pharyngeal basket, maximum diameter	PA	8.9	9.0	1.0	0.3	10.8	6.0	11.0	15
First nassulid organelle, length	CHL	7.7	8.0	1.4	0.4	17.9	5.0	10.0	15
Other nassulid organelles, length	CHL	3.4	3.0	0.7	0.2	21.7	2.0	5.0	15
Paroral membrane, length	CHL	9.4	9.0	2.4	0.8	25.7	6.0	15.0	10
Macronucleus, number	PA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Somatic ciliary rows, number	CHL	83.9	86.0	6.3	1.6	7.5	72.0	92.0	15
Pharyngeal basket, number of rods	CHL	18.1	18.0	1.2	0.3	6.4	15.0	19.0	15
Nassulid organelles, number	CHL	5.8	6.0	0.6	0.1	9.7	5.0	7.0	15

[a] Data based on silver-impregnated, mounted, and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, PA – protargol impregnation (FOISSNER's method), SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Naxella rosea (TUCOLESCO, 1962) **nov. comb.** (Fig. 102a–g; 270, 351a–k; Table 83)

1962 *Nassula rosea* TUCOLESCO, Arch. Protistenk., 106: 11.

Neotype material: Neotypified from Namibian site (57) population, according to reasons 1, 2, 4, 6 given in chapter 2.4.2.

Improved diagnosis: Size about 60 x 40 µm in vivo; broadly ellipsoidal. Two kinds of fusiform trichocysts: large type 6–9 µm long, small type 3–4 µm long. On average 44 ciliary rows and 13 pharyngeal rods extending to posterior body end. 3 nassulid organelles extending to left body margin. Paroral membrane distinct, composed of about 13 dikinetids.

Description of Namibian population: Size 50–75 × 30–50 µm in vivo, as calculated from measurements of live specimens and values shown in table 83, assuming a shrinkage of about 20% due to the preparation procedures. Overall shape ellipsoidal to broadly ellipsoidal with bluntly pointed anterior and widely rounded posterior end and shallow furrow underneath nassulid frange; length:width ratio about 1.5:1 in preparations (Fig. 102a, b, f; 351a–e, k; Table 83). Macronucleus usually in middle third of cell, broadly

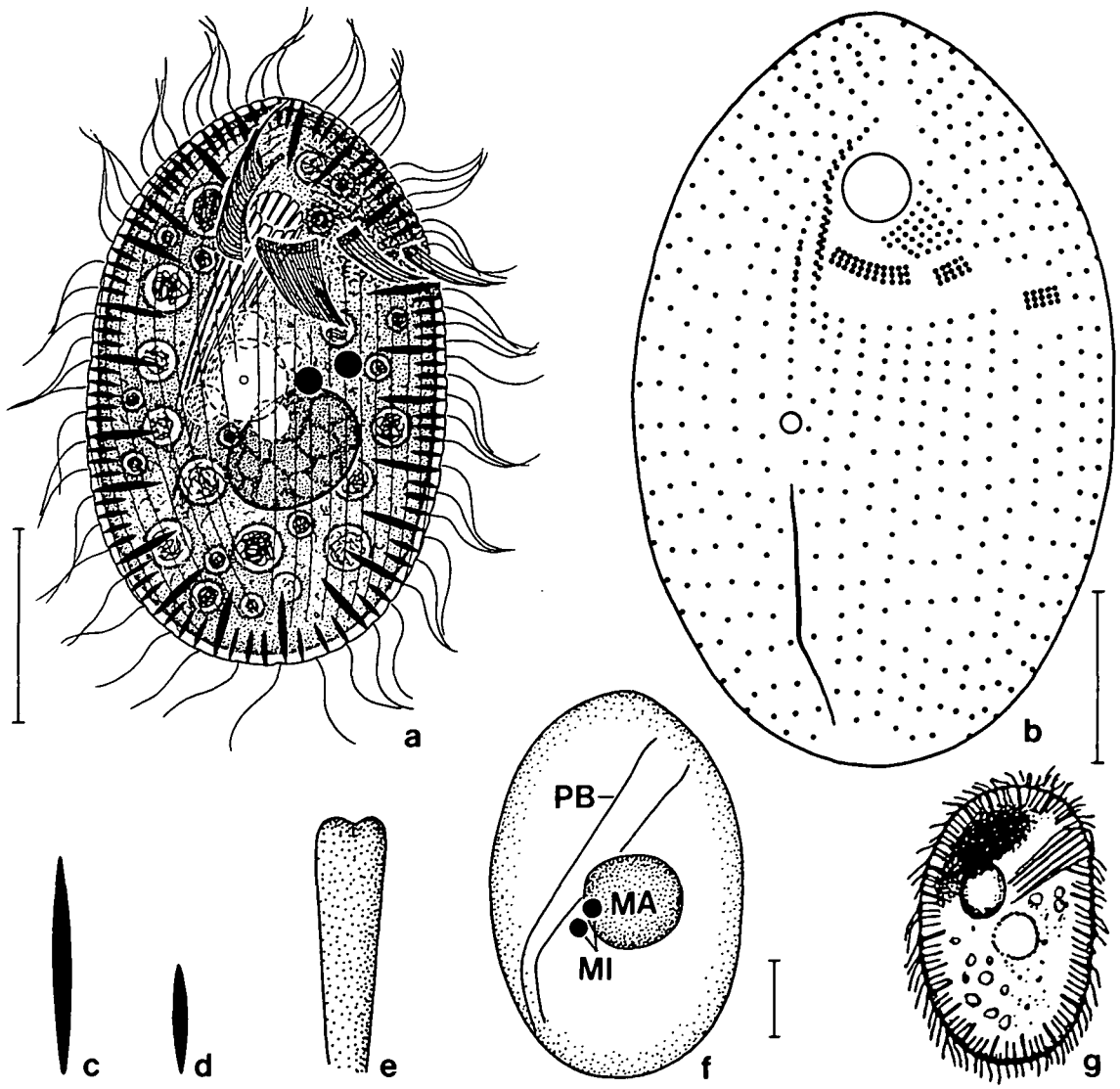


Fig. 102a–g. *Naxella rosea*, Namibian (a–f) and Romanian (g) specimens from life (a, c–e, g), after silver nitrate impregnation (b), and protargol impregnation (f). **a:** Ventral view of a representative specimen from neotype population showing the two types of trichocysts and the broadly ellipsoidal body with a bluntly pointed anterior end. **b:** Ciliary pattern of ventral side showing the distinct paroral membrane and the short nassulid frange, which invariably consists of three organelles and extends slightly obliquely to the left body margin. **c, d:** Large (6–9 µm long) and short (3–4 µm long) trichocyst drawn to scale. **e:** Anterior portion of a pharyngeal rod. **f:** Right lateral view showing the nuclear apparatus and the pharyngeal basket extending to rear end. **g:** Right lateral view of type specimen, length 55–69 µm (from TUCOLESCO 1962). MA – macronucleus, MI – micronuclei, PB – pharyngeal basket. Scale bar 20 µm (a) and 10 µm (b, f).

ellipsoidal, with reticular nucleolus. Micronuclei adjacent to macronucleus, globular, difficult to distinguish from similarly sized cytoplasmic inclusions. Contractile vacuole near mid-body, surrounded by small contributory vesicles during diastole; excretory pore at end of kinety 2. Cytopyge slit underneath excretory pore, extends to near posterior body end, about 15 µm long. Resting trichocysts attached almost perpendicularly to cortex, equidistantly arranged in longitudinal rows, form distinct fringe, fusiform (Fig. 102a, c, d; 351b–e, j, k): large type 6–9 × 0.7–1 µm and sparse, small type 3–4 × 0.5–0.7 µm and numerous. Occurrence of mucocysts not investigated. Cortex about 1 µm thick and bright, punctated by ciliary pits and trichocysts. Cells greenish and/or yellow-brown due to ingested cyanobacteria and citrine patch of 0.2 µm-sized granules in left anterior body portion. Feeds mainly on coccal cyanobacteria digested in vacuoles 2–5 µm across.

Somatic cilia about 10 µm long in vivo, arise from shallow cortical pits, loosened in posterior pole area; distances between individual cilia increase from anterior to posterior, especially in second kinety and ciliary rows underneath first nassulid organelle. Ciliary rows longitudinally and equidistantly arranged, except for more closely spaced postoral kineties and first (paroral) and second kinety, which end near mid-body; leave blank an about 2 µm wide stripe underneath nassulid frange and form distinct preoral suture. Kinety 2 usually commences with some dikinetids at level of mid-oral opening and ends at excretory pore of contractile vacuole (Fig. 102b; 270, 351f, h, i; Table 83).

Oral opening subapical. Pharyngeal basket extends obliquely to dorsal side and posterior end of cell, funnel-shaped, composed of about 13 thick, untwisted rods with shallow indentation anteriorly; annulus and distal microtubular sheath not recognizable in vivo and protargol preparations. Distal basket region about 6–7 µm wide, composed of heavily impregnated, ellipsoidal structures (seemingly?) connected by a ring-shaped, membranous structure (Fig. 102a, e, f; 270, 351f, h, i, k). Nassulid frange extends slightly obliquely posteriad on ventral side, invariably composed of three staggered organelles. Nassulid organelles composed of three kineties each, decrease in size from right to left, that is, first organelle with about 10–13 cilia per kinety, last with only three to five; length of cilia increases from about 7 µm at right to about 10 µm at left end of organelles (Fig. 102a, b; 270, 351a, f, h, i, k; Table 83). Paroral membrane rather conspicuous, continuous with first somatic ciliary row, commences at level of oral opening and extends in flat bow to blank stripe underneath nassulid frange, composed of about 12–14 clockwise inclined dikinetids (Fig. 102a, b; 270, 351a, f, h, i).

Occurrence and ecology: TUCOLESCO (1962) discovered *Naxella rosea* in a freshwater affluent to a Romanian lake. We found it in highly saline soils of the Etosha Pan region (sites 57, 70). Thus, *N. rosea* seems to be a euryhaline and cosmopolitan species.

Comparison with original description and related species: Assigned to genus *Naxella* for reasons explained in introduction to family. In vivo difficult to distinguish from → *Nassula longinassa*. The Namibian population resembles two species, *Nassula rosea* TUCOLESCO, 1962 (Fig. 102g) and → *Nassula lucida* REUTER, 1961. The description of *N. rosea* is based on live observations of a single specimen. Thus, it is fairly incomplete and lacks, for instance, information about nassulid organelles and pharyngeal rods. However, our population matches this species in an important feature, namely, the occurrence of two types of trichocysts ("les uns vigoureux et rares, les autres plus fins et plus serrés"; TUCOLESCO 1962). Furthermore, shape and size (length 55–69 µm after TUCOLESCO 1962) are very similar. Only the colour (grey-pink vs. greenish to yellow-brown) and the habitat (freshwater

vs. highly saline soil) are different. Colour is a weak feature in nassulids because it depends on food organisms and life cycle. The habitat is a more serious difference. However, some (many?) nassulids are euryhaline, as exemplified by → *Nassulides labiatus*. Our population also resembles → *Nassula lucida* REUTER, 1961, especially in body shape, colour (bright yellow-orange), habitat (rock-pools; NaCl 0.1–21.6‰), and number of pharyngeal rods (14). However, REUTER (1961) did not mention two types of trichocysts. Thus, we prefer identifying our population with *N. rosea* TUCOLESCO, 1962, while another, similar population with only one type of trichocysts and only two nassulid organelles matches → *N. lucida* REUTER, 1961.

Naxella rosea differs from its congeners in the trichocysts (only one type in → *Naxella lucida* and *N. australis* FOISSNER & O'DONOGHUE, 1990; lacking in *N. minima* DRAGESCO & DRAGESCO-KERNÉIS, 1986), the number of nassulid organelles (only two in → *N. lucida*; 5–8 in *N. minima*, which thus belongs very likely to *Nassula*), and in the location of the excretory pore of the contractile vacuole (distinctly left of paroral membrane and underneath first or second nassulid organelle in *N. faurei* FOISSNER & O'DONOGHUE, 1990). There are two other similarly sized nassulids, → *Nassula parva* KAHL, 1928 and *N. pusilla* KAHL, 1931; however, these species lack trichocysts (at least, none were mentioned by KAHL) and should thus not be identified (synonymized) with *Naxella rosea*.

Cyclogramma viridis DINGFELDER, 1962 is probably a senior synonym of *Naxella faurei* FOISSNER & O'DONOGHUE, 1990 because it is very similar in shape, size, number of nassulid organelles (not mentioned by DINGFELDER but his assignment of the species to *Cyclogramma* implies three nassulid organelles), and freshwater habitat (DINGFELDER 1962, FAURÉ-FREMIET 1967, FOISSNER & O'DONOGHUE 1990).

Table 83. Morphometric data on *Naxella rosea* (upper line) and *N. lucida* (lower line).

Characteristics [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	CHL	53.1	50.0	7.5	2.4	14.2	44.0	65.0	10
	CHL	40.1	39.0	5.6	2.0	13.9	32.0	50.0	8
Body, width in ventral view	CHL	35.3	34.0	4.4	1.4	12.6	30.0	45.0	10
	CHL	26.8	26.5	2.8	1.0	10.5	24.0	31.0	8
Body length:width, ratio	CHL	1.5	1.5	0.1	0.1	8.0	1.4	1.8	10
	CHL	1.5	1.6	0.2	0.1	12.3	1.1	1.6	8
Anterior body end to macronucleus, distance	CHL	28.9	26.0	6.1	1.9	21.0	23.0	41.0	10
	CHL	20.0	19.0	3.3	1.3	16.6	15.0	25.0	7
Anterior body end to cyrtos, distance	CHL	10.5	9.0	2.4	0.8	23.0	8.0	14.0	10
	CHL	5.8	5.0	2.6	0.9	45.3	3.0	9.0	8
Anterior body end to last nassulid organelle,	CHL	14.8	14.0	3.5	1.4	23.5	11.0	21.0	6
distance	CHL	10.1	10.5	3.4	1.2	34.0	6.0	14.0	8
Macronucleus, length	CHL	13.1	13.0	1.8	0.6	13.5	9.0	15.0	9
	CHL	9.6	10.0	1.0	0.4	10.2	8.0	11.0	7
Macronucleus, width	CHL	9.8	9.0	1.9	0.6	19.7	8.0	13.0	9
	CHL	8.6	8.0	0.8	0.3	9.2	8.0	10.0	7
Micronucleus, diameter [b]	CHL	3.0	3.0	0.0	0.0	0.0	3.0	3.0	5
Pharyngeal basket, maximum diameter	CHL	6.0	6.0	1.2	0.4	19.2	5.0	9.0	10

(continued)

Characteristics [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	PA	5.0	5.0	0.0	0.0	0.0	5.0	5.0	8
First nassulid organelle, length	CHL	5.5	5.5	–	–	–	5.0	6.0	6
	CHL	5.7	6.0	–	–	–	5.0	6.0	3
Last nassulid organelle, length	CHL	3.0	3.0	0.0	0.0	0.0	3.0	3.0	6
	CHL	3.0	3.0	0.0	0.0	0.0	3.0	3.0	5
Macronucleus, number	SC	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	CHL	1.0	1.0	0.0	0.0	0.0	1.0	1.0	8
Micronuclei, number [c]	SC	2.4	2.0	–	–	–	2.0	3.0	7
	CHL	2.3	2.0	–	–	–	2.0	3.0	4
Somatic ciliary rows, number	SC	44.3	44.0	1.7	0.6	3.8	42.0	46.0	7
	SC	34.7	35.0	1.7	0.5	5.0	32.0	37.0	12
Kinetids in a dorsal kinety, number	SC	24.0	23.0	2.7	1.4	11.3	22.0	28.0	4
	SC	22.6	23.0	1.9	0.6	8.3	18.0	25.0	9
Pharyngeal basket, number of rods	SC	12.9	13.0	0.7	0.3	5.4	12.0	14.0	7
	SC	12.7	13.0	0.9	0.3	7.0	11.0	14.0	12
Nassulid organelles, number	SC	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
	SC	2.0	2.0	0.0	0.0	0.0	2.0	2.0	12

[a] Data based on silver-impregnated, randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, PA – protargol impregnation (FOISSNER's method), SC – silver carbonate impregnation, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] *Naxella rosea*.

[c] *Naxella lucida*: Of four specimens investigated, one has 3 micronuclei.

Naxella lucida (REUTER, 1961) **nov. comb.** (Fig. 103a–g; 352a–f; Table 83)

1961 *Nassula lucida* REUTER, Acta zool. fenn., 99: 12.

Neotype material: Neotypified from Namibian site (67) population, according to reasons 1, 2, 4, 6 given in chapter 2.4.2.

Improved diagnosis: Size about 55–75 × 30–45 µm in vivo; broadly ellipsoidal. Two types of extrusomes: fusiform, about 5 µm long trichocysts, and platelet-like, minute mucocysts. On average 35 ciliary rows and 13 pharyngeal rods extending to posterior body end. 2 nassulid organelles underneath oral area. Paroral membrane distinct, composed of about 13 dikinetids.

Description of Namibian population: Size 40–60 × 25–35 µm in vivo, as calculated from some measurements of live specimens and values shown in table 83, assuming a shrinkage of about 20% due to the preparation procedures. Overall shape broadly ellipsoidal with shallow oral depression and flat furrow underneath nassulid frange;

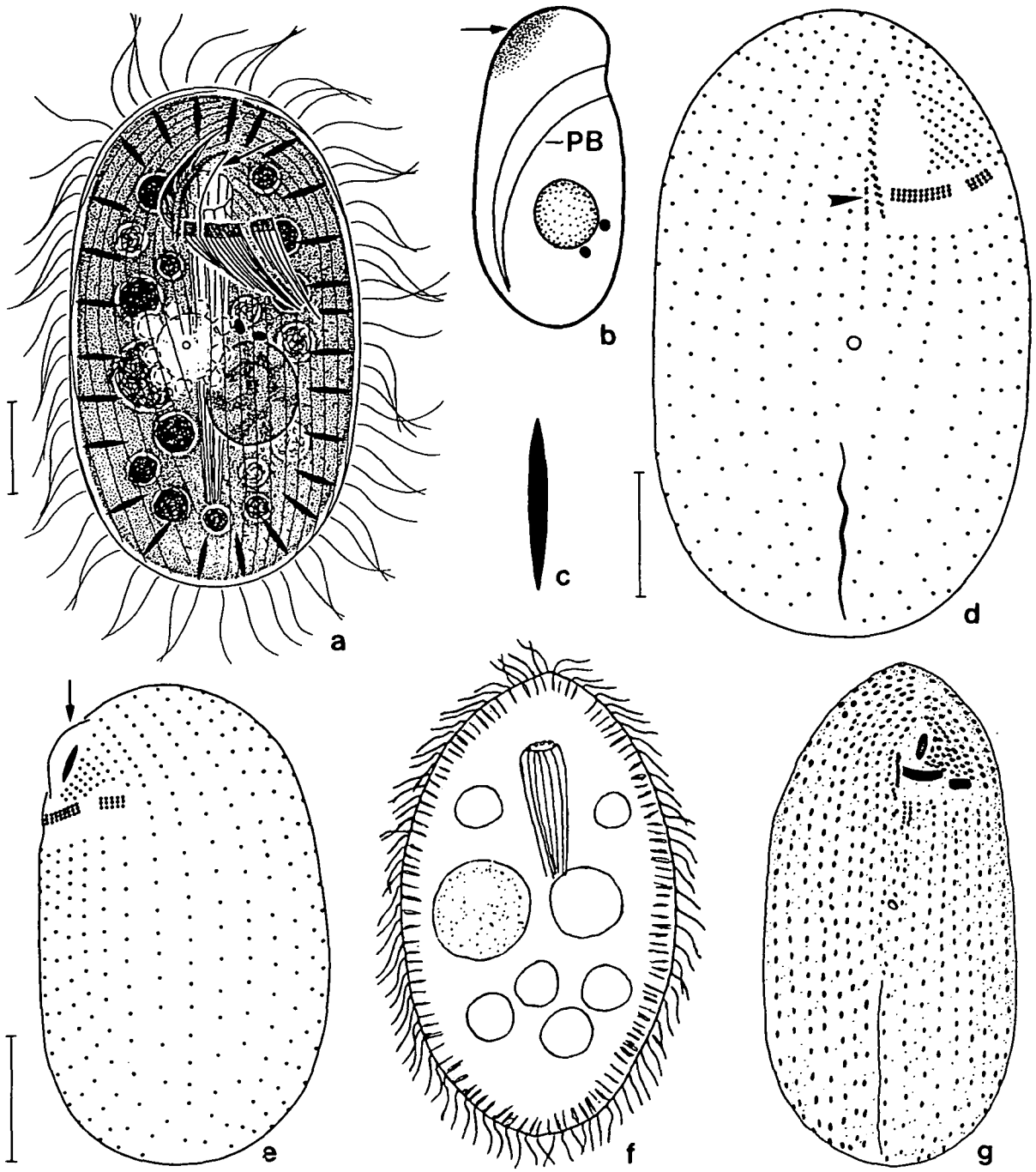


Fig. 103a–g. *Naxella lucida*, Namibian (a–e) and Finnish (f) specimens and similar species (g) from life (a–c, f) and after silver nitrate impregnation (d, e, g). **a:** Ventral view of a representative specimen showing the two nassulid organelles underneath the oral area, the conspicuous paroral membrane, and the distinct fringe of fusiform trichocysts. A hyaline lip (arrow) covers the right third of the oral area. **b:** Right lateral view showing the nuclear apparatus, the long pharyngeal basket, and the distinct patch of golden granules (arrow) in the anterior portion of the dorsal side. **c:** Resting trichocysts are about 5 µm long. **d, e:** Ciliary pattern of ventral and left side showing the nassulid frange composed of two organelles only. The paroral membrane consists of clockwise inclined dikinetids. Note dikinetids in kinety 2 (arrowhead). Arrow in (e) marks buccal lip. **f:** Specimen from type population, length 70–80 µm (from REUTER 1961). **g:** *Nassula* sp. (about 52 µm long) from the South Shetland Islands (from THOMPSON 1978). PB – pharyngeal basket. Scale bar 10 µm.

length:width ratio about 1.6:1, dorsoventrally slightly flattened (Fig. 103a, b). Macronucleus usually in posterior half of cell, about 14 µm across in vivo, with reticular nucleolus. Micronuclei adjacent to macronucleus, ellipsoidal, about 1–2 x 0. 5–1 µm in silver carbonate-impregnated specimens; difficult to distinguish from similarly sized cytoplasmic inclusions. Contractile vacuole near mid-body, surrounded by small contributory vesicles during diastole; excretory pore near end of second kinety. Cytopyge slit underneath excretory pore, extends to near posterior body end, about 15 µm long; food remnants leave cell as fluffy bale (Fig. 352f). Resting trichocysts attached almost perpendicularly to cortex within ciliary rows, form distinct fringe, fusiform, about 5 x 0.6 µm (Fig. 103a, c; 352c, e). Resting mucocysts hardly recognizable, produce bright, about 1 µm thick cortical layer, released as 1–2 µm-sized, polygonal platelets, which form a membranous cover when methyl green-pyronin is added (Fig. 352d). Cells blue-green to orange-yellow due to ingested cyanobacteria in various stages of digestion and golden patch of about 1 µm-sized, greasy granules in anterior portion of dorsal side. Feeds mainly on filamentous cyanobacteria digested in vacuoles 3–20 µm across (Fig. 352a, e). Swims rapidly.

Somatic cilia 10–12 µm long in vivo, loosened in posterior pole area; distances between individual cilia increase from anterior to posterior, especially in second kinety and ciliary rows underneath first nassulid organelle. Ciliary rows longitudinally and equidistantly arranged, except for more closely spaced postoral kineties and first (paroral) and second kinety, which end slightly above mid-body; form short, but distinct preoral suture and postorganellar stripe both about 3 µm wide. Second kinety with some dikinetids in anterior portion, commences at level of mid-oral opening; occasionally kineties 3 and 4 also shortened anteriorly (Fig. 103d, e; 352a, c; Table 83).

Oral opening subapical, fusiform; a hyaline cortical lip covers right third of oral area (Fig. 352a, e). Pharyngeal basket extends obliquely to dorsal side and posterior end of cell, funnel-shaped, composed of about 13 thick, untwisted rods; annulus and distal microtubular sheath not recognizable in vivo and protargol preparations. Distal basket region about 5 µm wide, of same structure as in → *Naxella rosea*, that is, composed of heavily impregnated, ellipsoidal structures (seemingly?) connected by a ring-shaped, membranous structure (Fig. 352a, b). Nassulid frange underneath oral area, invariably composed of only two organelles arranged parallel to frange axis. Both organelles consist of three kineties each, which are composed of 12–13 cilia in first and 5–7 cilia in second organelle; length of cilia increases from about 5 µm at right to 12 µm at left end of organelles (Fig. 103d, e; 352a, c, f; Table 83). Paroral membrane rather conspicuous in silver nitrate, silver carbonate, and protargol preparations; continuous with first somatic ciliary row, commences at level of oral opening and extends in flat bow to postorganellar stripe, composed of about 11–14 clockwise inclined dikinetids with 5 µm long cilia (Fig. 103a, d, e; 352a, c).

Occurrence and ecology: REUTER (1961) discovered *Naxella lucida* in rock-pools (NaCl 0.1–21.6‰) at the Finnish coast. We found few specimens in highly saline soil from the margin of the Etosha Pan (site 67). Thus, *N. lucida* is very likely euryhaline and cosmopolitan.

Comparison with original description and related species. Assigned to genus *Naxella* for reasons explained in introduction to family. The Namibian specimens resemble *Nassula lucida* REUTER, 1961, whose description is entirely based on live observation. Thus, it is fairly incomplete, that is, lacks information about ciliary rows and nassulid

organelles, which REUTER (1961) could not "feststellen" (~ recognize). Our population matches *N. lucida* in some important characters, namely, the presence of trichocysts, the number of pharyngeal rods (14), and the saline habitat. The few differences remaining, namely, body shape (broadly ellipsoidal vs. ovoidal with bluntly pointed anterior end) and size (40–60 µm vs. 70–80 µm) are inconspicuous and insufficient to separate the populations. Our specimens also resemble *Nassula* sp. found by THOMPSON (1978) in a meltwater pool on King George Island (South Shetland Islands; Fig. 103g): both have only two nassulid organelles and a similar size in silver nitrate preparations (32–50 × 24–31 µm vs. 43–59 × 20–35 µm); however, the number of ciliary rows is slightly different (32–37 vs. 40–45). Unfortunately, THOMPSON (1978) gives no information about extrusomes and number of pharyngeal rods. Thus, his population cannot be definitely assigned.

Naxella lucida differs from its congeners mainly by the number of nassulid organelles: three in *N. australis* FOISSNER & O'DONOGHUE, 1990 and → *N. rosea*, as redescribed above; three to four in *N. faurei* FOISSNER & O'DONOGHUE, 1990; five to eight in *N. minima* DRAGESCO & DRAGESCO-KERNÉIS, 1986, which thus very likely belongs to *Nassula*. There are also two similarly sized *Nassula* species: → *N. longinassa* (6–8 nassulid organelles) and *N. pusilla* KAHL, 1931 (about 40 pharyngeal rods).

Nassulides labiatus (KAHL, 1933) **nov. comb.** (Fig. 104a–r; 353a–z, 354a–o; Table 84)

1933 *Nassula labiata* KAHL, Tierwelt N.- und Ostsee, 23: 66.
1934 *Nassula halophila* GURWITSCH, Acta Univ. Asiae mediae, 12: 19 (new synonym).
1935 *Nassula labiata* KAHL, 1933 — KAHL, Tierwelt Dtl., 30: 826.
1972 *Nassula labiata* KAHL, 1933 — BORROR, Acta Protozool., 10: 43 (redescription after silver nitrate impregnation).
1980 *Nassula labiata* KAHL and *Zosterographus labiatus* (KAHL) — FRYD-VERSAVEL, IFTODE & DEROUX, J. Protozool., 27: 79A (nomenclature, see introduction to family).
1986 *Zosterographus labiatus* (KAHL, 1933) — DRAGESCO & DRAGESCO-KERNÉIS, Faune tropicale, 26: 263 (redescription from life and after silver nitrate impregnation; nomenclature, see introduction to family).
1998 *Nassula labiata* KAHL, 1933 — SONG & WEI, Acta hydrobiol. sin., 22: 361 (redescription from life and after silver nitrate impregnation).

Neotype material: Neotypified from a cultivated population of a saline grassland soil about 200 m inshore and behind a coastal dune in the surroundings of Armação de Pêra, a small town at the Algarve coast, Portugal (37°N 08°W), according to reasons 1–4, 6 discussed in chapter 2.4.2.

Synonymy and comparison of populations: *Nassula halophila* GURWITSCH, 1934 is virtually identical to *N. labiatus* in morphology and habitat (Fig. 104c). Thus, it is synonymized with that species. Several populations of *N. labiatus* have been studied (BORROR 1972, DRAGESCO & DRAGESCO-KERNÉIS 1986, KAHL 1933, SONG & WEI 1998). They are very similar and match the Portuguese and Namibian specimens well, especially in body shape, trichocysts, and length of first nassulid organelle, as well as in the number of

somatic ciliary rows, nassulid organelles, and pharyngeal rods. In contrast, most metric features show strong interpopulation variability, for instance, body size, which is conspicuously smaller in the Namibian specimens (Table 84). The improved diagnosis given below summarizes the data available, including the detailed results from the Portuguese and Namibian populations.

Improved diagnosis: Size usually 85–220 × 65–145 µm in vivo; broadly ellipsoidal. Two types of extrusomes: fusiform, about 4 µm long trichocysts and platelet-like, minute mucocysts. Usually 130–170 ciliary rows and 12–18 nassulid organelles extending onto dorsal side of cell. Pharyngeal basket usually composed of 28–35 rods extending to posterior body third. Paroral membrane indistinct. Type II resting cysts.

Description: We document this species by an abundance of micrographs, which are not available in the literature. In contrast, excellent illustrations of the infraciliature were provided by DRAGESCO & DRAGESCO-KERNÉIS (1986). Thus, we show it by only one drawing (Fig. 104b) and refer to DRAGESCO & DRAGESCO-KERNÉIS (1986) and the micrographs for further information. Most of the observations are from a Portuguese population, which could be cultivated on Eau de Volvic and filamentous cyanobacteria as food source. The culture also contained several other ciliates.

Size in vivo about 200 µm in German population (KAHL 1933), 190–200 × 135–140 µm in Russian (GURWITSCH 1934), 160–280 µm in Benin (DRAGESCO & DRAGESCO-KERNÉIS 1986), 80–180 × 50–110 µm in Chinese (SONG & WEI 1998), 80–185 × 50–125 µm in Portuguese, and 75–105 × 60–80 µm in Namibian population. Size of silver nitrate-impregnated specimens 117–154 × 83–106 µm (BORROR 1972), 110–175 µm (FRYD-VERSAVEL cited in DRAGESCO & DRAGESCO-KERNÉIS 1986), and 94–199 × 70–180 µm (DRAGESCO & DRAGESCO-KERNÉIS 1986), which matches the Portuguese population very well (101–175 × 75–118 µm), but is considerably larger than that of the Namibian specimens (71–99 × 58–75 µm). Overall shape broadly ellipsoidal to obovoidal, length:width ratio after silver nitrate impregnation 1.5:1 in North American (BORROR 1972), 1.4:1 in Portuguese, and 1.3:1 in Namibian population (Table 84); cultivated specimens from Portuguese population often obliquely truncate preorally producing rounded triangular outline as depicted in figures 104a, f, g. Macronucleus usually in middle third of cell, broadly ellipsoidal, about 45 × 35 µm in vivo, with reticular nucleolus, surrounded by distinct, about 1 µm thick membrane in Portuguese specimens. Usually 5–7, according to DRAGESCO & DRAGESCO-KERNÉIS (1986) up to 16 micronuclei adjacent to macronucleus; individual micronuclei about 5 µm across in vivo and difficult to distinguish from similarly sized cytoplasmic inclusions. Contractile vacuole near or slightly above mid-body, surrounded by small contributory vesicles during diastole; excretory pore almost in line with first kinety, about 2.5 µm in diameter. Cytopyge slit underneath excretory pore, extends to posterior body end, about 27 µm long. Resting trichocysts attached almost perpendicularly to cortex, fusiform, about 4 × 0.6–0.7 µm, rather numerous forming more or less distinct fringe; exploded trichocysts also fusiform but up to 40 µm long and 1.5 µm wide, with minute, compact tip (Fig. 104a, i, j; 353u–w). Resting mucocysts hardly recognizable, produce bright, about 1 µm thick cortical layer, only rarely released when methyl green-pyronin is applied, appearing as 1–2 µm-sized, polygonal platelets swelling to a voluminous, up to 100 µm thick coat (Fig. 104k; 353x–z). Cortex about 1 µm thick and bright, indistinctly separated from cytoplasm. Cortical units pentagonal to hexagonal, each containing a heavily impregnated granule (very likely a basal body) and usually one posteriorly situated bright hole, either the parasomal sac or a trichocyst attach

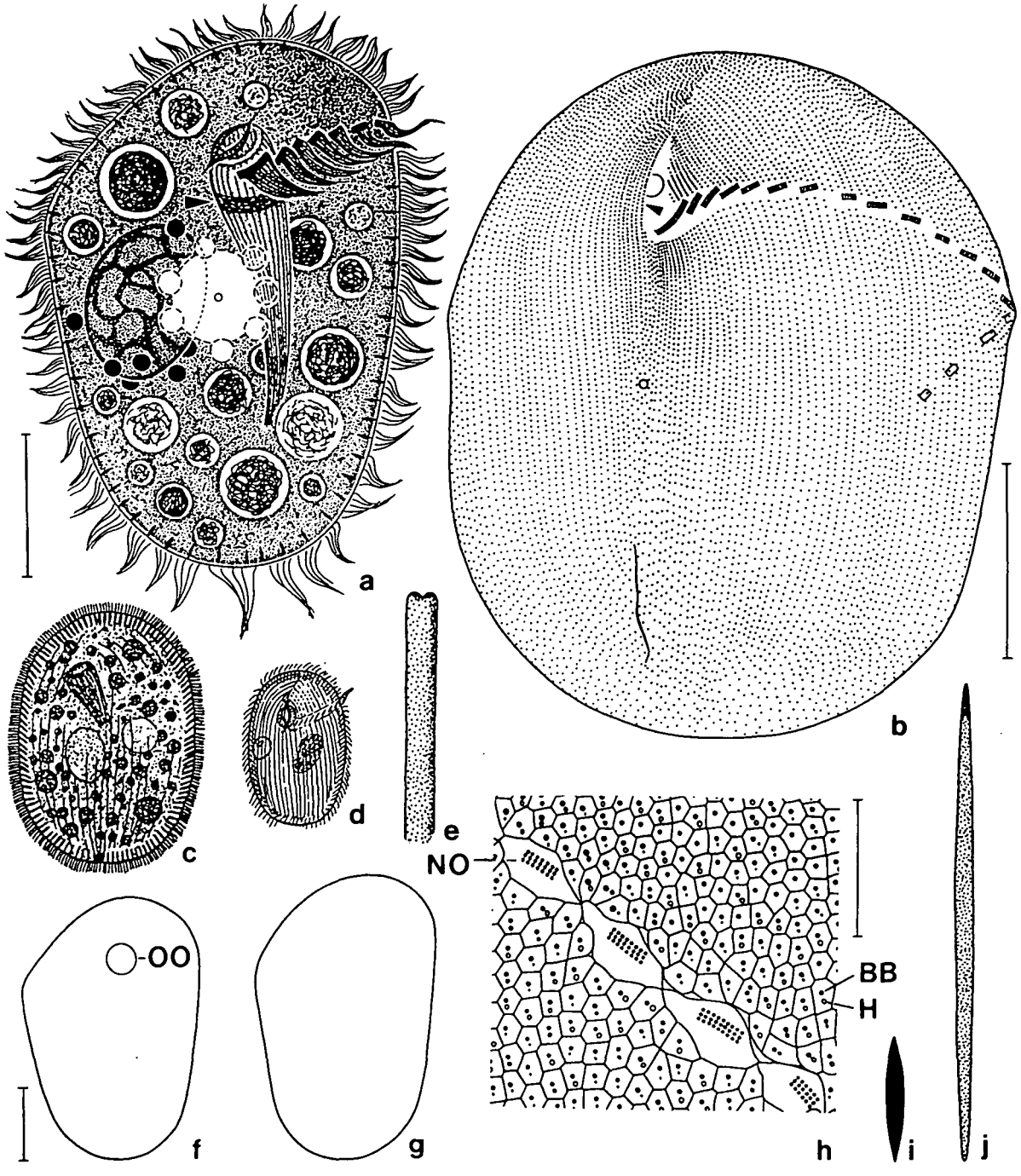


Fig. 104a–j. *Nassulides labiatus*, Portuguese (a, b, e–g, i, j), Namibian (h), and German (d) specimens from life (a, c–g, i, j), after silver nitrate impregnation (b), and silver carbonate impregnation (h). **a:** Ventral view of a representative specimen from a flourishing culture. Note triangular outline and pharyngeal basket with distinct annulus (arrowhead). **b:** Ciliary pattern of ventral side showing shape of nassulid frange and indistinct paroral membrane (arrowhead). **c:** *Nassula halophila*, a junior synonym, length 190–200 µm (from GURWITSCH 1934). **d:** Specimen from type population, length 200 µm (from KAHL 1933). **e:** Anterior portion of a pharyngeal rod. **f, g:** Body shape of a well-fed specimen from a flourishing culture and of a specimen without food vacuoles. **h:** Cortical units near end of nassulid frange. **i, j:** Resting (4 µm) and exploded (40 µm) trichocyst. BB – basal body, H – parasomal sac or trichocyst attachment site, NO – nassulid organelle, OO – oral opening. Scale bars 40 µm (a, b, f, g) and 10 µm (h).

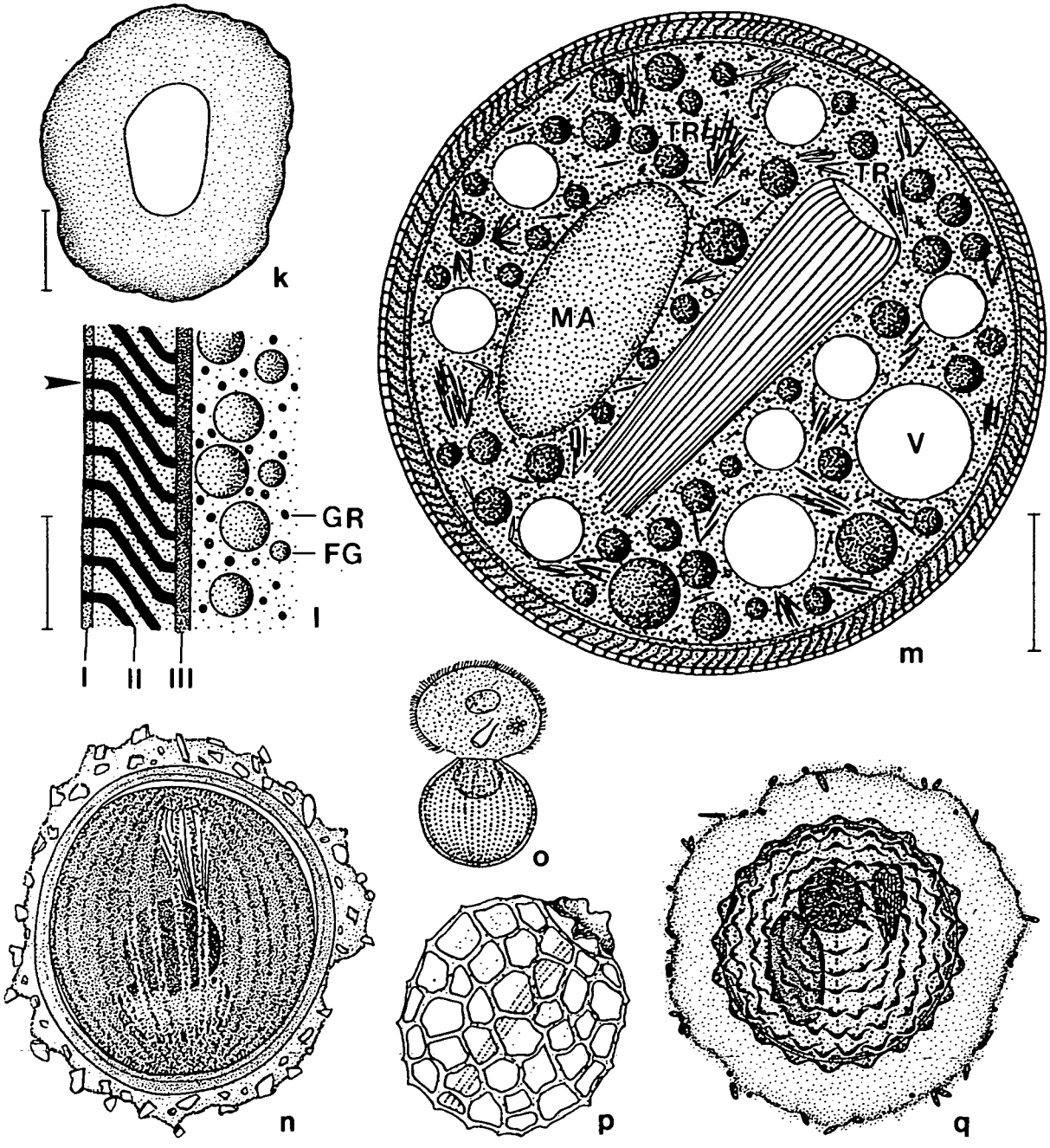


Fig. 104k–r. *Nassulides labiatus* from Portuguese population (k–m) and cyst types in nassulids (n–q) after methyl green-pyronin staining (k) and from life (l–q). **k:** Mucocysts are extruded and swell to a voluminous, about 100 µm thick coat when methyl green-pyronin is applied. **l, m:** The resting cyst has a conspicuous wall, in which the ecto- and endocyst are connected by curious, Z-shaped filaments (arrowhead) arranged in the same pattern as the basal bodies (cp. Fig. 354j–n). **n:** Type I cysts with smooth and amorphous wall in → *Nassula granata*, 50 µm across. **o:** Type II cysts with Z-shaped structures in *Nassula ambigua* (65–80 µm across; from STEIN 1854) and *Nassulides labiatus* (Fig. 104 l, m). **p:** Type III cysts with faceted surface in, e.g., *Nassula ornata* (120–150 µm across, only three of the somatic ciliary rows are shown; from BEERS 1966). **q:** Type IV cysts with tubercular wall in → *Nassula tuberculata*, 45 µm across. I, II, III – ecto-, meso-, and endocyst, FG – fat globules, GR – granules, MA – macronucleus, TR – trichocysts, V – clear vesicles. Scale bars 100 µm (k), 20 µm (m), and 5 µm (l).

ment site; units large and irregularly elliptical around nassulid organelles (Fig. 104h; 353r–t). Cells orange or brownish due to ingested cyanobacteria and innumerable, about 0.2 µm-sized granules forming distinct, golden patch in left anterior body portion of Portuguese specimens (Fig. 104a); granules very likely residues of filamentous cyanobacteria digested in vacuoles 8–40 µm across. Movement without peculiarities.

Somatic cilia about 13 µm long, in posterior pole area slightly elongated and loosely arranged; distances between individual cilia increase from anterior to posterior, especially in ciliary rows underneath first nassulid organelle. Ciliary rows longitudinally and equidistantly arranged, except for more closely spaced postoral kineties and rows underneath leftmost nassulid organelles; form indistinct preoral suture, but rather distinct, 2–3 µm wide post-organellar stripe. Number of ciliary rows fairly similar in all populations: 120–165 in North American (BORROR 1972), 140–160 in French (FRYD-VERSAVEL cited in DRAGESCO & DRAGESCO-KERNÉIS 1986), 140–200 in Benin (DRAGESCO & DRAGESCO-KERNÉIS 1986), about 150 in Chinese (SONG & WEI 1998), 133–192 in Portuguese, and 108–158 in Namibian specimens (Fig. 104b; 353b, c, f–j, m, n; Table 84).

Oral opening in anterior quarter of cell, membranous and fusiform. Pharyngeal basket extends obliquely to dorsal side and posterior third of cell, about 25 µm wide and bulbous distally due to the microtubular sheath, basket annulus distinct and recognizable even in vivo; composed of about 25 (GURWITSCH 1934), 25–30 (BORROR 1972) or 30–40 rods (DRAGESCO & DRAGESCO-KERNÉIS 1986), which matches the Portuguese (29–30) and Namibian (29–32) populations. Rods not twisted, about 1.5 µm thick, with shallow indentation anteriorly and conspicuous crests winding around whole basket length (Fig. 104a, e; 353 l, 354a, e, f; Table 84). Nassulid frange extends in flat bow onto dorsal side and terminates near mid-body, composed of 13 (BORROR 1972), 12–15 (FRYD-VERSAVEL cited in DRAGESCO & DRAGESCO-KERNÉIS 1986), 16–19 (DRAGESCO & DRAGESCO-KERNÉIS 1986) or 14–16 organelles (SONG & WEI 1998), which matches the Portuguese (12–18) and Namibian (13–15; n = 2) specimens; rightmost organelles overlapping proximally because closely spaced and obliquely orientated to main axis of frange, left organelles more widely spaced and orientated parallel to frange. First nassulid organelle 10–12 µm long and curved, other organelles only 3–5 µm long and straight; individual organelles composed of three kineties and usually unciliated in right quarter, length of cilia decreases from about 20 µm at left to about 17 µm at right end of organelles (Fig. 104b; 353f–i, o, q; Table 84). Paroral membrane continuous with first kinety, indistinct, that is, only some closely spaced basal bodies are recognizable after silver impregnation (Fig. 104b; 353 l).

Resting cysts globular, on average 98 µm across, deep-orange due to countless granules about 0.2 µm across (Fig. 104m; 354g–k, n, o; Table 84). Wall smooth, colourless, trilaminar, 3–5 µm thick, except for a small, thickened and protruding area, probably the emergence site. Ectocyst 0.5–1 µm thick, mesocyst 3–4 µm, endocyst 1–2 µm and opaque; ectocyst and endocyst connected by conspicuous, Z-shaped filaments, each possibly related in some way to a somatic basal body because the infraciliary pattern is mirrored by these structures, except for the nassulid organelles, where only two of the three basal body rows are associated with Z-filaments (Fig. 104 l, m; 354j–n). However, when encysted specimens occasionally retract from the cyst wall, the filaments remain between ecto- and endocyst, indicating that they are weakly, or not at all, connected with the basal bodies (Fig. 354j, k). Cytoplasm with innumerable, orange granules, as described above; many colourless fat globules 2–5 µm across; some clear, large vesicles; and few dark food inclusions. Pharyngeal basket and trichocysts

maintained.

Information about nassulid resting cysts is sparse; however, four types of walls can be distinguished (Fig. 104 l–q): (i) smooth and amorphous in *Nassula hesperidae* (ENTZ 1884), *Parafurgasonia sorex* (PENARD 1922), → *Nassula granata*, and possibly *Nassulides pictus* as described by PENARD (1922) and BUSSERS (1976); (ii) punctated in infraciliary pattern and with Z-shaped filaments in *Nassula ambigua* (STEIN 1854) and *Nassulides labiatus*; (iii) faceted due to distinct ridges in *Nassula ornata* (FABRE-DOMERGUE 1888), *Furgasonia trichocystis* (now *theresae*; FAURÉ-FREMIET 1967), *Nassula terricola* (FOISSNER 1989), *Obertrumia aurea* (FOISSNER et al. 1994), and *Parafurgasonia protectissima* (PENARD 1922); (iv) tubercular in → *Nassula tuberculata*. The cyst wall of *Nassulides labiatus* is most similar to that of *Nassula ambigua*, a species, which has not yet been redescribed.

Occurrence and ecology: KAHL (1933) discovered *Nassulides labiatus* in a sea water channel on the Island of Sylt, Germany. Later, it was found in brackish waters of Russia (GURWITSCH 1934), tropical Africa (DRAGESCO & DRAGESCO-KERNÉIS 1986), the Baltic Sea (CZAPIK & FYDA 1992), and the USA (BORROR 1972b) as well as in marine waters of China, where it formed red tides (SONG & WEI 1998). These records agree with our findings, that is, the neotype location contains many flat pools, most of which were dry and had a white salt crust when the material was collected. The sample consisted of the upper (0–3 cm) soil layer and of algal crusts between halophytes; it was highly saline and had pH 8.4. Likewise, *N. labiatus* was found only in the highly saline soils from sites (54, 56, 57, 58, 70) of the Etosha Pan region. Thus, *N. labiatus* is euryhaline and cosmopolitan and probably restricted to marine environments and saline inland biotopes.

Table 84. Morphometric data on two populations of *Nassulides labiatus*: PO – Portugal, NA – Namibia.

Characteristics [a]	Pop [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	PO	CHL	133.7	136.0	19.1	4.9	14.3	101.0	175.0	15
	NA	CHL	81.5	80.0	8.2	2.6	10.1	71.0	99.0	10
Body, width	PO	CHL	98.9	98.0	13.2	3.4	13.3	75.0	118.0	15
	NA	CHL	61.9	60.5	5.1	1.6	8.3	58.0	75.0	10
Body length:width, ratio	PO	CHL	1.4	1.3	0.1	0.0	7.4	1.2	1.6	15
	NA	CHL	1.3	1.3	0.1	0.0	6.9	1.2	1.5	10
Anterior body end to macronucleus, distance	PO	CHL	57.8	55.5	8.4	3.0	14.5	50.0	75.0	8
	NA	CHL	44.9	44.0	6.1	1.7	13.5	35.0	55.0	13
Anterior body end to excretory pore, distance	PO	CHL	61.7	63.0	7.9	2.0	12.8	46.0	73.0	15
	NA	CHL	48.7	48.0	4.0	2.3	8.3	45.0	53.0	3
Anterior body end to cyrtos, distance	PO	CHL	21.0	19.0	5.0	1.3	23.8	15.0	34.0	15
	NA	CHL	16.2	16.0	2.6	0.7	16.0	13.0	19.0	13
Anterior body end to last nassulid organelle, distance	PO	CHL	55.0	54.0	6.0	1.5	10.9	46.0	69.0	15
	NA	CHL	45.8	46.0	7.0	2.1	15.2	31.0	60.0	11
Macronucleus, length	PO	PA	33.2	34.0	2.2	0.6	6.6	28.0	36.0	15
	NA	PA	27.4	28.0	4.4	1.3	16.0	21.0	33.0	11
Macronucleus, width	PO	PA	28.3	28.0	3.4	0.9	12.1	23.0	34.0	15
	NA	PA	20.3	21.0	2.0	0.6	9.9	16.0	23.0	11

(continued)

Characteristics [a]	Pop [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Micronucleus, length	PO	PA	3.0	3.0	0.0	0.0	0.0	3.0	3.0	6
	NA	PA	2.5	2.5	–	–	–	2.0	3.0	4
Micronucleus, width	PO	PA	3.0	3.0	0.0	0.0	0.0	3.0	3.0	6
	NA	PA	2.5	2.5	–	–	–	2.0	3.0	4
Pharyngeal basket, maximum diameter	PO	CHL	17.3	18.0	1.8	0.5	10.6	14.0	20.0	15
	NA	CHL	16.2	16.0	1.3	0.4	7.8	14.0	18.0	12
First nassulid organelle, length	PO	CHL	10.5	10.0	1.5	0.4	13.9	9.0	14.0	15
	NA	CHL	9.7	10.0	–	–	–	9.0	10.0	6
Other nassulid organelles, length	PO	CHL	4.9	5.0	1.5	0.4	30.1	3.0	8.0	15
	NA	CHL	4.4	5.0	1.0	0.3	22.8	3.0	6.0	9
Macronucleus, number	PO	PA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	NA	PA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13
Micronuclei, number	PO	PA	6.6	7.0	2.6	1.2	39.5	3.0	9.0	5
Somatic ciliary rows, number	PO	CHL	145.9	138.5	20.0	7.1	13.7	133.0	192.0	8
	NA	CHL	129.0	125.0	16.3	5.2	12.7	108.0	158.0	10
Kinetids in a dorsal kinety, number	PO	CHL	80.0	80.0	10.0	3.3	12.5	64.0	94.0	9
	NA	CHL	54.4	55.5	5.6	2.0	10.3	47.0	62.0	8
Pharyngeal basket, number of rods	PO	PA	30.0	30.0	0.7	0.2	2.2	29.0	31.0	10
	NA	SC	31.0	32.0	1.7	1.0	5.6	29.0	32.0	3
Nassulid organelles, number	PO	CHL	15.3	15.0	1.8	0.5	12.0	12.0	18.0	15
Resting cysts, length	PO	IV	98.6	100.0	6.3	1.7	6.4	90.0	110.0	14
Resting cysts, width	PO	IV	98.1	98.5	6.7	1.8	6.8	90.0	110.0	14

[a] Data based, if not otherwise stated, on silver-impregnated, randomly selected specimens from a non-flooded Petri dish culture (Namibian specimens) or a pure culture (Portuguese specimens). Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, IV – in vivo, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, PA – protargol impregnation (FOISSNER's method), Pop – population, SC – silver carbonate impregnation, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Comparison with related species: *Nassulides labiatus* differs from its congeners mainly in the number of nassulid organelles, which is distinctly lower in *N. pictus* (7–8; FOISSNER 1980e, 1989, FOISSNER et al. 1994) and *N. vernalis* (8–10; FOISSNER 1989), but considerably higher in *N. pratensis* (27–29; DRAGESCO & DRAGESCO-KERNÉIS 1986). A further difference concerns the number of somatic ciliary rows, which is distinctly lower in *N. pictus* (37–50; FOISSNER 1980e, 1989, FOISSNER et al. 1994) and *N. vernalis* (48–65; FOISSNER 1989). *Nassulides labiatus* resembles *Nassula* sp., found by THOMPSON (1972) in a meltwater pool of the Antarctic Peninsula, in the oblique orientation of the rightmost nassulid organelles, body size (silver-impregnated: 103–148 × 66–109 µm), and number of nassulid organelles (12–16) and somatic ciliary rows (95–120); however, both differ slightly in the number of pharyngeal rods (25–32 vs. 20). Unfortunately, THOMPSON (1972) gives no information about extrusomes. Thus, his population cannot be definitely assigned. *Nassulides labiatus* is also similar to several *Nassula* species: *N. enormis* VUXANOVICI, 1962a (length 250–270 µm; possibly a senior synonym of *N. pratensis*), *N. pluvialis* DINGFELDER, 1962 (18 pharyngeal rods; possibly a junior synonym of *N. labiatus*), *N. rotunda* GELEI, 1950 (very

similar to *N. labiatus*, but a true *Nassula* according to the redescription by FOISSNER 1980e), and *N. nahchivanica* ALEKPEROV, 1984 (length 250–300 µm, 17 pharyngeal rods, 35 nassulid organelles; and a true *Nassula* according to the arrangement of the nassulid organelles).

Family Furgasoniidae CORLISS, 1979

1975 Cyclogrammidae JANKOWSKI, Akad. Nauk SSSR, Zool. Inst. Leningrad: 27 (invalid because without diagnosis).
1976 Cyclogrammidae PUYTORAC & GRAIN, Protistologica, 12: 62 (invalid because without diagnosis).
1979 Furgasoniidae CORLISS, The ciliated protozoa: 226.

Improved diagnosis: Small to medium-sized nassulids with usually conspicuous pharyngeal basket extending posteriorly. Up to 3 nassulid organelles restricted to basket area and composed of more or less numerous ciliary rows with usually 3 basal bodies each. Paroral membrane distinct.

Type genus (by monotypy): *Furgasonia* JANKOWSKI, 1964.

Remarks: The diagnosis of the Furgasoniidae has been improved because the family enlarged since it was established by CORLISS (1979), and a related family, the → Colpodidiidae FOISSNER, 1995, was discovered. Now, the Furgasoniidae comprise four genera: → *Furgasonia* JANKOWSKI, 1964; → *Parafurgasonia* FOISSNER & ADAM, 1981; *Urliella* FOISSNER, 1989; and → *Wolfkosia*, a new genus described below.

Members of the Furgasoniidae and Colpodidiidae may look very similar at first glance due to the nassulid organelles restricted to the basket area, the distinct paroral membrane, and the similar body shape and size [see also introduction to family Colpodidiidae and "comparison with similar species" under → *Apocolpodidium (Apocolpodidium) etoschense*]. Indeed, these families differ only in one main feature, namely, the oral basket, which extends posteriorly in the former and anteriorly in the latter.

Certainly, several furgasoniids highly resemble ordinary Nassulidae, to which they were formerly assigned. However, the fine structure of the nassulid organelles is different (GRAIN et al. 1978, EISLER 1986, 1988, 1989), although they appear very similar in the light microscope, and the somatic ciliary pattern shows an important difference easily recognizable in silver preparations: the ciliary rows left of the oral apparatus are uninterrupted in the Furgasoniidae and Colpodidiidae, while intersected by the nassulid organelles in the Nassulidae.

Furgasonia JANKOWSKI, 1964

1852 *Cyclogramma* PERTY, Zur Kenntniss kleinster Lebensformen: 146 (junior synonym of *Cyclogramma* DOUBLEDAY, 1847).
1964 *Furgasonia* n. gen., JANKOWSKI, Arch. Protistenk., 107: 272.
1979 *Furgasonia* JANKOWSKI, 1964 — CORLISS, The ciliated protozoa: 226 (detailed discussion of nomenclature).

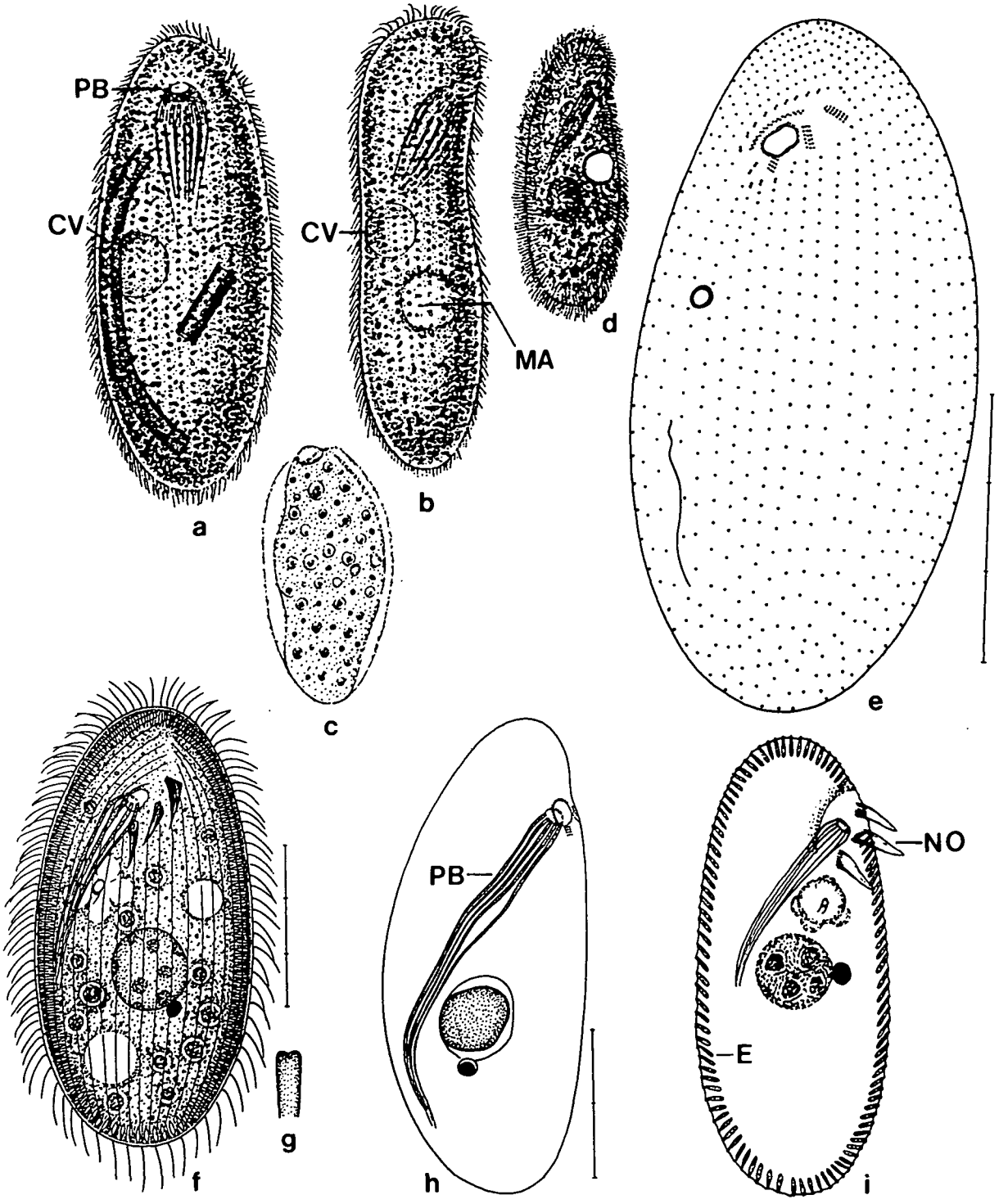


Fig. 105a–i. *Furgasonia theresae* from life (a, b, d, f, g, i), after cytological staining (c), CHATTON-LWOFF silver nitrate impregnation (e), and protargol impregnation (h). Figures 105a–c are from FABRE-DOMERGUE (1891); figure 105d is from STOKES (1894); figures 105e–h are from FOISSNER (1989) and show the neotype population; and figure 105i is from FOISSNER (1979b). **a–c:** Ventral and lateral view and nuclear apparatus, length 60–70 µm. **d:** *Nassula trichocystis*, length 70 µm. **e–i:** *Furgasonia trichocystis*, ventral and lateral views, length 70–100 µm, and anterior end of a pharyngeal rod (g). CV – contractile vacuole, E – extrusomes, MA – macronucleus, NO – nassulid organelles, PB – pharyngeal basket. Scale bar division 10 µm.

Improved diagnosis: Furgasoniidae CORLISS, 1979 with three distinct nassulid organelles arranged radially around lower and left margin of oral opening.

Type species (by original designation): *Nassula tricirrata* GELEI, 1932.

Furgasonia theresae (FABRE-DOMERGUE, 1889) **nov. comb.** (Fig. 105a–i)

1889 *Nassula Theresae* FABRE-DOMERGUE, Annls Microgr., 2: 53 (without figures).
1891 *Nassula Theresae* FABRE-DOMERGUE, Annls Microgr., 3: 219 (figures and figure explanations).
1894 *Nassula trichocystis* STOKES, Proc. Am. phil. Soc., 33: 342 (new synonym).
1967 *Cyclogramma trichocystis* STOKES — FAURÉ-FREMIET, J. Protozool., 14: 459 (identification doubtful because of pink colour; genus name invalid because of homonymy).
1989 *Furgasonia trichocystis* (STOKES, 1894) — FOISSNER, Sber. Akad. Wiss. Wien, 196 (year 1987): 207 (neotypification).

Justification of synonymy: KAHL (1931), the first reviser of the group, could not obtain the papers of FABRE-DOMERGUE (1889, 1891) and thus did not recognize the obvious identity of *Nassula theresae* FABRE-DOMERGUE, 1889 and *Nassula trichocystis* STOKES, 1894. Both descriptions match perfectly in all main features, such as body size and shape, nucleus, location of the contractile vacuole, pharyngeal basket, and trichocysts (definitely mentioned by FABRE-DOMERGUE in the description). Furthermore, the descriptions match the redescription by FOISSNER (1989), who neotypified the species. Thus, we synonymize *Nassula trichocystis* STOKES, 1894 with *N. theresae* FABRE-DOMERGUE, 1889 and transfer the species to the genus *Furgasonia: Furgasonia theresae* (FABRE-DOMERGUE, 1889) nov. comb. This action is in accordance with article 23.9. of the ICZN (1999).

Urliella FOISSNER, 1989

Improved diagnosis: Furgasoniidae CORLISS, 1979 without nassulid organelles.

Type species (by original designation): *Urliella terricola* FOISSNER, 1989.

Remarks: This genus is unique among the nassulids because it lacks nassulid organelles. FOISSNER (1989) also mentions two minor features, viz. the nearly apical location of the oral apparatus and the position of the paroral membrane right of the oral opening. Both features are now outdated because other genera show transitions in these characters (FOISSNER 1999b, present work).

Parafurgasonia FOISSNER & ADAM, 1981

Improved diagnosis: Furgasoniidae CORLISS, 1979 with single distinct nassulid organelle underneath oral opening.

Type species (by original designation): *Nassula sorex* PENARD, 1922.

Remarks: FOISSNER & ADAM (1981) mention in the diagnosis also "paroral membrane semicircular along anterior margin of oral opening". However, there are transitions in this feature, suggesting that it should be removed from the genus diagnosis (FOISSNER 1999b).

A reinvestigation of *P. sorex* showed that the paroral is composed of dikinetids orientated perpendicularly to the kinety axis (Fig. 355e–h). As in other furgasoniids, for instance, → *Wolfkosia loeffleri*, the posterior (left) basal body of the dikinetids often impregnates only faintly, or not at all, probably because it is unciliated. In the preparations by FOISSNER & ADAM (1981), obviously only the anterior (right) basal bodies impregnated and were thus misinterpreted as dikinetids orientated parallel to kinety axis.

Wolfkosia nov. gen.

Diagnosis: Furgasoniidae CORLISS, 1979 with somatic kinety 1 bipartited into long, C-shaped, densely ciliated anterior portion and short, straight, sparsely ciliated posterior fragment. 1 distinct and 1 or 2 indistinct nassulid organelles along posterior margin of oral opening. Anterior fragment of kinety 1, paroral membrane, and nassulid organelles form conspicuous, circular pattern around oral opening. Distal end of pharyngeal basket with teeth-like projections.

Type species: *Wolfkosia loeffleri* nov. spec.

Etymology: Wilhelm FOISSNER dedicates this new genus to Dr. Wolfgang KOS (Salzburg), an excellent surgeon, who made it possible that he could contribute to this work (see also species dedication).

Classification and comparison with related genera: *Wolfkosia* belongs to the Furgasoniidae, according to the features mentioned in the family diagnosis. It differs from the other genera mainly by somatic kinety 1: bipartited with C-shaped anterior portion vs. continuous and only slightly curved. Furthermore, a unique, circular oral pattern is created by the particular location and shape of the anterior fragment of kinety 1, the paroral membrane, and the nassulid organelles (Fig. 106m; 356q, r, t, u). The pharyngeal basket is also unique, having a fish-snout like distal end, that is, a pattern which we have never seen in any other nassulid (Fig. 106a, n; 356b, e, g, h). → *Furgasonia* has like *Wolfkosia* three nassulid organelles, which are, however, of same size and radially arranged around the lower and left margin of the oral opening. → *Urliella* lacks nassulid organelles entirely. → *Parafurgasonia* has only a single nassulid organelle. However, this difference must not be overinterpreted because we cannot entirely exclude that the scattered basal bodies underneath the oral opening of *W. loeffleri* do not represent nassulid organelles 1 and 2 but belong to nassulid organelle 3. Thus, the particular pattern of the oral structures, especially the C-shaped anterior

fragment of kinety 1, distinguishes *Wolfkosia* from → *Parafurgasonia*. As concerns separation from → *Apocolpodidium*, see "comparison with similar species" below.

Wolfkosia loeffleri has as conspicuous mitochondria like most members of the family Colpodidiidae. The Furgasoniidae lack such distinct mitochondria, at least the genera → *Furgasonia* and → *Parafurgasonia*, which we reinvestigated for this feature. Indeed, the mitochondria are hardly recognizable, although having a similar size and shape as in *W. loeffleri* and → *Colpodidium* spp., because they are much less refractive.

***Wolfkosia loeffleri* nov. spec.** (Fig. 106a–o; 356a–z; Table 85)

Diagnosis: Size about 45 × 23 μm in vivo; obovoidal. Contractile vacuole underneath subapical oral apparatus at end of C-shaped fragment of kinety 1. Extrusomes fusiform. On average 14 somatic ciliary rows and 13 paroral dikinetids. C-shaped fragment of kinety 1 with about 9 dikinetids. Pharyngeal basket composed of about 12–15 distinctly twisted rods. Nassulid organelle 3 composed of approximately 6–9 ciliary rows.

Type location: Rock-pools at bank of Rio Corobici at the hacienda "La Pacifica" (Centro Ecológico "La Pacífica") near the town of Cañas in Costa Rica, Central America, 10°28'N 85°10'W.

Etymology: Wilhelm FOISSNER dedicates this new species to Dr. Karl LÖFFLER (Salzburg), who recognized, by simple palpation, the abdominal aneurysm Dr. Wolfgang KOS later operated (see genus dedication).

Description: This small ciliate has a complex ciliary pattern. See figure 106m for a semidiagrammatic interpretation and terminology.

Size 35–50 × 20–25 μm in vivo. Lateral view conspicuously obovoidal with minute subapical process at oral apparatus; ventral and dorsal view ellipsoidal to elongate ellipsoidal because slightly to distinctly flattened laterally; when squeezed, preoral portion flattens (Fig. 106a, h, i; 356g–i; Table 85). Macronucleus usually in middle third of cell, globular, with indistinct, possibly reticular nucleolus. Micronucleus usually attached to macronucleus, globular. Contractile vacuole in second quarter of cell, surrounded by contributory vesicles during diastole, with short canal having pore underneath C-shaped portion of somatic kinety 1 (Fig. 106a, d, m; 356w–z). Cytopyge slit in line with excretory pore, extends in posterior half of cell, becomes a fusiform opening when faecal mass with ellipsoidal crystals leaves cell. Resting extrusomes attached almost perpendicularly to cortex and usually close to left posterior margin of somatic kinetids in anterior half of cell and to left anterior margin in posterior half of cell; fusiform, conspicuous because large compared to size of cell, namely, 4–5 × 0.7 μm, but do not form a distinct fringe because as sparse as cilia (Fig. 106a, f; 356k). No mucocysts extruded after methyl green-pyronin application. Cortex about 1 μm thick and bright, with distinct ribs along ciliary rows and ciliary pits (Fig. 106o). Mitochondria underneath cortex, conspicuous because numerous, up to 8 μm long, and serpentine and occasionally even branched (Fig. 106j; 356a, d). Cytoplasm colourless, contains colourless food vacuoles 4–15 μm across and some fat inclusions 1–3 μm across. Movement without peculiarities, that is, swims rather rapidly by rotation about main body axis.

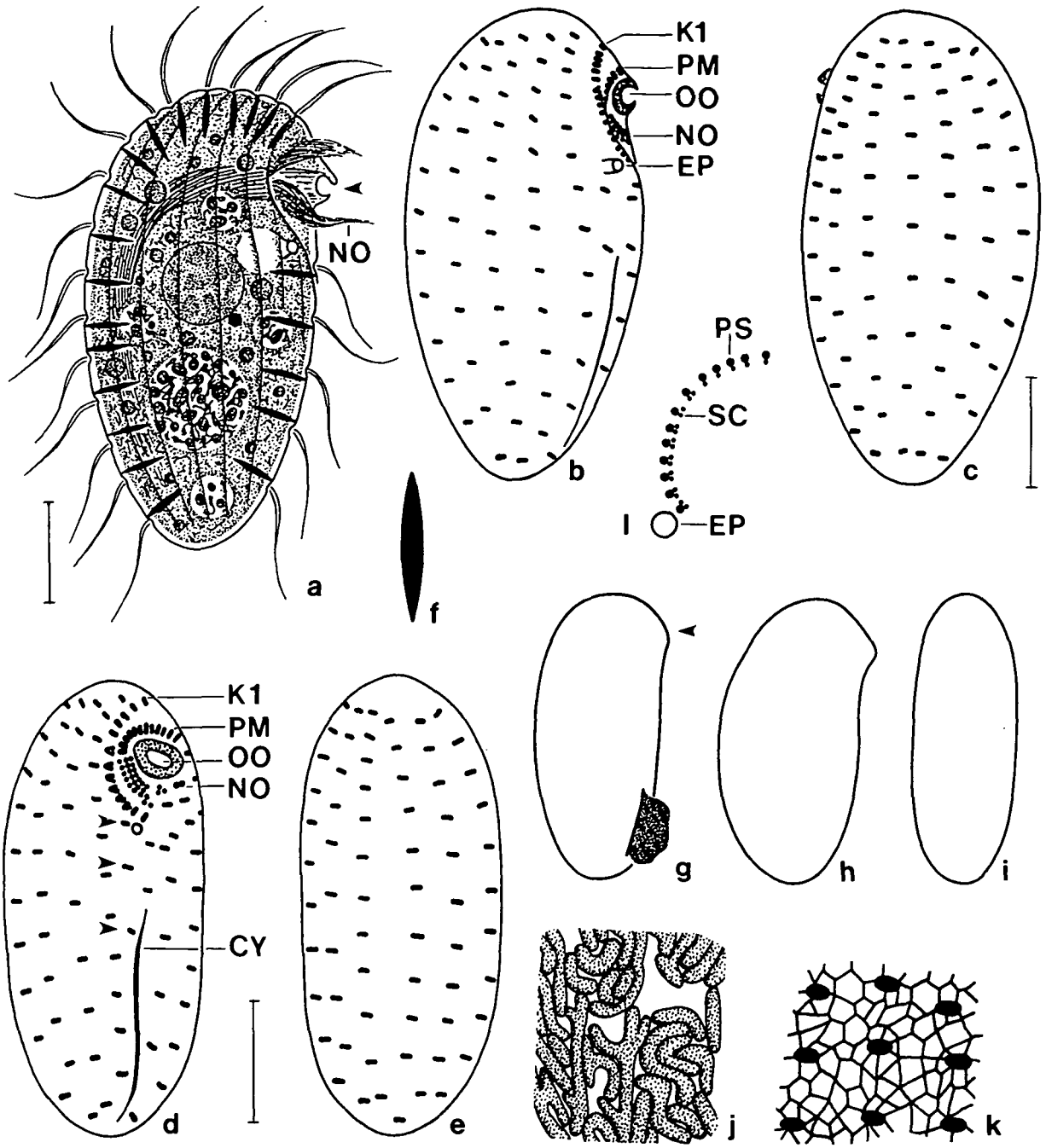


Fig. 106a–l. *Wolfkosia loeffleri*, Costa Rican (a–f, i–l) and Saudi Arabian (g, h) specimens from life (a, f, g–j) and after silver nitrate impregnation (b–e, k, l). **a:** Right lateral view of a representative specimen showing the obovoidal body shape and the teeth-like processes of the pharyngeal basket (arrowhead). **b–e, l:** Ciliary pattern of right, left, ventral, and dorsal side. The anterior portion of somatic kinety 1 is C-shaped and composed of dikinetids along the oral apparatus, while the posterior portion is straight and composed of only a few monokinetids (arrowheads). **f:** Resting extrusome, length 4–5 µm. **g:** Representative, defecating specimen from Saudi Arabian population with slight subapical projection (arrowhead) at oral apparatus. **h:** When slightly squeezed, the preoral dome flattens. **i:** Ventral view of a flat specimen. **j:** The serpentine mitochondria are up to 8 µm long and branched. **k:** Silverline system. CY – cytopyge, EP – excretory pore of contractile vacuole, K1 – C-shaped anterior portion of somatic kinety 1, NO – nassulid organelles, PM – paroral membrane, PS – parasomal sac, OO – oral opening, SC – somatic cilium. Scale bars 10 µm.

Ciliary rows meridionally and equidistantly arranged, except for slightly more closely spaced postoral kineties. Dorsal and lateral ciliary rows bipolar. Preoral suture very short and inconspicuous because formed by only two to three rows on each side, merges into elliptical, barren anterior pole area. Kinety 1 (first row right of paroral) bipartited (Fig. 106d, m; 356c, k, j, q–u, w–z; Table 85): anterior portion long and C-shaped, commences subapically with some rather closely spaced monokinetids and extends with closely spaced dikinetids[14] to excretory pore along a furrow right of the oral apparatus; posterior portion short (one to four kinetids) and straight, monokinetidal, commences slightly underneath and right of excretory pore and abuts obliquely on cytopyge. Usually four monokinetidal postoral kineties: kinety 1 commences underneath left end of paroral membrane; kineties 2 and 3 commence underneath scattered basal bodies (nassulid organelle 2?) left of nassulid organelle 3; and kinety 4 commences underneath and slightly left of the excretory pore (Fig. 106d, m; 356c, k, q, w).

Somatic cilia about 10 μm long in vivo, single except for 9–10 pairs in C-shaped anterior portion of somatic kinety 1. Distances between kinetids rather large, except for C-shaped portion of somatic kinety 1, where they are closely spaced. Silver carbonate preparations reveal each somatic kinetid to be composed of (i) an rather irregular (possibly due to attached

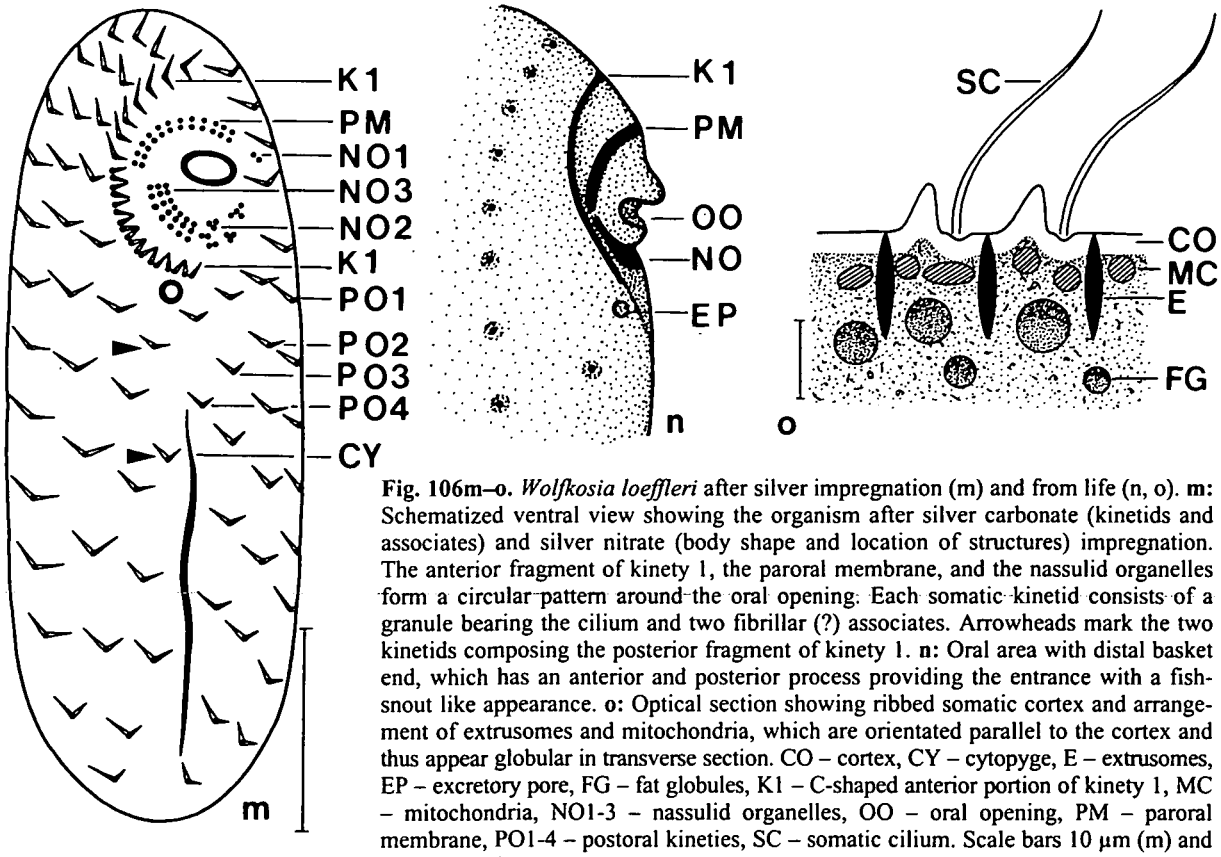


Fig. 106m–o. *Wolfkosia loeffleri* after silver impregnation (m) and from life (n, o). **m:** Schematized ventral view showing the organism after silver carbonate (kinetids and associates) and silver nitrate (body shape and location of structures) impregnation. The anterior fragment of kinety 1, the paroral membrane, and the nassulid organelles form a circular pattern around the oral opening. Each somatic kinetid consists of a granule bearing the cilium and two fibrillar (?) associates. Arrowheads mark the two kinetids composing the posterior fragment of kinety 1. **n:** Oral area with distal basket end, which has an anterior and posterior process providing the entrance with a fish-snout like appearance. **o:** Optical section showing ribbed somatic cortex and arrangement of extrusomes and mitochondria, which are orientated parallel to the cortex and thus appear globular in transverse section. CO – cortex, CY – cytopyge, E – extrusomes, EP – excretory pore, FG – fat globules, K1 – C-shaped anterior portion of kinety 1, MC – mitochondria, NO1-3 – nassulid organelles, OO – oral opening, PM – paroral membrane, PO1-4 – postoral kineties, SC – somatic cilium. Scale bars 10 μm (m) and 2.5 μm (n, o).

[14] The posteriormost dikinetids are frequently slightly out of line, indicating that they might not belong to the C-shaped portion of somatic kinety 1 but, as in the → Colpodidiidae, surround the excretory pore.

parasomal sac and/or alveolocyst and/or extrusome) granule bearing the cilium; (ii) a short structure (kinetodesmal fibre?) extending obliquely anteriad at right side of basal body, except for dikinetids in somatic kinety 1; and (iii) a short structure (transverse fibre?) extending almost perpendicularly to kinety axis at left side of basal body (Fig. 106m; 356k, q, r, t, u). No elongated caudal cilia.

Oral apparatus with subapical opening in anterior quarter of cell, composed of four distinct components: pharyngeal basket, nassulid organelles, paroral membrane, and, at right, a conspicuous, C-shaped kinety. Pharyngeal basket extends straight to dorsal side, where it curves sharply posteriad, composed of about 12–15 fine, distinctly twisted rods lightly impregnating with silver carbonate; distal end heavily impregnated with silver nitrate and of unique structure, that is, with an anterior and posterior tooth-like process providing entrance with a fish-snout like appearance (Fig. 106a, b, d, m, n; 356b, e, f, g, h, s, w–z). Nassulid organelles in semicircular furrow along posterior margin of pharyngeal basket, without distinct fibres; only organelle 3 clearly recognizable, slightly curved, consists of about 6–9 ciliary rows each composed of three basal bodies bearing about 6 µm long, mobile cilia; organelle 1 likely between left end of paroral membrane and anterior end of first postoral kinety, consists of two to three basal bodies only; organelle 2 possibly composed of scattered basal bodies between organelles 1 and 3. Paroral membrane above pharyngeal basket, right portion extends into furrow left of dikinetidal portion of kinety 1, distinctly curved, composed of 11–14 dikinetids orientated perpendicularly to kinety axis and bearing about 6 µm long cilia; left (proximal) basal body of dikinetids very likely barren because often faintly impregnated, or not at all (Fig. 106a, m; 356c, k, q–z). C-shaped kinety represents anterior portion of ciliary row 1, consists of some monokinetids anteriorly and closely spaced dikinetids posteriorly; easily misinterpreted as paroral membrane because curved, long, conspicuous, and close to the oral apparatus, seemingly forming a semicircle with the paroral (Fig. 106a, m; 356b, j, k, s, t).

Silverline system as in *Furgasonia blochmanni* (FOISSNER 1989) and *Parafurgasonia sorex* (FOISSNER & ADAM 1981), that is, narrowly meshed in somatic and oral cortex, forms two similarly sized polygons between each two ciliary rows in anterior half of cell and 3–4 polygons each in posterior half of cell (Fig. 106k; 356m–p, v).

Observations on other populations: The Saudi Arabian specimens match those from the type location in most features (Table 85). They have, however, a greater size range (silver nitrate-impregnated specimens: 38–73 × 20–28 µm vs. 33–48 × 19–25 µm), a slightly stouter shape (length:width ratio: 1.8:1 vs. 2:1; Table 85), and two size types of extrusomes (5 µm and 7 µm). The Namibian population was not studied in detail because of its apparent similarity with the Costa Rican specimens (Fig. 356f, l).

Occurrence and ecology: *Wolfkosia loeffleri* was discovered in dry mud from rock-pools in volcanic bedrock at the bank of Rio Corobici, Costa Rica. A second population was found in slightly saline and acidic (pH 6.4) soil from a vegetable field near the village of Al-Jubailah, about 20 km north of Riyadh, Saudi Arabia. The sample contained mainly weed litter and the greyish upper (1 cm) soil layer. The ciliate community was highly diverse, comprising about 80 species. Furthermore, *W. loeffleri* occurred in a mud sample taken from rock-pools in the dolomite hills near the Halali Lodge at the south margin of the Etosha Pan, Namibia (site 66). Based on these records, it is impossible to decide whether *W. loeffleri* prefers limnetic or terrestrial habitats, but a world-wide distribution is likely.

Comparison with similar species: *Wolfkosia loeffleri* is easily distinguished from other furgasoniids and the colpodidiids by the "circular" oral structures, the highly characteristic distal end of the pharyngeal basket, and the obovoidal body shape. These features distinguish it also from → *Apocolpodidium (Apocolpodidium) etoschense*, which is otherwise very similar. As concerns shape and size, it is also easily confused with *Sathrophilus muscorum*, a very common soil and moss ciliate. The pharyngeal basket of *Wolfkosia* is not only peculiar because of the fish-snout like distal end, but also because of its orientation, viz., it extends straight to dorsal side and then curves sharply posteriad. A similar pattern is shown only by marine, microthoracid discotrichids (FOISSNER 1997a).

Table 85. Morphometric data on two populations of *Wolfkosia loeffleri*: CR – Costa Rican population, SA – Saudi Arabian population.

Characteristics [a]	Pop [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	CR	CHL	41.5	41.5	3.9	0.7	9.3	33.0	48.0	30
	SA	CHL	45.2	42.0	9.4	1.7	20.7	38.0	73.0	30
Body, width in lateral view	CR	CHL	22.2	23.0	2.1	0.6	9.7	19.0	25.0	15
	SA	CHL	23.3	24.0	2.3	0.6	9.7	20.0	28.0	15
Body, width in ventral view	CR	CHL	17.1	18.0	2.3	0.6	13.2	14.0	21.0	15
	SA	CHL	23.3	21.0	5.4	1.4	23.1	17.0	35.0	15
Body length:width, ratio in lateral view	CR	CHL	2.0	1.9	0.1	0.1	7.2	1.7	2.2	15
	SA	CHL	1.8	1.8	0.2	0.1	8.2	1.6	2.2	15
Body length:width, ratio in ventral view	CR	CHL	2.3	2.3	0.3	0.1	14.2	1.7	3.1	15
	SA	CHL	2.1	2.1	0.2	0.1	10.2	1.8	2.4	15
Anterior body end to macronucleus, distance	CR	CHL	13.6	14.0	2.6	0.7	19.2	10.0	19.0	15
	SA	CHL	19.6	19.0	4.5	1.2	22.8	15.0	29.0	15
Anterior body end to excretory pore, distance	CR	CHL	12.9	13.0	1.3	0.3	9.9	11.0	15.0	15
	SA	CHL	14.2	14.0	3.0	0.8	21.0	9.0	21.0	15
Anterior body end to nassulid organelle 3, distance	CR	CHL	7.2	8.0	1.2	0.3	16.8	5.0	9.0	15
	SA	CHL	7.5	8.0	2.1	0.5	27.9	4.0	12.0	15
Anterior body end to somatic kinety 1, distance	CR	CHL	2.4	2.0	0.8	0.2	34.5	1.0	4.0	15
	SA	CHL	3.0	3.0	1.1	0.3	37.8	1.0	6.0	15
Anterior body end to summit of paroral membrane, distance	CR	CHL	4.4	4.0	1.0	0.3	22.4	3.0	6.0	15
	SA	CHL	5.1	5.0	1.4	0.4	27.4	3.0	9.0	15
Macronucleus, length	CR	PA	8.5	8.0	1.1	0.3	12.4	6.0	10.0	15
	SA	CHL	7.0	6.0	1.1	0.3	16.2	6.0	9.0	15
Macronucleus, width	CR	PA	7.5	8.0	0.9	0.2	12.5	6.0	9.0	15
	SA	CHL	7.0	6.0	1.1	0.3	16.2	6.0	9.0	15
Micronucleus, length	CR	PA	1.3	1.0	–	–	–	1.0	2.0	15
Micronucleus, width	CR	PA	1.2	1.0	–	–	–	1.0	2.0	15
Paroral membrane, length [b]	CR	CHL	5.5	5.0	–	–	–	5.0	6.0	15
Macronucleus, number	CR	PA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	SA	CHL	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Micronucleus, number	CR	PA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Somatic ciliary rows, number	CR	CHL	14.4	14.5	0.6	0.2	4.5	13.0	15.0	15
	SA	CHL	14.6	14.0	1.9	0.5	12.9	13.0	19.0	15
Kinetids in a dorsal kinety, number	CR	CHL	11.1	11.0	1.4	0.4	13.0	9.0	14.0	15
	SA	CHL	11.4	11.0	2.9	0.8	25.4	9.0	21.0	15

(continued)

Characteristics [a]	Pop [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Somatic kinety 1, number of dikinetids	CR	CHL	9.3	9.0	0.5	0.1	4.9	9.0	10.0	15
Nassulid organelle 3, number of ciliary rows [c]	CR	CHL	7.0	7.0	0.9	0.2	12.5	6.0	9.0	15
Paroral membrane, number of dikinetids	CR	CHL	12.6	12.5	0.9	0.2	6.8	11.0	14.0	15

[a] Data based on silver-impregnated, mounted, and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, PA – protargol impregnation (FOISSNER's method), Pop – population, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Measured as chord of organelle.

[c] Rather rough estimate because ciliary rows difficult to separate from scattered basal bodies at organelle's left end.

Order Colpodidiida nov. ordo

Diagnosis: Medium-sized (length 50–100 µm) Nassulia JANKOWSKI, 1967 with distinct dikinetidal paroral membrane, 3 nassulid (adoral) organelles within more or less distinct buccal cavity, and 4 postoral ciliary rows. Oral basket extends anteriorly, where it curves dorsally and posteriorly; composed of very fine fibres and thus inconspicuous. Nassulid organelles 1 and 2 minute, that is, composed of only few dikinetids, organelle 3 conspicuous and composed of several minute kineties each consisting of 3 cilia. Proter's paroral produces, by transverse and longitudinal splitting, a new proter paroral, the opisthe paroral, proter's postoral kinety 4, and dikinetidal anlagen for the nassulid organelles. Somatic kinety 1 oralized, that is, produces part of nassulid organelle 3, while the other part is generated by paroral anlagen. Nasse kinetosomes distinct in dividers.

Type family: Colpodidiidae FOISSNER, 1995.

Classification and comparison with related orders: We discovered several new colpodidiid nassulids in Namibia and soils globally. All are described here to firmly establish the new order. Fortunately, we could even study the ontogenesis of the type species, → *Colpodidium caudatum*. This and a few observations on other species [*Pedohymena australiensis* FOISSNER, 1995; → *Apocolpodidium (Apocolpodidium) etoschense*] showed that colpodidiids have a unique stomatogenic pattern, although it is mixokinetal as in other members of the subclass (for review and terminology, see FOISSNER 1996c). Thus, we separated them at ordinal level. As yet, the order is monotypic. However, the family consists of three genera and four subgenera, of which → *Apocolpodidium* and → *Pedohymena* might compose a second family. Such classification, however, should await more detailed data on ontogenesis and ultrastructure.

As concerns the overall classification, the Colpodidiida very likely belong to the Nassulia because their general organization and stomatogenesis are more similar to the Nassulia than to any other ciliates. Furthermore, the silver preparations provide strong evidence for the

presence of alveolocysts, a main apomorphy of the nassulids (EISLER & BARDELE 1983).

The classic nassulid genera, such as → *Nassula,* → *Furgasonia, Chilodontopsis,* and *Microthorax*, have been raised to ordinal rank, based, however, mainly on morphostatic features (for review, see DEROUX 1994). In contrast, we define the new nassuline order by a combination of morphostatic and ontogenetic features, emphasizing the latter. → *Colpodidium* has a mixokinetal stomatogenesis, that is, the opisthe oral structures are produced by parental oral and somatic ciliature. The mixokinetal mode is typical for nassulids (FOISSNER 1996c), to which *Colpodidium* accordingly belongs. Although the ontogenesis of *Colpodidium* shows some similarities with that of *Furgasonia* (order Parahymenostomatida) and *Pseudomicrothorax/Leptopharynx* (order Microthoracida), it is so different that relationships can hardly be recognised. At best, it can be interpreted as a mixture of parahymenostomatid and microthoracid features. In both *Colpodidium* and *Furgasonia* the paroral plays a leading role in that it splits transversely and longitudinally (EISLER & BARDELE 1986; Fig. 357m–u). The posterior fragment generates, as in → *Colpodidium*, the opisthe's paroral, while the split outer part of the paroral becomes a new somatic kinety 1, which is, like the origin of the nassulid organelles, completely different from *Colpodidium*. *Colpodidium* and *Pseudomicrothorax/Leptopharynx* are similar in that somatic kinety 1 contributes to the nassulid organelles and distinct nasse kinetosomes occur (NJINE 1979a, PECK 1974). The origin and role of the paroral, in contrast, is totally different.

The leading role of the parental oral structures in the ontogenesis of the Colpodidiidae is highly reminiscent of hymenostome scuticociliates (for review, see FOISSNER 1996c). This might indicate a closer relationship between nassulid and oligohymenophorean ciliates than presently shown by gene sequence data (SCHLEGEL & EISLER 1996).

Members of the orders Colpodidiida, Nassulida, and Parahymenostomatida may look very similar at first glance. There is, however, a simple feature distinguishing the Colpodidiida from the Nassulida and Parahymenostomatida (e.g. → *Wolfkosia*, → *Furgasonia*), namely the pharyngeal basket, which is directed anteriorly and inconspicuous in the former and usually conspicuous in the latter, where it is directed posteriorly and composed of thick, stiff rods. Thus, this is a main morphological feature of the new order; interestingly, such a basket pattern is also found in certain species of the order Microthoracida, where it probably evolved convergently. The inconspicuousness of the colpodidiid pharyngeal basket, even after protargol impregnation, strongly indicates a special ultrastructure; in some species, e.g., → *Colpodidium trichocystiferum*, → *C. microstoma*, → *Apocolpodidium (Apocolpodidium) etoschense*, and → *A. macrostoma*, basket structures are not recognizable at all. On the other hand, the basket may be inconspicuous also in other nassulids, especially in some Parahymenostomatida, e.g., *Parafurgasonia protectissima* and *P. terricola*, as described by FOISSNER (1999b).

A further important feature is the buccal cavity. All other Nassulia, except for most microthoracids, lack a distinct buccal cavity, while that of the Colpodidiida is usually conspicuous and contains the adoral ciliature, much like the Parahymenostomatida. In the Nassulida, the adoral ciliature extends left, splitting some or many somatic ciliary rows. Finally, the known Colpodidiida have only one distinct nassulid organelle because the organelles 1 and 2 are minute and thus easily overlooked (FOISSNER 1995, MIRABDULLAYEV 1986, WILBERT 1982). This is a main difference to the Parahymenostomatida, which either have three conspicuous nassulid organelles of same size (→ *Furgasonia*) or only a single nassulid organelle (→

Parafurgasonia, and possibly also → *Wolfkosia*) or none at all (→ *Urliella*). According to its ontogenesis, the nassulid organelle 3 consists, like the organelles of → *Furgasonia* and *Pseudomicrothorax*, of more or less numerous ciliary rows with three basal bodies each, while the nassulid organelles in the order Nassulida are composed of three ciliary rows with more or less numerous basal bodies each (EISLER 1986, 1988, 1989). As concerns the paroral membrane, the dikinetidal organization is usually much more distinct in the Colpodidiidae than in the Nassulidae.

We also included "four postoral ciliary rows" in the diagnosis because all known species of the order have this number. In contrast, the Nassulida have many kineties under the oral opening and nassulid frange, and the Parahymenostomatida have few (e.g. → *Parafurgasonia*) or many (→ *Furgasonia*) postoral ciliary rows.

Family Colpodidiidae FOISSNER, 1995

Improved diagnosis: With characteristics of order.

Type genus (original designation): *Colpodidium* WILBERT, 1982.

Remarks: The family greatly enlarged since 1982, when it consisted of a single genus and species only. Now nine species distributed over three genera (→ *Colpodidium* WILBERT, 1982; → *Pedohymena* FOISSNER, 1995; → *Apocolpodidium* nov. gen.) and four subgenera (→ *Colpodidium* WILBERT, 1982 stat. nov.; → *Pseudocolpodidium* nov. subgen.; → *Apocolpodidium* nov. subgen., → *Phagoon* nov. subgen.) are known. All, except for *C. viride* (MIRABDULLAYEV, 1986) JANKOWSKI, 1992, occur in terrestrial habitats. → *Pedohymena* and → *Colpodidium* need improved diagnoses according to the emended family characterization provided above.

Pedohymena FOISSNER, 1995 (Fig. 283–285)

Improved diagnosis: Colpodidiidae FOISSNER, 1995 with broadly conical buccal cavity directed dorsally. Paroral membrane long and loop-shaped. Nassulid organelle 3 orientated obliquely to main body axis. Postoral kineties basically monokinetidal.

Type species (original designation): *Pedohymena australiensis* FOISSNER, 1995 (nom. corr. for *P. australiense* FOISSNER, 1995).

Colpodidium WILBERT, 1982

Improved diagnosis: Colpodidiidae FOISSNER, 1995 with horn-shaped or pocket-shaped buccal cavity directed anteriorly or to right side. Paroral membrane slightly to distinctly curved. Nassulid organelle 3 orientated obliquely or perpendicularly to main body

axis. At least postoral kinety 2, which commences in buccal cavity, possesses some dikinetids anteriorly.

Type species (by monotypy): *Colpodidium caudatum* WILBERT, 1982.

Remarks: In addition to the new genus → *Apocolpodidium*, described below, we discovered four other new *Colpodidium* species, of which one (*Colpodidium bradburyarum*) looks rather different due to the shape and orientation of the buccal cavity. However, the infraciliature is very similar to that of *Colpodidium*. Thus, we separate this new species from *Colpodidium* not at genus but at subgenus level. Accordingly, *Colpodidium* is split into two subgenera: *Colpodidium* WILBERT, 1982 stat. nov. and *Pseudocolpodidium* nov. subgen.

Subgenus *Colpodidium* WILBERT, 1982 nov. stat.

Diagnosis: Buccal cavity horn-shaped and directed anteriorly. Paroral membrane slightly curved. Nassulid organelle 3 orientated obliquely to main body axis. Postoral kineties 2 and 3 with several dikinetids anteriorly.

Remarks: This subgenus contains → *Colpodidium* (*Colpodidium*) *caudatum* WILBERT, 1982; *Colpodidium* (*Colpodidium*) *viride* (MIRABDULLAYEV, 1986) JANKOWSKI, 1992 [nom. corr. for *Colpodidium viridis* (MIRABDULLAEV, 1986) JANKOWSKI, 1992]; → *Colpodidium* (*Colpodidium*) *horribile* nov. spec.; → *Colpodidium* (*Colpodidium*) *trichocystiferum* nov. spec.; and → *Colpodidium* (*Colpodidium*) *microstoma* nov. spec.

Colpodidium (*Colpodidium*) *caudatum* WILBERT, 1982 nov. stat. (Fig. 357h–y, 358a–d; Table 86)

Colpodidium caudatum is rather frequent in Namibian soils. We could study ontogenesis in a population grown on Eau de Volvic and crushed wheat grains to stimulate growth of the indigenous bacteria and flagellate protist community, which served as food.

Colpodidium caudatum has been redescribed in great detail by FOISSNER (1995), including some ontogenetic stages which showed, for the first time, the three nassulid organelles; other details, however, were misinterpreted: somatic kinety 1 in FOISSNER's micrograph 57 is the outer, split part of the parental paroral membrane, and the "developing pharyngeal basket" in figure 56, which was reproduced side-inverted, is the new excretory pore.

As the species is well-known, we shall provide only a brief description of the Namibian population, emphasizing ontogenetically important structures. Further details are shown in the figures and table 86; see also description of Chinese population, below. In vivo, the Namibian *Colpodidium caudatum* is a 40–55 × 15–25 µm-sized, slightly reniform ciliate with a horn-shaped vestibulum in mid-body. It usually has 21 ciliary rows, which form a distinct preoral suture. The ciliary rows are monokinetidal, except for a few dikinetids in the postoral portion of kinety 1, a few dikinetids around the excretory pore, and some dikinetids at the anterior

end of postoral kineties 2 and 3 (Fig. 357a–g and FOISSNER 1995). The excretory pore of the contractile vacuole is slightly underneath the right end of the paroral. The oral apparatus consists of a slightly curved, dikinetidal paroral membrane (with only one basal body ciliated!) and three nassulid organelles. Organelle 1 consists of a single dikinetid between left end of paroral and anterior end of postoral kinety 1. Organelle 2 consists of one or two dikinetids at anterior end of postoral kinety 2. Organelle 3, which is rather conspicuous and extends on the dorsal vestibular wall, consists of 13 short ciliary rows each composed of three cilia.

Table 86. Morphometric data on *Colpodidium (Colpodidium) caudatum* from Namibian site (3).

Characteristics [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	CHL	47.0	47.0	3.9	0.8	8.3	39.0	53.0	21
Body, width	CHL	18.4	18.0	1.8	0.4	9.8	14.0	21.0	21
Anterior body end to paroral, distance	CHL	15.3	15.0	1.3	0.3	8.6	13.0	18.0	21
Anterior body end to end of paroral, distance	CHL	22.0	22.0	1.5	0.3	7.0	19.0	25.0	21
Depth of buccal cavity	CHL	6.5	6.0	0.7	0.2	11.6	5.0	8.0	21
Somatic ciliary rows, number	SC	21.0	21.0	1.5	0.4	7.0	20.0	25.0	13
Kinetids in a dorsal kinety, number	SC	23.9	24.0	2.6	0.8	11.1	19.0	28.0	12
Nassulid organelle 3, number of ciliary rows	SC	13.0	13.0	0.5	0.1	4.1	12.0	14.0	15
Paroral membrane, number of dikinetids	SC	11.8	12.0	0.8	0.2	6.8	10.0	13.0	14

[a] Data based on cultivated, silver-impregnated and randomly selected specimens. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SC – silver carbonate impregnation, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Ontogenesis (Fig. 357h–y, 358a–d): The ontogenesis of *C. caudatum* could be followed in non-permanent silver carbonate preparations[15]. Accordingly, the process is not documented by line drawings but by 23 excellent micrographs, which are arranged and described in the figure explanations in such a way that the successive stages can be easily followed. Thus, the description concentrates on the key events, that is, how the main structures behave and originate during ontogenesis.

Nassulid organelles: The opisthe nassulid organelles have an unusual and complex origin (Fig. 357a–r). Organelle 3, the largest one, is a **composite** of anlagen formed by somatic kinety 1 and the two dikinetids above and left of the excretory pore. This is not only clear from the sequence of events shown in figures 357m–q, but also from the structure of the completed organelle (Fig. 357q), whose 15–17 ciliary rows are obtained only if the three anlagen are united. Furthermore, only kinety 1 produces such an anlage, showing that it is not an ordinary somatic kinety. As the dikinetids around the excretory pore are generated by the

[15] All trials to get usable protargol preparations failed. Silver nitrate preparations were easily obtained, but too crude for following the fine ontogenetic processes. However, slides with many dividers have been deposited.

paroral, organelle 3 is a composite of somatic and oral ciliature. The organelles 1 and 2, each consisting of only few dikinetids, are very likely produced by a split part of the proter paroral. However, we cannot entirely exclude, due to the close spatial relationships, that they originate from the dikinetid above the excretory pore. Anyway, in both cases the nassulid organelles 1 and 2 originate from the paroral because the proliferating dikinetids are of paroral origin, that is, are separated from the new paroral in late dividers (Fig. 357v–y).

Paroral membrane: The proter's paroral has a leading role in stomatogenesis because it produces, by transverse and longitudinal splitting, a new proter paroral, the opisthe paroral, the proter's postoral kinety 4, a dikinetidal anlage for nassulid organelle 3 and, possibly, also for organelles 1 and 2 (see above). The paroral separates its posterior portion very early and then splits longitudinally (Fig. 357 l–p). The posterior portion migrates rearwards and produces the opisthe paroral and, very likely, also nassulid organelles 1 and 2 (Fig. 357p–r). The inner split part of the proter's paroral is reorganized and becomes the proter's new paroral, which separates two dikinetids at the posterior end; these dikinetids migrate to the excretory pore (Fig. 357u–y, 358a, b), where they become nassulid anlagen in early dividers (Fig. 357n–l). The outer split part (marked by PM*) of the proter's paroral elongates and produces the proter's postoral kinety 4, which is lacking because the opisthe gets the entire parental postoral 4 (Fig. 357 l–r); later, it is resorbed. Accordingly, there is no shift of kineties like, for instance, in *Nassula* and *Furgasonia* (EISLER & BARDELE 1986).

Somatic kineties (except kinety 1 and postoral kineties treated below): The somatic kineties divide as in other ordinary ciliates, that is, new basal bodies for the filial products are produced intrakinetally, forming typical triplets (Fig. 357r, s, v–y).

Somatic kinety 1: Somatic kinety 1 plays a key role in ontogenesis by producing part of nassulid organelle 3 (Fig. 357g–q). Accordingly, it is an "oralized somatic kinety" in the sense of FOISSNER & FOISSNER (1988). The lost basal bodies are replaced by intrakinetal proliferation, as in ordinary somatic kineties.

Postoral kineties: Postoral kineties 1–3 divide like ordinary somatic kineties. However, basal body proliferation commences much earlier in kinety 1 than in the other ciliary rows (Fig. 357i, j), and the anterior, dikinetidal portion of postoral kinety 2 is reorganized, that is, resorbed and rebuilt (Fig. 357t–v). Proter's postoral kinety 4 is produced by the outer split part of the paroral (Fig. 357t–x), while the opisthe obtains the parental postoral 4.

Nuclear apparatus: The nuclear apparatus divides as in other ordinary ciliates. It is in the posterior end of the cell in interphase specimens and migrates to body centre before division commences (Fig. 357m, p, r, v–y).

Reorganization: The parental oral structures are partially or fully reorganized, especially the paroral membrane and the "nasse kinetosomes". The nasse kinetosomes (and/or the distal end of the oral basket) behave very strangely: first they become very distinct in early dividers (Fig. 357j, m–o), then they disappear for a short period (Fig. 357r–v) and become very distinct again in late dividers producing a semicircular array of granules (Fig. 357w–y) and, finally, they become pygnotic (Fig. 358a–d). Certainly, these processes are very difficult to analyze because the structures are so small. Thus, misinterpretations are possible. But the basic observation that *Colpodidium* possesses nasse kinetosomes is undoubtedly correct (Fig. 357w–y). The nassulid organelles are also partially reorganized, as indicated by the following observation: in morphostatic specimens, organelle 3 is composed of 12–14 short kineties

(Table 86), while both the proter and opisthe organelle 3 consist of 15–17 rows in middle and late dividers (Fig. 357q, t, v, w, 358a, c, d).

Post-divider changes: Early post-dividers have more distinct "nasse kinetosomes" (cp. Fig. 358a–d with Fig. 357f) and some kineties of nassulid organelle 3 are resorbed (see above). Possibly, there are also some changes in the anterior portion of somatic kinety 1 which appears more conspicuous in late dividers and post-dividers than in morphostatic cells (Fig. 357d, e, g, 358a–d). Cell shaping also occurs mainly in post-dividers because newly divided cells are ellipsoidal and have a rather flat buccal cavity.

Colpodidium (*Colpodidium*) *caudatum* WILBERT, 1982 – Chinese population (Fig. 107a–g; 359a–j; Tables 87, 88)

Description: Size 70–90 × 25–40 µm, usually 80 × 30 µm in vivo. Shape fairly constant and conspicuous because elongate fusiform to fusiform, anterior end considerably and frequently more tapered than posterior, widest at level of oral apparatus, dorsal side moderately convex, ventral more or less flattened with a triangular, shallow preoral groove; cross section circular (Fig. 107a, g; 359a–c; Table 87). Macronucleus underneath mid-body, broadly ellipsoidal to spherical, about 13 µm across in vivo, with reticular nucleolus. Micronucleus globular, difficult to recognize because usually in shallow indentation of macronucleus. Contractile vacuole subequatorial underneath buccal cavity, surrounded by contributory vesicles during diastole; excretory pore in line with paroral membrane underneath right margin of buccal entrance, distinct even in vivo. Cytopyge slit underneath excretory pore, extends in posterior body end (Fig. 107d; 359h, i). No extrusomes. Cortex thinner (only 0.5–0.7 µm) and more flexible than in other populations and congeners, furrowed by ciliary rows, especially in anterior body half (Fig. 359a, c). Mitochondria underneath cortex, rod-shaped or reniform, occasionally irregular, numerous and thus conspicuous although only 1.5–3 µm long (Fig. 107f; 359b, d). Cytoplasm colourless and bright, contains some fat globules 1–2 µm across. Food vacuoles with remnants of bacilli, mainly spores, 3–4 µm across during acidic phase, up to 15 µm in the alkaline state, where the condensed content becomes fluffy. Swims rapidly by rotation about main body axis.

Ciliary rows equidistantly arranged, those of left and dorsal side sinistrally twisted, gradually shortened from anterior body end to oral apparatus, terminate subapically and subterminally, forming barren pole areas. Kinety spiralling mainly caused by about ten left lateral and dorsal kineties, which extend at angles of about 45° across preoral ventral surface and abut on about six ventral and right lateral ciliary rows. Thus, a long, sigmoidal, groove-like depressed preoral suture is formed with a small, triangular blank area above the paroral membrane (Fig. 107b, c; 359i, j; Table 87). Kinety 1 (first right of paroral) sigmoidally curved, commences pre-equatorially with closely spaced monokinetids, extends along oral apparatus with closely spaced dikinetids restricted to the area between paroral and excretory pore, and usually terminates near posterior quarter of cell with a rather short tail (4–6 kinetids) of ordinarily spaced monokinetids. Four postoral kineties (Fig. 107b, d, e; 359e, h, i): kinety 1 at left margin of buccal cavity, slightly curved, usually commences underneath minute nassulid organelle 1, monokinetidal throughout; kinety 2 performs sharp right bend, causing

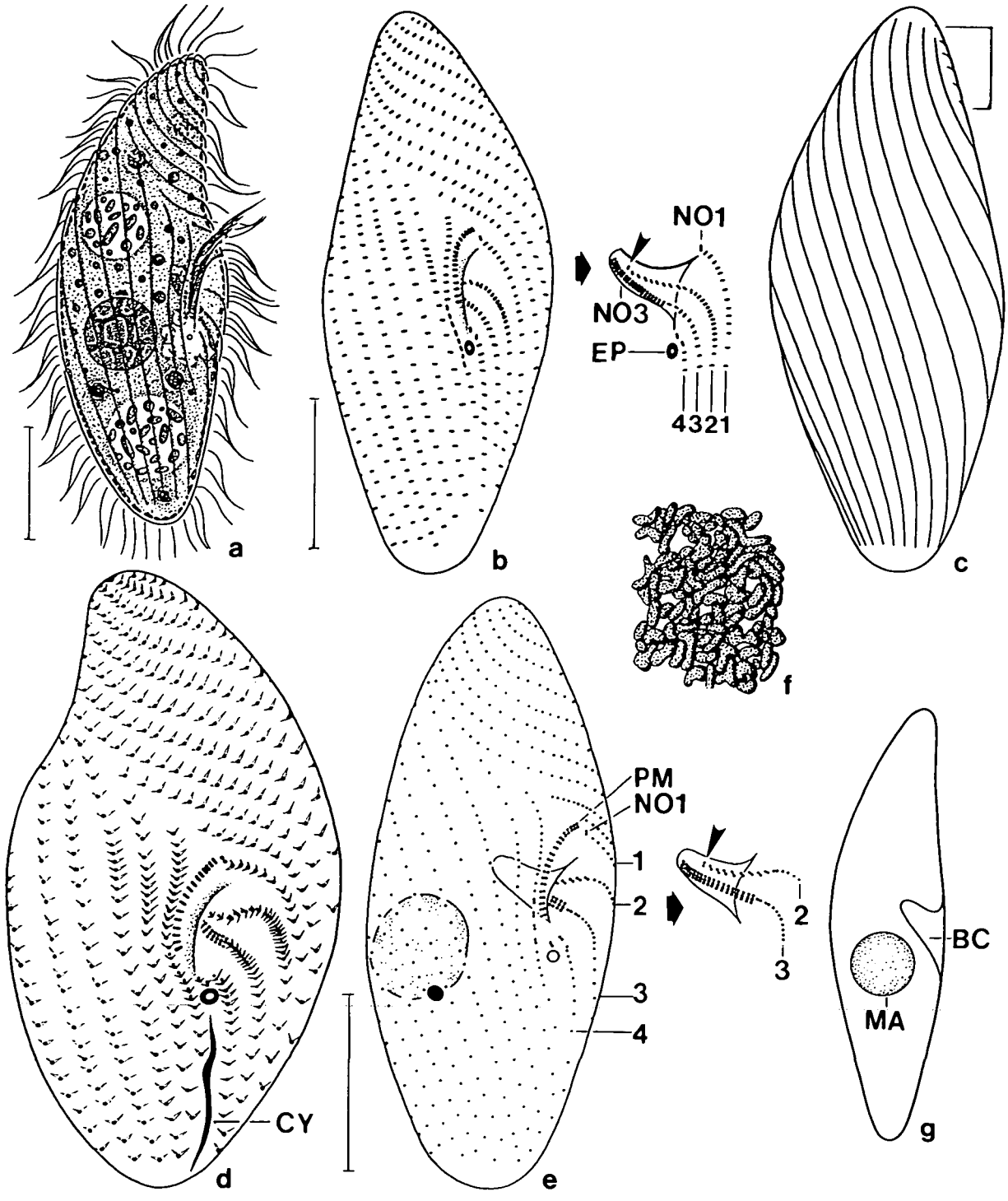


Fig. 107a–g. *Colpodidium caudatum*, Chinese specimens from life (a, f, g) and after silver nitrate (b, c), silver carbonate (d), and protargol (e) impregnation. **a:** Ventrolateral view of a fusiform specimen. **b, c:** Ciliary pattern of same specimen showing left lateral kineties spiralling over ventral to dorsal side (bracket). Arrowhead marks presumed organelle 2. **d:** Infraciliature of ventral side. **e:** Ciliature of ventral side at two focal planes. Arrowhead marks presumed nassulid organelle 2. **f:** Mitochondria. **g:** Right lateral view of shape variant. 1-4 – postoral kineties, BC – buccal cavity, CY – cytopyge, EP – excretory pore, MA – macronucleus, NO1, 3 – nassulid organelles, PM – paroral membrane. Scale bars 20 µm.

dikinetidal anterior portion to become located within buccal cavity; kinety 3 almost straight, commences underneath nassulid organelle 3, dikinetidal anteriorly, monokinetidal posteriorly; kinety 4 almost straight, commences left and at level of excretory pore, monokinetidal throughout.

Somatic cilia about 10 µm long in vivo, single, except for two to four dikinetids around excretory pore, four to eight dikinetids in kinety 1 as described above, about eight to twelve dikinetids in anterior portion of postoral kinety 2, and two to three dikinetids at anterior end of postoral kinety 3. Cilia very closely spaced in kineties 2 and 3 at level of oral apparatus and in anterior region of kinety 1 and postoral kineties. Fibrillar (?) associates of somatic kinetids as described in → *C. horribile* and shown in figures 107d and 359e–j. Special features are: (i) kinetodesmal fibres not elongated in postoral kineties; (ii) transverse fibres not elongated in preoral portion of kineties 1–3; (iii) transverse fibre probably lacking in anterior, possibly unciliated basal body of dikinetids.

Table 87. Morphometric data on Chinese population of *Colpodidium* (*Colpodidium*) *caudatum*.

Characteristics [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	CHL	75.5	76.0	5.4	1.4	7.2	63.0	83.0	15
Body, width	CHL	28.3	28.0	3.4	0.9	12.0	23.0	36.0	15
Body length:width, ratio	CHL	2.7	2.7	0.2	0.1	8.7	2.3	3.2	15
Anterior body end to macronucleus, distance	CHL	38.1	39.0	4.1	1.1	10.7	30.0	48.0	15
Anterior body end to excretory pore, distance	CHL	45.1	45.0	3.3	0.9	7.4	40.0	50.0	13
Anterior body end to nassulid organelle 3, distance	CHL	34.3	35.0	2.6	0.7	7.7	29.0	40.0	15
Anterior body end to somatic kinety 1, distance	CHL	27.8	29.0	2.3	0.6	8.1	24.0	31.0	13
Anterior body end to paroral membrane, distance	CHL	29.9	30.0	2.8	0.7	9.2	26.0	36.0	14
Macronucleus, length	PA	14.0	13.0	3.1	0.8	22.1	11.0	22.0	15
Macronucleus, width	PA	11.3	10.0	2.1	0.5	18.2	10.0	16.0	15
Micronucleus, length	PA	2.3	2.0	0.7	0.2	31.0	1.0	3.0	15
Micronucleus, width	PA	2.0	2.0	0.7	0.2	32.7	1.0	3.0	15
Macronucleus, number	PA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Micronucleus, number	PA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Somatic ciliary rows, number	CHL	21.5	22.0	1.4	0.6	6.4	19.0	23.0	6
Somatic ciliary rows between anterior body end and paroral, number	CHL	10.1	10.0	0.8	0.2	7.9	8.0	11.0	15
Kinetids in a dorsal kinety, number	CHL	36.6	37.0	7.2	3.2	19.8	27.0	44.0	5
Postoral kinety 2, number of dikinetids	PA	10.0	10.0	2.0	1.2	20.0	8.0	12.0	3
Postoral kinety 3, number of dikinetids	PA	2.1	2.0	–	–	–	2.0	3.0	10
Nassulid organelle 3, number of ciliary rows	CHL	20.0	19.0	1.7	1.0	8.7	19.0	22.0	3
Paroral membrane, number of dikinetids	CHL	16.4	16.0	1.2	0.3	7.6	14.0	19.0	15

[a] Data based on silver-impregnated, mounted, and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, PA – protargol impregnation (FOISSNER's method), SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Anterior end of paroral on average 40% back from anterior body end, buccal cavity thus in mid-body. Buccal opening elliptical and about 5 µm long; buccal cavity horn-shaped and approximately 10 µm deep, contains nassulid organelle 3 and anterior portion of postoral kinety 2. Nassulid organelles without distinct fibres, details difficult to recognize due to their small size (Fig. 107b, d, e; 359e, g–i): organelle 1 between left end of paroral and anterior end of postoral kinety 1, minute because consisting of only two granules, often lighter impregnated than paroral and somatic kinetids; organelle 2 probably at proximal end of postoral kinety 2, where a slightly separated dikinetid occurs; organelle 3 extends on dorsal wall of buccal cavity to cytostome, orientated obliquely to main body axis, slightly concave, composed of about 19–22 ciliary rows with three basal bodies each. Paroral membrane extends in flat bow along right and upper margin of buccal entrance; conspicuous because consisting of 14–19 dikinetids orientated perpendicularly to kinety axis, distances between dikinetids increase slightly from left to right (Fig. 107b, d, e, g; 359a, e–i; Table 87). Pharyngeal basket recognizable neither in vivo nor silver preparations.

Silverline system as in Kenyan population (FOISSNER 1995), that is, irregularly meshed in somatic and oral cortex.

Occurrence and ecology: WILBERT (1982) discovered *C. caudatum* in savannah soil from Afghanistan. Later, FOISSNER (1995, 1998a) recorded it from soils world-wide. The Chinese population is from soil (mud) of a river overflow in Beijing. *Colpodidium caudatum* is a rare species distinctly more frequent in Gondwanan than Laurasian areas.

Comparison of populations: The Chinese specimens look very different, especially when compared with the Namibian site (3) population (cp. figures 107a–g and 359a–j with figures 357a–g), because they are large, conspicuously fusiform, and have strongly spiralling ciliary rows. However, a separation at subspecies level does not seem justified at the present state of knowledge because there are transitions in all features (Table 88), that is, *Colpodidium caudatum* shows a strong interpopulation and intraspecific variability. On the other hand, the differences of the Chinese population are considerable, especially in body shape and size as well as in the strongly spiral kinety course, indicating that *C. caudatum* might be a complex of sibling species. The Benin population described by DRAGESCO & DRAGESCO-KERNÉIS (1996) differs from the other populations mainly in the longer paroral membrane and in that kinety 1 commences more anteriorly; thus, it is very similar to → *C. horribile* (see "comparison with related species" by this species).

Table 88. Comparison of main features in four populations of *Colpodidium (Colpodidium) caudatum*.

Characteristics [a]	Afghanistan (WILBERT 1982)	Kenya [b] (FOISSNER 1995)	Namibia, site 3 (see above)	China
Body shape	fusiform to slenderly ovoidal	slightly reniform	reniform	conspicuously fusiform
Body length in vivo	40–50	55–70	40–55	70–90
Body width in vivo	15–20 [d]	25–35	15–25	25–40
Mean body size after silver impregnation	45 x 15	55 x 22	47 x 18	76 x 28
Macronucleus [c]	70 [d]	68	?	50

(continued)

Characteristics [a]	Afghanistan (WILBERT 1982)	Kenya [b] (FOISSNER 1995)	Namibia, site 3 (see above)	China
Excretory pore [c]	65 [d]	53	?	60
Buccal opening, upper margin [c]	51	~ 33	~ 33	~ 40
Somatic ciliary rows, number	19–20	16–19	20–25	19–23
Somatic ciliary rows between anterior body end and paroral, number	8	5–7 [d]	5–6 [d]	8–11
Kinetids in a dorsal kinety, number	25–31	23–32	19–28	27–44
Nassulid organelle 3, number of ciliary rows	?	15 [d]	12–14	19–22
Paroral membrane, number of dikinetids	18 [d]	12–14	10–13	14–19
Cortex	rigid	rigid	rigid	very flexible
Dorsal kineties, course	± straight	± straight	± straight	spiral
Preoral suture, course	slightly curved, commences on right side	± straight, commences ventrally	± straight, commences ventrally [e]	spiral, commences dorsally [e]

[a] Data based, if not otherwise stated, on CHATTON-LWOFF silver nitrate-impregnated, mounted specimens. Measurements in µm.

[b] Protargol-impregnated specimens.

[c] Mean distance between anterior body end and organelle, in % of mean body length.

[d] Not mentioned, thus estimated from figures and/or micrographs.

[e] Both features are intermediate in a population from Namibian site (8; Fig. 112a–f).

Colpodidium (Colpodidium) horribile nov. spec. (Fig. 108a–t, 109a–g; 275–278, 360a–s; Table 89)

Diagnosis: Size about 60 × 30 µm in vivo; ellipsoidal. Macronucleus in middle third of cell. Trichocysts pin-shaped, highly refractive. On average 25 somatic ciliary rows and paroral dikinetids. Buccal opening rather large and slightly underneath mid-body. Nassulid organelle 3 composed of about 16 ciliary rows.

Type location: Highly saline soil from littoral of Lake Nakuru, Kenya, East Africa, 00°N 37°E.

Etymology: The Latin adjective *horribile* (horrible) refers to the highly characteristic trichocysts.

Description: Size 55–75 × 25–40 µm in vivo. Shape fairly constant, lateral view ellipsoidal to slightly ovoidal with flat ventral and more or less distinctly vaulted dorsal side; length:width ratio 1.7–2.1:1, usually 1.9:1 in protargol preparations, cells thus appear rather broad, especially if compared with most → *C. caudatum* populations (2.5:1). Laterally slightly flattened, ventral and dorsal view elongate ellipsoidal to ovoidal (Fig. 108a, f, m; 360a–d; Table 89). Macronucleus usually in middle third of cell, about 13 µm across in vivo,

with reticular nucleolus. Micronucleus usually attached to macronucleus, globular to ellipsoidal, difficult to recognize in vivo because very hyaline (blister-like). Contractile vacuole subequatorial, underneath buccal cavity, with short excretory canal having pore in line with paroral membrane underneath right margin of buccal entrance. Cytopyge slit close underneath excretory pore, extends in posterior quarter of cell; faecal mass globular and mucilaginous, contains some minute refractive granules. Resting trichocysts scattered in cytoplasm and attached almost perpendicularly to cortex close to left side of ciliary rows, moderately numerous forming indistinct fringe; conspicuous, although having a size of only 4 × 1 μm, because highly refractive appearing as about 1 μm-sized, brilliant granules in surface view (Fig. 108a, n; 360b, c, f, j). Shape also peculiar and as shown in figures 108r, s, that is, pin-like with a dome-shaped head and a cuneate, slightly inflated shaft. Exploded trichocysts in vivo with highly refractive, conical tip and hyaline, 25–30 μm long shaft narrowing posteriorly (Fig. 108t; 360e, f, h). Trichocysts do not impregnate with protargol, but tip stains, occasionally, intensely with silver carbonate, producing a peculiar, spotted appearance of impregnated cells; tips appear hat-like after silver carbonate impregnation and in vivo, if observed with phase contrast, that is, have a conical centre surrounded by a minute collar (Fig. 108q; 360i, k, m, n). Under cover glass pressure and possible also other, as yet unspecified conditions, the trichocysts partially explode internally showing a highly remarkable behaviour reminiscent of cnidocysts: they quickly and irregularly jump and swirl twice at irregular intervals, becoming ellipsoidal and appearing partially uncoiled, showing the highly refractive tip (Fig. 108g–l). Cortex distinctly furrowed by ciliary rows, thinner than in → *Nassula* spp., but slightly notched by the extrusomes; mitochondria underneath cortex, conspicuous because numerous and 2–3 × 0.5 μm in size, rod-shaped to dumb-bell-shaped (Fig. 108n–p; 360a, f, g, h). Cytoplasm colourless, contains many bright fat globules about 1 μm across and 4–10 μm-sized food vacuoles with bacterial remnants, especially spores. Movement without peculiarities.

Ciliary rows meridionally and equidistantly arranged, except for more widely spaced postoral kineties; dorsal kineties bipolar, those on ventral side form comparatively large, triangular, blank area above oral apparatus and long preoral suture in midline because left side kineties abut obliquely on right side kineties, which gradually shorten from anterior end of cell to oral apparatus (Fig. 109a, c, g; 275–278, 360p; Table 89). Kinety 1 (first right of paroral) commences pre-equatorially with closely spaced monokinetids, extends along oral apparatus with rather widely spaced dikinetids, and ends terminally or subterminally with a tail of widely spaced monokinetids. Four postoral kineties (Fig. 109a, b, d, e, g; 275–278, 360m–s): kinety 1 commences left of minute nassulid organelle 1, monokinetidal throughout; kinety 2 commences in proximal portion of buccal cavity, dikinetidal in anterior half, monokinetidal in posterior; kinety 3 commences at distal end of nassulid organelle 3, dikinetidal anteriorly, monokinetidal posteriorly; kinety 4 commences at level of excretory pore of contractile vacuole, monokinetidal throughout.

Somatic cilia about 10–11 μm long and rather stiff in vivo, single, except for four to ten dikinetids in kinety 1 at level of oral apparatus, two to three dikinetids around excretory pore, ten to thirteen dikinetids in anterior portion of postoral kinety 2, and one to three dikinetids at anterior end of postoral kinety 3. Cilia very closely spaced in anterior region of somatic kinety 1 and postoral kineties 1–3; distances between cilia increase from anterior to posterior, ciliature thus loosened in rear pole area. Silver carbonate preparations reveal each somatic kinetid to be composed of (i) an irregular (possibly due to attached parasomal sac and/or

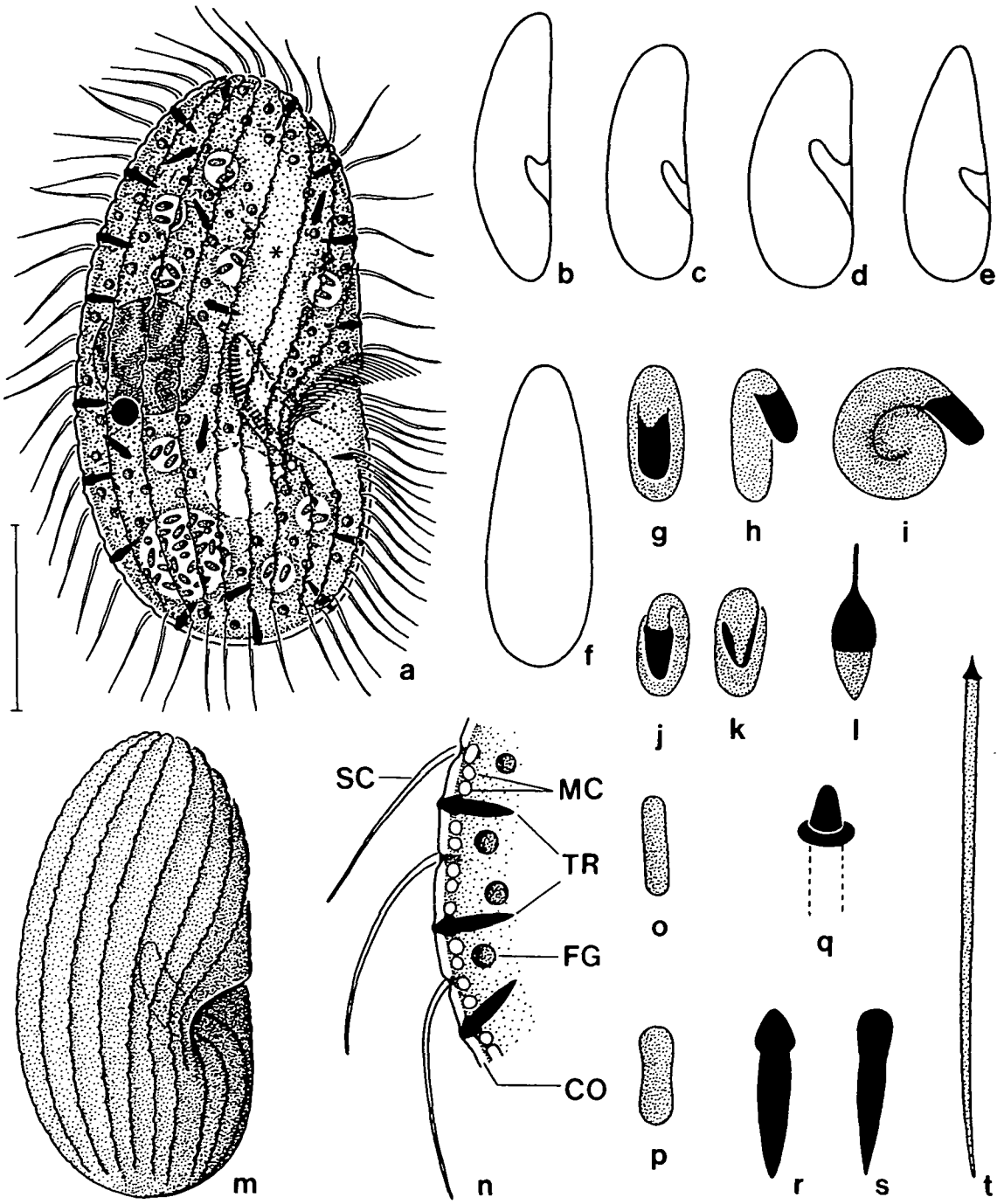


Fig. 108a–t. *Colpodidium horribile*, Kenyan (a, f–p, r) and Chinese (b–e, q, s, t) specimens from life (a–p, r–t) and after silver carbonate impregnation (q). **a, m:** Right lateral views of a representative specimen showing surface distinctly furrowed by ciliary rows and buccal entrance. The pharyngeal basket area appears as bright cone (*). The peculiar trichocysts are scattered in the cytoplasm and attached to the cortex forming an indistinct fringe. **b–e:** Shape variability in Chinese population. **f:** Ventral view. **g–l:** Shapes of trichocysts exploding in the cytoplasm under cover glass pressure. **n:** Optical section of cortex showing arrangement of trichocysts and mitochondria. **o, p:** Mitochondria are 2–3 µm long. **q:** Trichocyst tip appears hat-like when impregnated with silver carbonate. **r, s:** Resting trichocysts (4 × 1 µm) have a dome-shaped head and a cuneate shaft. **t:** Exploded trichocysts (25–30 × 1 µm) have a minute, highly refractive tip. CO – cortex, FG – fat globule, MC – mitochondria, SC – somatic cilium, TR – trichocysts. Scale bar 20 µm.

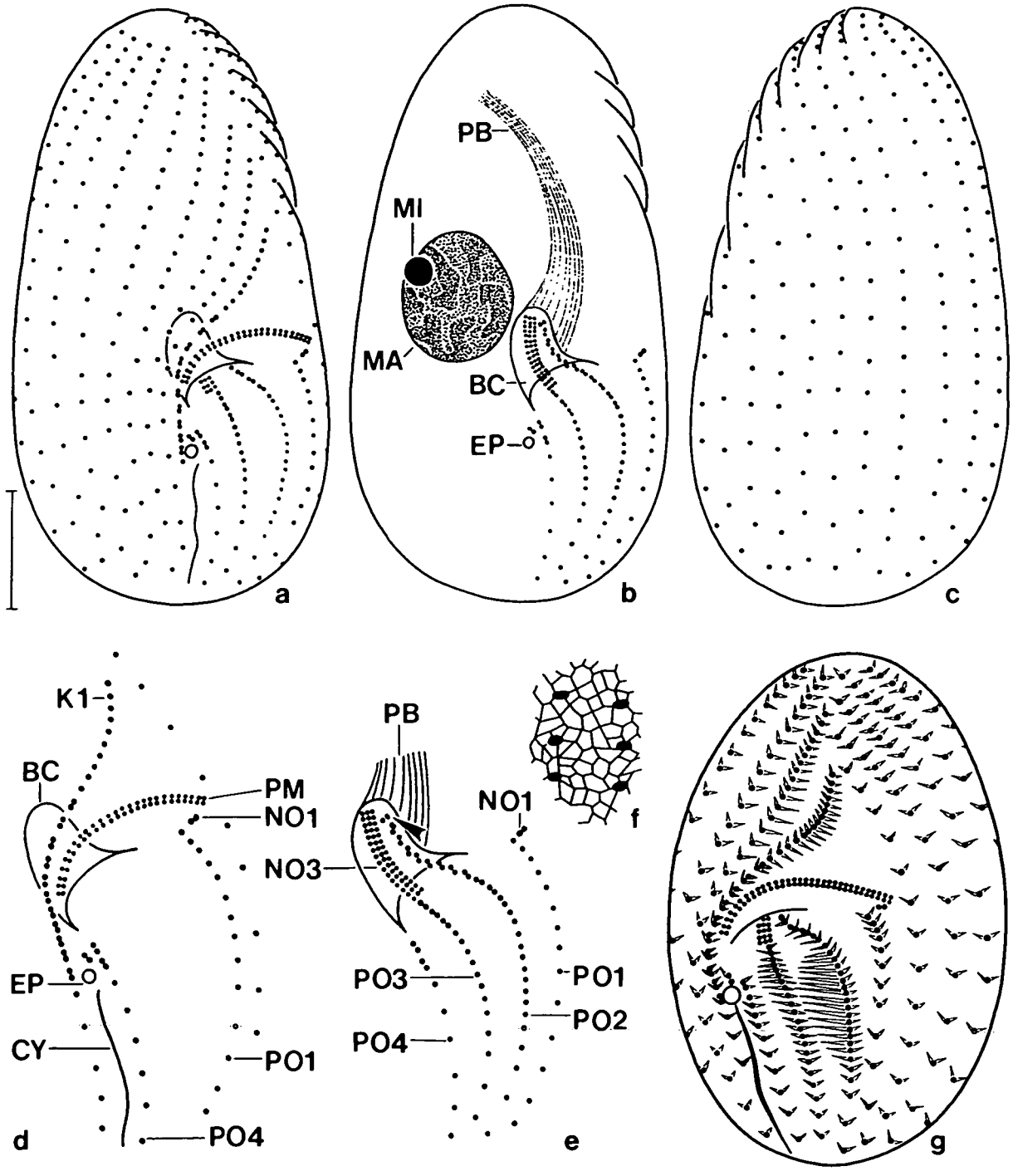


Fig. 109a–g. *Colpodidium horribile*, Kenyan (a–f) and Chinese (g) specimens after protargol (a–e), silver nitrate (f), and silver carbonate impregnation (g). **a–c:** Ventrolateral and dorsolateral view of same specimen showing ciliary pattern and main cell organelles. **d, e:** Oral ciliature at two focal planes showing dikinetids around excretory pore, in somatic kinety 1 at level of the oral apparatus, and in the anterior portion of postoral kineties 2 and 3. Arrowhead marks presumed nassulid organelle 2. **f:** Silverline pattern. **g:** Infraciliature of ventral side. Note elongated kinetodesmal fibres (?) in anterior portion of postoral kineties 2 and 3 and elongated transverse fibres (?) in preoral half of somatic kineties 1–3. BC – buccal cavity, CY – cytopyge, EP – excretory pore, K1 – somatic kinety 1, MA – macronucleus, MI – micronucleus, NO1, 3 – nassulid organelles, PB – pharyngeal basket, PM – paroral membrane, PO1–4 – postoral kineties. Scale bar 10 μm.

alveolocyst and/or trichocyst) granule bearing the cilium; (ii) a short structure (kinetodesmal fibre?) extending obliquely anteriad at right side of basal body, except for anterior basal body of dikinetids, where it is lacking, and anterior portion of postoral kineties 2 and 3, where it is very long and extends almost perpendicularly to kinety axis; and (iii) a short structure (transverse fibre?), slightly elongated in preoral portion of somatic kineties 1–3 and lacking in the anterior basal body of the postoral dikinetids, extending almost perpendicularly to kinety axis at left side of basal body (Fig. 109g; 275–278, 360p, s).

Summit of paroral on average 50% back from anterior body end, about 6–8 μm wide buccal opening thus slightly underneath mid-body. Buccal cavity conspicuous, horn-shaped, contains nassulid organelles 2 and 3 and anterior portion of postoral kinety 2 (Fig. 108a–e, m; 275–278, 360a–d; Table 89). Nassulid organelles without distinct fibres, details difficult to recognize due to their small size (Fig. 108a, b, d, e, g; 275–278, 360o, r, s). Nassulid organelle 1 between left end of paroral and anterior end of postoral kinety 1, minute because consisting of only two granules, lighter impregnated than paroral and somatic kinetids. Nassulid organelle 2 probably at proximal end of postoral kinety 2, where a few faintly impregnated and thus hardly recognizable basal bodies occur. Nassulid organelle 3 extends on dorsal wall of buccal cavity to cytostome, orientated obliquely to main cell axis, slightly concave, composed of 13–19 ciliary rows with three basal bodies each. Paroral membrane conspicuous, even in vivo, because composed of closely spaced cilia increasing in length from 3–4 μm at right end to 12 μm at left, extends in flat bow along right and upper margin of buccal opening; composed of 19–33 dikinetids orientated perpendicularly to kinety axis and having only one basal body ciliated, distances between dikinetids increase slightly from left to right (Fig. 109b, e; 275–278, 360n, r). Pharyngeal basket large but hardly recognizable in vivo and even protargol preparations because composed of about 18 very thin rods; extends as a wide funnel, which sometimes appears as a bright stripe in live specimens, from proximal vertex of buccal cavity to near anterior end of cell, where it curves dorsally (Fig. 109a, b).

Silverline system as in → *C. caudatum* (FOISSNER 1995), that is, irregularly meshed in somatic and oral cortex, producing about four minute polygons between each two ciliary rows; meshes partially filled with argyrophilic substance in suboptimal preparations (Fig. 109f; 360 l).

The Chinese specimens match those from the type population in all main morphometrics (Table 89). They show, however, a much greater shape variability (Fig. 108b–e).

Occurrence and ecology: *Colpodidium horribile* was discovered in a sample containing grass roots and grey, highly saline mineral soil from the littoral of Lake Nakuru, one of the famous soda lakes in Kenya, East Africa. A second population was found in a sample containing litter and loamy, dark-brown soil (pH 6.7) from the bottom of a moist overflow 1 km from a river in Beijing, China (40°N 117°E). Furthermore, *C. horribile* occurred in a sample from the Etosha Pan region (site 54), which contained highly saline soil (pH 8) mixed with grass roots. Abundant at all sites. Likely, *C. horribile* is a euryhaline cosmopolitan.

Comparison with related species: → *Colpodidium caudatum* WILBERT, 1982 lacks trichocysts, which we consider as species character, and has a kinety 1 commencing more anteriorly (about 20% vs. 40% back from anterior body end) as well as slightly fewer somatic ciliary rows (16–23 vs. 23–26) and paroral dikinetids (12–19 vs. 19–33). In vivo, *C. horribile* and → *C. caudatum* can be rather reliably distinguished not only by the trichocysts

but also by the length:width ratio (1.9:1 vs. 2.5:1) and the location of the macronucleus (in middle vs. posterior third). DRAGESCO & DRAGESCO-KERNÉIS (1986) redescribed → *C. caudatum* from Benin, Africa. However, their specimens differ from those studied by WILBERT (1982) and FOISSNER (1995), especially in the number of paroral dikinetids (about

Table 89. Morphometric data on two populations of *Colpodidium* (*Colpodidium*) *horribile*: CK – Kenyan type population, CC – Chinese population.

Characteristics [a]	Pop [a]	Me [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	CK	PB	54.3	53.0	3.8	1.0	6.9	50.0	63.0	15
	CC	CHL	56.9	58.0	5.2	1.3	9.1	48.0	68.0	15
Body, width in lateral view	CK	PB	28.8	29.0	2.7	0.7	9.3	24.0	34.0	15
Body, width in ventral view	CC	CHL	25.7	26.0	3.4	0.9	13.4	20.0	30.0	15
Body length:width, ratio in lateral view	CK	PB	1.9	1.9	0.1	0.0	6.3	1.7	2.1	15
Body length:width, ratio in ventral view	CC	CHL	2.2	2.1	0.3	0.1	13.5	1.9	2.9	15
Anterior body end to macronucleus, distance	CK	PB	20.5	21.0	5.2	1.3	25.2	8.0	26.0	15
	CC	CHL	24.7	24.0	2.9	0.8	11.9	21.0	30.0	15
Anterior body end to excretory pore of	CK	PB	35.5	35.0	1.5	0.4	4.1	34.0	40.0	15
contractile vacuole, distance	CC	CHL	35.5	36.0	2.8	0.7	7.9	30.0	41.0	15
Anterior body end to cytostome (proximal	CK	PB	24.9	25.0	1.2	0.3	4.7	23.0	28.0	15
end of buccal cavity), distance	CC	CHL	23.0	23.0	2.4	0.6	10.5	19.0	28.0	15
Anterior body end to somatic kinety 1,	CK	PB	17.0	16.0	1.5	0.4	8.9	15.0	19.0	15
distance	CC	CHL	16.6	16.0	2.0	0.5	11.8	14.0	21.0	15
Anterior body end to summit of paroral	CK	PB	26.9	26.0	1.7	0.4	6.2	25.0	31.0	15
membrane, distance	CC	CHL	26.7	26.0	2.1	0.5	7.8	23.0	31.0	15
Macronucleus, length	CK	PB	11.9	11.0	1.3	0.3	11.2	10.0	15.0	15
Macronucleus, width	CK	PB	10.5	11.0	1.0	0.3	9.4	9.0	13.0	15
Micronucleus, length	CK	PB	2.5	3.0	–	–	–	2.0	3.0	15
Micronucleus, width	CK	PB	2.3	2.0	–	–	–	2.0	3.0	15
Macronucleus, number	CK	PB	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	CC	CHL	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Micronucleus, number	CK	PB	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	CC	CHL	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Somatic ciliary rows, number	CK	PB	24.6	25.0	1.1	0.3	4.3	23.0	26.0	15
	CC	CHL	23.8	24.0	1.1	0.3	4.5	22.0	26.0	15
Kinetids in a dorsal kinety, number	CK	PB	23.9	24.0	2.9	0.7	12.0	19.0	28.0	15
Postoral kinety 2, number of dikinetids	CK	PB	11.4	11.0	1.0	0.3	8.6	10.0	13.0	15
Postoral kinety 3, number of dikinetids	CK	PB	2.1	2.0	0.5	0.1	22.1	1.0	3.0	15
Nassulid organelle 3, number of ciliary rows	CK	PB	16.3	16.0	1.8	0.5	11.3	13.0	19.0	15
Paroral membrane, number of dikinetids	CK	PB	25.3	25.0	4.0	1.0	15.6	19.0	33.0	15

[a] Data based on silver-impregnated, mounted, and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Me – methods, Min – minimum, n – number of individuals investigated, PB – protargol impregnation (WILBERT's method), Pop – population, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

25–30 vs. 12–14); thus, DRAGESCO & DRAGESCO-KERNÉIS (1986) supposed that it is a new species. In fact, the Benin population matches *C. horribile* in the long paroral membrane but differs by the lack of trichocysts, a slightly smaller size (silver nitrate-impregnated specimens: 20–58 × 10–20 µm), and fewer ciliary rows (12–14). While body size and number of ciliary rows are rather weak features, the lack of trichocysts is much more important. However, DRAGESCO & DRAGESCO-KERNÉIS (1986) apparently did not study live specimens and may thus have overlooked extrusomes. *Colpodidium viride* (MIRABDULLAYEV, 1986) JANKOWSKI, 1992 has symbiotic green algae, lacks trichocysts, and has a hook-shaped nassulid organelle.

The pin-shaped extrusomes of *C. horribile* are highly remarkable because all other nassulids have fusiform extrusomes or none at all. To the best of our knowledge, only *Pseudourostyla cristata*, a hypotrichous ciliate, has similarly-shaped extrusomes (OBERSCHMIDLEITNER & AESCHT 1996, SUGANUMA 1973).

Colpodidium (Colpodidium) trichocystiferum nov. spec. (Fig. 110a–l; 271–274, 361a–m; Table 90)

Diagnosis: Size about 50 × 25 µm in vivo; ellipsoidal. Macronucleus in middle third of cell. Trichocysts fusiform. On average 18 somatic ciliary rows and 17 paroral dikinetids. Buccal opening rather large and in mid-body. Nassulid organelle 3 composed of about 10 ciliary rows.

Type location: Saline inland soil from Zicksee region, Burgenland, Austria, 47°50'N 16°50'E.

Etymology: Composite of *trichocyst* and *ferum* (Latin suffix; bearing), referring to the fusiform extrusomes.

Description: Size 40–60 × 20–30 µm in vivo. Shape rather variable, ellipsoidal to slightly ovoidal or cylindroidal with flat to slightly concave ventral and usually conspicuously vaulted dorsal side, laterally rather distinctly flattened (lost in preparations; Table 90); length:width ratio 1.7–2.2:1, usually 1.9–2:1 in vivo and protargol preparations, cells thus appear rather broad, especially if compared with most → *C. caudatum* populations (2.5:1; Fig. 110a, k; 361a, b, d). Macronucleus in middle third of cell on average, rarely in anterior or posterior third, about 10 µm across in vivo and with reticular nucleolus. Micronucleus globular, difficult to recognize because usually in shallow indentation of macronucleus and faintly impregnated with protargol. Contractile vacuole subequatorial underneath buccal cavity; excretory pore in line with paroral membrane underneath right margin of buccal entrance. Cytopyge slit close underneath excretory pore, extends in posterior third of cell, becomes a large, fusiform opening during defecation (Fig. 110k). Resting trichocysts scattered in cytoplasm and attached almost perpendicularly to cortex close to posterior or left posterior margin of somatic kinetids in anterior half of cell and to left anterior margin of kinetids in posterior half of cell, form indistinct fringe, fusiform, about 3–4 × 0.4 µm in size (Fig. 110a, g; 361d, e, g, i, j). Exploded trichocysts about 6 µm long, composed of a short, refractive anterior rod attached to a minute globule and a comparatively large, hyaline, obclavate

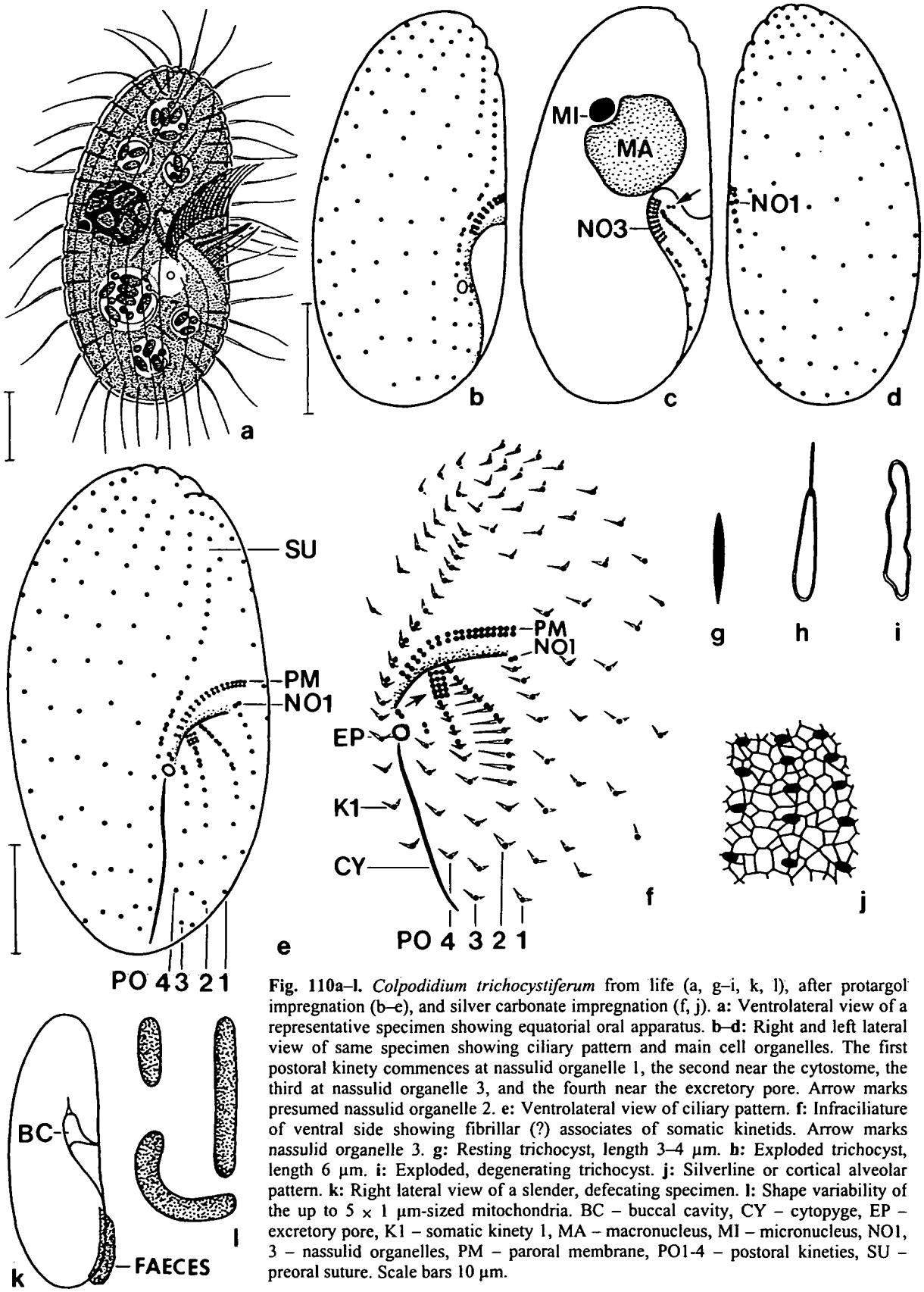


Fig. 110a–l. *Colpodidium trichocystiferum* from life (a, g–i, k, l), after protargol impregnation (b–e), and silver carbonate impregnation (f, j). **a:** Ventrolateral view of a representative specimen showing equatorial oral apparatus. **b–d:** Right and left lateral view of same specimen showing ciliary pattern and main cell organelles. The first postoral kinety commences at nassulid organelle 1, the second near the cytostome, the third at nassulid organelle 3, and the fourth near the excretory pore. Arrow marks presumed nassulid organelle 2. **e:** Ventrolateral view of ciliary pattern. **f:** Infraciliature of ventral side showing fibrillar (?) associates of somatic kinetids. Arrow marks nassulid organelle 3. **g:** Resting trichocyst, length 3–4 µm. **h:** Exploded trichocyst, length 6 µm. **i:** Exploded, degenerating trichocyst. **j:** Silverline or cortical alveolar pattern. **k:** Right lateral view of a slender, defecating specimen. **l:** Shape variability of the up to 5 × 1 µm-sized mitochondria. BC – buccal cavity, CY – cytopyge, EP – excretory pore, K1 – somatic kinety 1, MA – macronucleus, MI – micronucleus, NO1, 3 – nassulid organelles, PM – paroral membrane, PO1-4 – postoral kineties, SU – preoral suture. Scale bars 10 µm.

posterior portion; degenerate to irregular blisters within a few minutes (Fig. 110h, i). Cortex distinctly punctated by ciliary pits, thinner than in → *Nassula* spp.; mitochondria underneath cortex, conspicuous because numerous and up to 5 × 1 µm in size, rod-shaped or more or less distinctly curved. Cytoplasm colourless, contains 5–10 µm-sized food vacuoles with bacterial remnants, especially spores (Fig. 361m). Swims rather rapidly.

Ciliary rows meridionally and equidistantly arranged; dorsal kineties bipolar, those on ventral side form a preoral suture, which is, however, indistinct and confined to the anterior body fifth due to the low number of ciliary rows and the comparatively large, triangular, blank preoral area (Fig. 110e, f; 271–274, 361f, i, k). Kinety 1 (first right of paroral) commences subapically with rather closely spaced monokinetids, extends along oral apparatus with rather closely spaced dikinetids, and terminates near posterior body end with a tail of widely spaced monokinetids. Four postoral kineties: kinety 1 commences underneath nassulid organelle 1, monokinetidal throughout; kinety 2 commences in proximal portion of buccal cavity, dikinetidal in anterior half, monokinetidal in posterior; kinety 3 commences at distal end of nassulid organelle 3, dikinetidal anteriorly, monokinetidal posteriorly; kinety 4 commences at level of excretory pore of contractile vacuole, monokinetidal throughout (Fig. 110b–f; 271–274, 361c, f, i; Table 90).

Somatic cilia about 10 µm long in vivo, single except for four to six dikinetids in kinety 1 at level of oral apparatus, usually two dikinetids around excretory pore, six to seven dikinetids in anterior portion of postoral kinety 2, and two to four dikinetids at anterior end of postoral kinety 3. Cilia closely spaced in anterior region of somatic kinety 1 and postoral kineties 1–3; distances between cilia increase from anterior to posterior, ciliature thus loosened in rear pole area. Fibrillar (?) associates of somatic kinetids as described in → *C. horribile* and shown in figure 110f. Special features are: (i) kinetodesmal fibres not elongated in anterior portion of postoral kinety 3, and slightly elongated only in anterior portion of postoral kinety 2; (ii) transverse fibres not elongated in preoral portion of kineties 1–3; (iii) transverse fibre probably lacking in anterior, possibly unciliated basal body of dikinetids, at least in kinety 1.

Summit of paroral on average 40% back from anterior body end, about 6–8 µm wide buccal entrance thus near mid-body. Buccal cavity conspicuous, horn-shaped, contains nassulid organelle 3 and anterior portion of postoral kinety 2 (Fig. 110a, c, k; 271–274, 361a–d, k, l; Table 90). Nassulid organelles without distinct fibres, details difficult to recognize due to their small size (Fig. 110c, e, f; 361i). Nassulid organelle 1 between left end of paroral and anterior end of postoral kinety 1, minute because consisting of only two granules lighter impregnated than paroral and somatic kinetids. Nassulid organelle 2 probably left of proximal end of postoral kinety 2, where a few faintly impregnated and thus hardly recognizable basal bodies occur. Nassulid organelle 3 extends on dorsal wall of buccal cavity to cytostome, orientated obliquely to main cell axis, slightly concave, composed of 9–11 ciliary rows with three basal bodies each. Paroral membrane conspicuous, even in vivo, because composed of closely spaced, about 10 µm long cilia, extends in flat bow along right and upper margin of buccal entrance; composed of 15–19 dikinetids orientated perpendicularly to kinety axis, distances between dikinetids increase slightly from left to right (Fig. 110a, c, e, f; 271–274, 361c, d, i). Pharyngeal basket recognizable neither in vivo nor in silver preparations.

Silverline system as in *C. caudatum* (FOISSNER 1995), that is, irregularly meshed in somatic and oral cortex, producing 3–4 minute polygons between each two ciliary rows (Fig. 110j; 361f, h).

Table 90. Morphometric data on *Colpodidium* (*Colpodidium*) *trichocystiferum*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	42.3	41.0	4.0	0.8	9.5	35.0	50.0	26
Body, width in lateral view	21.9	21.0	2.7	0.7	12.6	18.0	26.0	15
Body, width in ventral view	21.0	21.0	3.3	1.0	15.5	15.0	25.0	11
Body length:width, ratio in lateral view	1.9	2.0	0.1	0.0	7.6	1.7	2.2	15
Body length:width, ratio in ventral view	2.1	2.1	0.2	0.1	11.9	1.7	2.6	11
Anterior body end to macronucleus, distance	14.3	15.0	5.7	1.5	39.6	6.0	29.0	15
Anterior body end to excretory pore, distance	25.3	24.0	1.9	0.5	7.7	23.0	29.0	15
Anterior body end to cytostome, distance [b]	18.9	18.0	2.5	0.7	13.4	16.0	24.0	15
Anterior body end to somatic kinety 1, distance	8.2	8.0	1.1	0.3	14.0	6.0	10.0	15
Anterior body end to summit of paroral, distance	17.0	16.0	1.7	0.5	10.2	14.0	20.0	15
Macronucleus, length	11.1	11.0	1.2	0.3	10.5	9.0	13.0	15
Macronucleus, width	10.2	11.0	1.4	0.4	13.5	8.0	13.0	15
Micronucleus, length	2.1	2.0	1.1	0.3	52.8	1.0	4.0	15
Micronucleus, width	2.1	2.0	1.1	0.3	52.8	1.0	4.0	15
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Somatic ciliary rows, number	17.7	18.0	–	–	–	17.0	18.0	15
Kinetids in a dorsal kinety, number	12.7	13.0	0.8	0.2	6.3	12.0	14.0	15
Postoral kinety 2, number of dikinetids	6.3	6.0	–	–	–	6.0	7.0	15
Postoral kinety 3, number of dikinetids	2.5	2.0	0.7	0.2	30.1	2.0	4.0	15
Nassulid organelle 3, number of ciliary rows	10.3	10.0	0.7	0.2	7.0	9.0	11.0	15
Paroral membrane, number of dikinetids	17.1	17.0	1.2	0.3	7.2	15.0	19.0	15

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Proximal end of buccal cavity.

Occurrence and ecology: *Colpodidium trichocystiferum* was discovered in saline soil (pH 8.1) from the Zicksee region in Austria, that is, between the Neusiedlersee and the Hungarian borderline. Later, we found it at Namibian site (49), that is, in mud and soil from track puddles. According to these records, *C. trichocystiferum* is a euryhaline cosmopolitan preferring ephemeral habitats.

Comparison with related species: Within the genus *Colpodidium*, only → *C. horribile* has extrusomes, which, however, differ distinctly from those of *C. trichocystiferum* in shape (pin-like vs. fusiform) and structure (trichocyst-like vs. toxicyst-like). Furthermore, *C. trichocystiferum* is considerably smaller than *C. horribile* (protargol-impregnated specimens: 35–50 × 18–26 µm vs. 50–63 × 24–34 µm) and has fewer ciliary rows (17–18 vs. 23–26), kinetids in a dorsal ciliary row (12–14 vs. 19–28), paroral dikinetids (15–19 vs. 19–33), dikinetids in the second postoral (6–7 vs. 10–13), and ciliary rows in the large nassulid organelle (9–11 vs. 13–19). → *Colpodidium caudatum* differs from *C. trichocystiferum* not only by the lack of extrusomes (FOISSNER 1995, WILBERT 1982), but also in size (protargol-

impregnated specimens: 49–64 × 16–26 µm vs. 35–50 × 18–26 µm), number of basal bodies in a dorsal ciliary row (23–32 vs. 12–14), number of paroral dikinetids (12–14 vs. 15–19), and number of ciliary rows in the large nassulid organelle (about 15, as estimated from figure 63 in FOISSNER 1995 vs. 9–11). In vivo, *C. trichocystiferum* and → *C. caudatum* can be rather reliably distinguished not only by the lack of trichocysts but also by the body's length:width ratio (1.9:1 vs. 2.5:1) and the location of the macronucleus (in middle vs. posterior third of cell). Furthermore, the location of the buccal entrance is rather different (Fig. 111a–d): in mid-body in *C. trichocystiferum*, slightly underneath mid-body in *C. horribile*, slightly above or in mid-body in → *C. caudatum* (FOISSNER 1995, WILBERT 1986), and between first and second third of cell in → *C. microstoma*. *Colpodidium viride* (MIRABDULLAYEV, 1986) JANKOWSKI, 1992 has symbiotic green algae, lacks trichocysts, and has a large, hook-shaped nassulid organelle 3 (MIRABDULLAYEV 1986).

Colpodidium trichocystiferum is not to be confused with → *Apocolpodidium (Apocolpodidium) etoschense* and *Pedohymena australiensis*, whose resting extrusomes have a very similar size and shape. Interestingly, the exploded extrusomes of *C. trichocystiferum* look very similar to haptorid toxicysts, while those of → *C. horribile*, *P. australiensis*, → *A. etoschense*, → *A. macrostoma*, and many other nassulids look similar to hymenostome spindle trichocysts.

Generally, most colpodidids look rather similar at first glance, but on detailed observation they can be distinguished even in vivo by the presence/absence of trichocysts, the location and gross structure of the oral apparatus, and the location of the macronucleus.

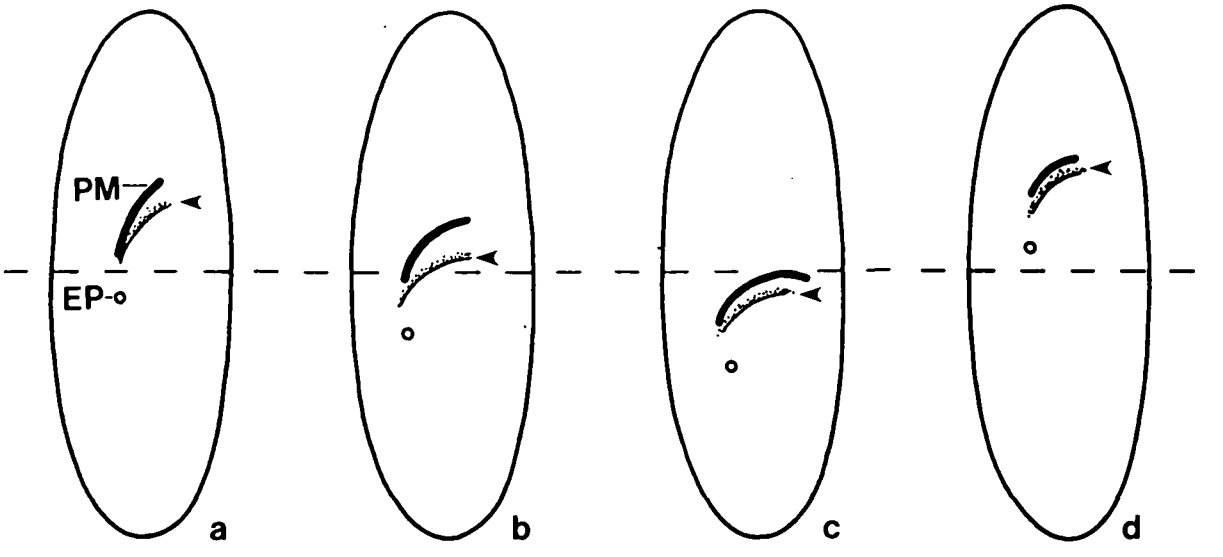


Fig. 111a–d. Schematized ventral views of *Colpodidium* species showing location of oral entrance (see also tables by these species): slightly above mid-body in Kenyan and Namibian population of → *C. caudatum* (a), in mid-body in *C. trichocystiferum* and Chinese population of → *C. caudatum* (b), slightly below mid-body in → *C. horribile* and Afghan population of → *C. caudatum* (c), and between first and second third of cell in → *C. microstoma* (d). Arrowheads mark upper margin of buccal opening, dashed line denotes mid-body. EP – excretory pore of contractile vacuole, PM – paroral membrane.

Colpodidium (*Colpodidium*) *microstoma* nov. spec. (Fig. 112a–i; 362a–k, 363i–r; Table 91)

Diagnosis: Size about 65 × 27 µm in vivo; reniform. Macronucleus in posterior third of cell. Cortical granules, possibly mucocysts, about 1 µm across. On average 24 somatic ciliary rows and 9 paroral dikinetids. Buccal opening uniquely small and pre-equatorial. Nassulid organelle 3 composed of about 11 ciliary rows.

Type location: Mud from granitic rock-pools on the Kruger Tablets in the Kruger National Park, Republic of South Africa, 23°S 31°E.

Etymology: Greek substantive in apposition, referring to the uniquely small buccal entrance.

Description: Size 55–80 × 23–35 µm in vivo. Shape fairly constant, lateral view slightly reniform due to more or less distinct indentation at oral apparatus, dorsal side convex; ventral and dorsal view elongate ellipsoidal because laterally slightly flattened (Fig. 112a, d; Table 91). Macronucleus invariably in posterior third of cell, globular, with reticular nucleolus. Micronucleus globular, difficult to recognize because usually in shallow indentation of macronucleus and faintly impregnated with protargol. Contractile vacuole near mid-body underneath buccal cavity, surrounded by contributory vesicles during diastole; excretory pore in line with paroral membrane underneath right margin of buccal entrance, distinct even in vivo. Cytopyge slit underneath excretory pore, about 21 µm long, extends in posterior body half. Cortex 1.0–1.2 µm thick and bright, furrowed by ciliary rows, especially in anterior body half, contains many minute, polygonal alveoli and curious granules, possibly some sort of extrusomes, which make surface rough; granules rather conspicuous because 0.8–1 µm across and bright, scattered, pale pink in bright field at certain light intensity and/or focal plane, stain red, but are not extruded, after methyl green-pyronin application (Fig. 112i; 362b, d, e). Subcortical mitochondria rather inconspicuous, although numerous, serpentine, and up to 5 µm long, because only slightly refractive (Fig. 362a). Cells dark at low magnification due to innumerable lipid droplets 1–3 µm across. Food vacuoles about 16 µm across, probably contain remnants of flagellates. Movement without peculiarities.

Ciliary rows meridionally and equidistantly arranged; dorsal kineties bipolar, those on ventral side form long, straight preoral suture because left side kineties abut obliquely on right side kineties, which gradually shorten from anterior end of cell to oral apparatus (Fig. 112b, f; 362g–i; Table 91). Kinety 1 (first right of paroral) commences slightly above anterior quarter of cell with monokinetids becoming more closely spaced from anterior to posterior, extends along oral apparatus with closely spaced dikinetids, and usually terminates near mid-body with a short tail of 1–4 ordinarily spaced monokinetids. Four postoral kineties: kinety 1 commences underneath, rarely left of minute nassulid organelle 1, monokinetidal throughout; kinety 2 commences in buccal cavity, dikinetidal in anterior half, monokinetidal in posterior; kinety 3 commences underneath nassulid organelle 3, dikinetidal anteriorly, monokinetidal posteriorly; kinety 4 commences left of and slightly below level of excretory pore, monokinetidal throughout (Fig. 112c, h; 362h).

Somatic cilia about 10 µm long in vivo, single except for four to five dikinetids in kinety 1 at level of buccal entrance, one to two dikinetids above excretory pore, probably three dikinetids

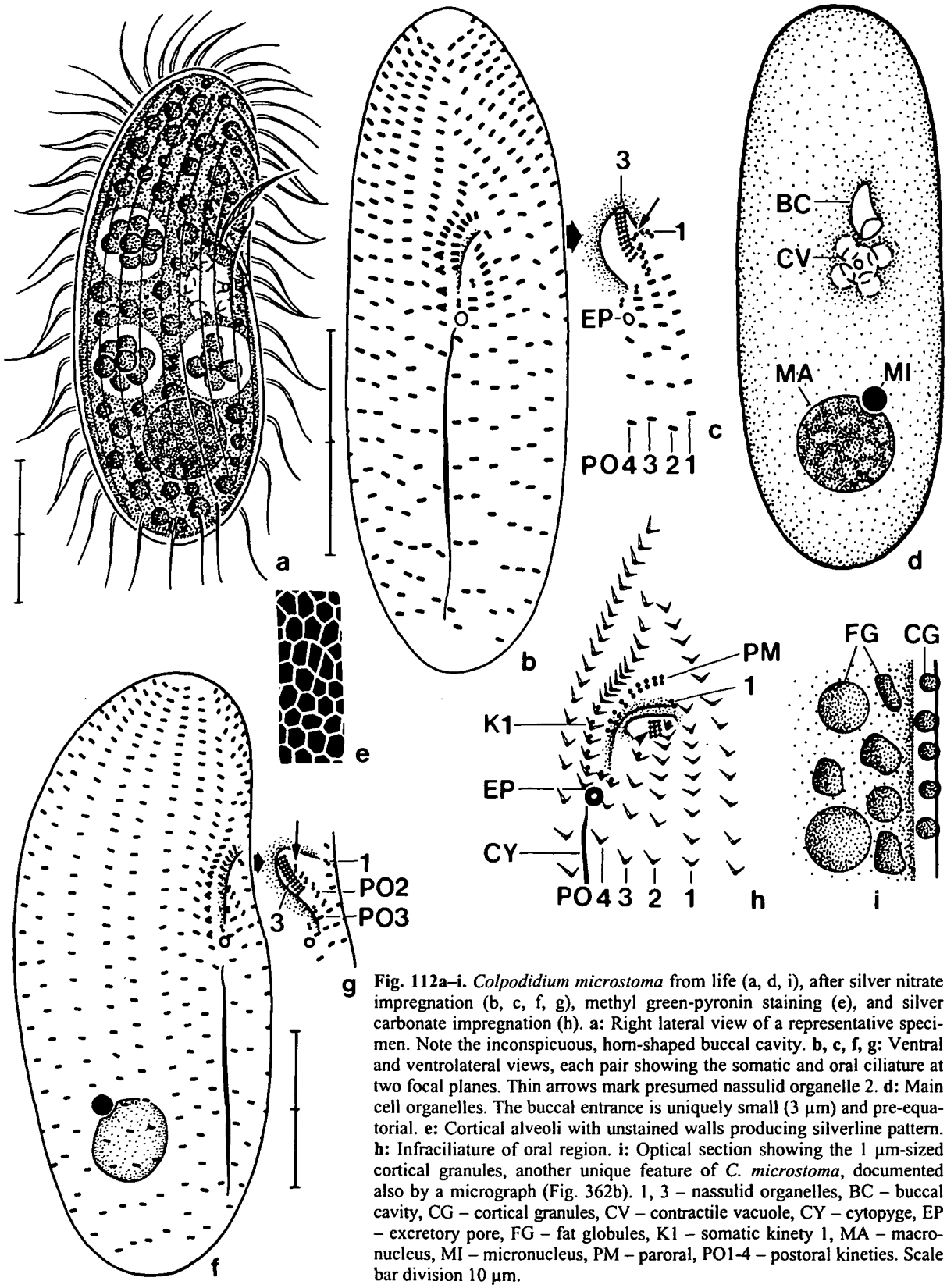


Fig. 112a–i. *Colpodidium microstoma* from life (a, d, i), after silver nitrate impregnation (b, c, f, g), methyl green-pyronin staining (e), and silver carbonate impregnation (h). **a:** Right lateral view of a representative specimen. Note the inconspicuous, horn-shaped buccal cavity. **b, c, f, g:** Ventral and ventrolateral views, each pair showing the somatic and oral ciliature at two focal planes. Thin arrows mark presumed nassulid organelle 2. **d:** Main cell organelles. The buccal entrance is uniquely small (3 µm) and pre-equatorial. **e:** Cortical alveoli with unstained walls producing silverline pattern. **h:** Infraciliature of oral region. **i:** Optical section showing the 1 µm-sized cortical granules, another unique feature of *C. microstoma*, documented also by a micrograph (Fig. 362b). 1, 3 – nassulid organelles, BC – buccal cavity, CG – cortical granules, CV – contractile vacuole, CY – cytopyge, EP – excretory pore, FG – fat globules, K1 – somatic kinety 1, MA – macronucleus, MI – micronucleus, PM – paroral, PO1-4 – postoral kineties. Scale bar division 10 µm.

in anterior portion of postoral kinety 2, and probably one dikinetid at anterior end of postoral kinety 3. Cilia closely spaced in anterior region of somatic kinety 1 and postoral kineties 2 and 3; distances between cilia increase from anterior to posterior, ciliature thus loosened in rear pole area. Fibrillar (?) associates of somatic kinetids as described in → *C. horribile* and shown in figures 112h and 362h. Special features are: (i) kinetodesmal fibres not elongated in postoral kineties; (ii) transverse fibres not elongated in preoral portion of kineties 1–3; (iii) transverse fibre lacking in anterior, possibly unciliated basal body of dikinetids, at least in kinety 1.

Upper end of paroral on average 29% back from anterior body end, buccal cavity thus between first and second third of body. Buccal opening elliptical and very small, that is, only about 3 µm wide; buccal cavity horn-shaped and rather inconspicuous because only up to 3 µm wide and 6 µm long, contains nassulid organelle 3 and anterior portion of postoral kinety 2 (Fig. 112a, c, d, g; 362a, h, j, k; Table 91). Nassulid organelles without distinct fibres, details difficult to recognize due to their small size. Nassulid organelle 1 usually between left end of paroral and anterior end of postoral kinety 1, minute because consisting of only two

Table 91. Morphometric data on *Colpodidium* (*Colpodidium*) *microstoma*.

Characteristics [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	CHL	62.8	63.0	4.7	0.9	7.5	53.0	78.0	30
Body, width in lateral view	CHL	26.7	25.0	4.3	1.1	16.1	21.0	35.0	15
Body, width in ventral view	CHL	22.8	23.0	2.3	0.6	10.2	19.0	26.0	15
Body length:width, ratio in lateral view	CHL	2.4	2.4	0.2	0.1	9.6	1.9	2.8	15
Body length:width, ratio in ventral view	CHL	2.7	2.7	0.3	0.1	11.3	2.4	3.3	15
Anterior body end to macronucleus, distance	CHL	43.1	44.0	4.5	1.2	10.3	36.0	53.0	15
Anterior body end to excretory pore, distance	CHL	28.1	28.0	2.4	0.6	8.4	23.0	33.0	15
Anterior body end to somatic kinety 1, distance	CHL	14.1	14.0	1.4	0.4	10.2	11.0	16.0	15
Anterior body end to cytostome, distance	CHL	17.7	18.0	1.6	0.4	9.2	14.0	20.0	15
Anterior body end to paroral membrane, distance	CHL	18.4	18.0	1.5	0.4	7.9	15.0	21.0	15
Depth of buccal cavity	CHL	5.5	6.0	0.8	0.2	15.3	4.0	7.0	15
Macronucleus, length	PA	13.7	14.0	1.3	0.4	9.8	11.0	16.0	15
Macronucleus, width	PA	11.9	12.0	1.1	0.3	9.2	10.0	14.0	15
Micronucleus, length	PA	2.7	3.0	0.7	0.2	27.1	1.0	4.0	15
Micronucleus, width	PA	2.5	3.0	0.9	0.2	36.1	1.0	4.0	15
Macronucleus, number	PA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Micronucleus, number	PA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Somatic ciliary rows, number	CHL	24.1	24.0	0.8	0.2	3.5	23.0	26.0	15
Kinetids in a dorsal kinety, number	CHL	28.3	28.0	2.9	0.8	10.4	25.0	37.0	15
Nassulid organelle 3, number of ciliary rows	CHL	10.5	10.0	0.6	0.2	6.1	10.0	12.0	15
Paroral membrane, number of dikinetids	CHL	9.3	9.0	0.7	0.2	7.8	8.0	10.0	15

[a] Data based on silver-impregnated, mounted, and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, PA – protargol impregnation (FOISSNER's method), SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

basal bodies. Nassulid organelle 2 probably at proximal end of postoral kinety 2, where a slightly separated dikinetid occurs. Nassulid organelle 3 extends on dorsal wall of buccal cavity to cytostome, orientated obliquely to main cell axis, slightly concave, composed of 10–12 ciliary rows with three basal bodies each. Paroral membrane extends in flat bow along right and upper margin of buccal entrance, fairly inconspicuous because composed of only 8–10 rather widely spaced dikinetids orientated perpendicularly to kinety axis (Fig. 112c, g, h; 362g–k). Pharyngeal basket recognizable neither in vivo nor silver preparations.

Methyl green-pyronin produces a pattern which is highly similar to the silverline system of, for instance, → *C. caudatum* (FOISSNER 1995) and → *Wolfkosia loeffleri*: the alveolar content stains red, while the alveolar walls remain unstained, showing the silverline pattern by negative contrast (Fig. 112e; 362f).

Occurrence and ecology: To date found in the circumneutral (pH 6.5) mud from type location and mud of an ephemeral puddle at the entrance to the Sydney Harbour National Park, Australia.

Comparison with similar species: *Colpodidium microstoma* has a uniquely small (≤ 3 μm), pre-equatorial buccal entrance. In the other members of the subgenus, the buccal opening is larger and usually slightly underneath mid-body. The differences to → *C. caudatum*, possibly the nearest relative, become obvious on comparison of micrographs and morphometrics: location of oral apparatus (29% vs. 33% of body length; Fig. 311), depth of buccal cavity (arithmetic mean: 5.5 μm vs. 6.5 μm), number of paroral dikinetids (8–10 vs. 10–13), and number of ciliary rows in nassulid organelle 3 (10–12 vs. 12–14). Certainly, these differences are not very conspicuous, especially considering the high variability of → *C. caudatum*. Thus, we emphasize as main species feature the minute oral entrance and the cortical granules, both documented by micrographs (Fig. 362a–c, 363a–r). The lack of trichocysts and symbiotic green algae distinguishes *C. microstoma* from → *C. horribile*, → *C. trichocystiferum*, and *C. viride* (MIRABDULLAYEV, 1986) JANKOWSKI, 1992.

Fortunately, we got useable SEM micrographs from the Australian population. They show convincingly the minuteness of the oral entrance (Fig. 363i–r) when compared with that of → *C. caudatum* (Fig. 357b, c, 363a–h). Further, the micrographs show the buccal entrance distinctly above mid-body (Fig. 363j, l, m), and the pellicle covered with a slimy layer from extruded mucocysts (Fig. 363p–r). Thus, *Colpodidium (Colpodidium) microstoma* is a distinct species easy to recognize both in vivo and preparations.

Pseudocolpodidium nov. subgen.

Diagnosis: Buccal cavity pocket-shaped and directed rightwards. Paroral membrane distinctly curved. Nassulid organelle 3 orientated perpendicularly to main body axis. Anterior, dikinetidal portion of postoral kinety 2 sharply curved rightwards and thus appearing as an additional nassulid organelle.

Type species: *Colpodidium (Pseudocolpodidium) bradburyarum* nov. spec.

Etymology: Composite of *pseudo* (Greek; resembling) and *Colpodidium*.

Comparison with related genera: *Pseudocolpodidium* is distinguished from the subgenus → *Colpodidium* mainly by the shape (pocket-like vs. horn-like) and orientation (rightwards vs. obliquely anteriad) of the buccal cavity. Correlated with these features are the orientation of the (large) nassulid organelle 3 (perpendicularly vs. obliquely to main body axis) and the sharp bend postoral kinety 2 performs anteriorly (Fig. 113d; 364f). Furthermore, *Pseudocolpodidium* has only one dikinetidal postoral kinety and a more distinctly curved paroral. However, these features must not be over-interpreted, not only because they are sometimes difficult to recognize but also because, e.g., → *Colpodidium horribile* has only one to three dikinetids in postoral kinety 3.

→ *Apocolpodidium* lacks dikinetidal postoral kineties, while → *Pedohymena* FOISSNER, 1995, which probably lacks postoral dikinetids too, has a loop-shaped paroral membrane.

Colpodidium (Pseudocolpodidium) bradburyarum nov. spec. (Fig. 113a–k; 364a–j; Table 92)

Diagnosis: Size about 55 × 30 in vivo; conspicuously obovoidal. Usually 2 macronuclear nodules. On average 23 somatic ciliary rows and 16 paroral dikinetids. Buccal cavity in second quarter of cell. Nassulid organelle 3 composed of about 17 ciliary rows.

Type location: Soil from bottom of river overflow in Beijing, China, 40°N 117°E.

Etymology: We dedicate this new species to Prof. Dr. Phyllis BRADBURY as a small piece of appreciation for her friendship over the years and her significant contributions to the morphology and biology of the apostome ciliates.

Description: Size 40–70 × 25–40 µm in vivo. Shape fairly constant and conspicuous because distinctly obovoidal making cells looking like swimming eggs; ventral view obovoidal, lateral view ellipsoidal to obovoidal with ventral side usually flattened and dorsal distinctly vaulted (Fig. 113a, i; Table 92); shape often poorly preserved in silver preparations. Nuclear apparatus usually in posterior half of cell. Macronuclear nodules globular and often abutting, with large globular nucleoli; of 29 specimens analyzed, 26 have two macronuclear nodules, one has three, and two have only one nodule (Table 92). Micronuclei recognizable neither in vivo nor in protargol and silver carbonate preparations. Contractile vacuole in mid-body underneath buccal cavity; excretory pore in line with paroral membrane close to right margin of buccal entrance. Cytopyge slit underneath excretory pore, extends in posterior half of cell. Cortex thick and bright, punctated by ciliary pits, rather inflexible, usually strongly wrinkled in protargol preparations. No trichocysts, but about 2 µm-sized blisters (special kind of mucocysts ?) are released on slight cover glass pressure providing cells with peculiar, pustulated appearance; blisters do not stain with methyl green-pyronin or protargol, but occasionally impregnate faintly with silver nitrate (Fig. 113j, k; 364a–c). Cells dark at low magnification, especially in posterior half, due to countless, 1–2 µm-sized, angular fat inclusions. Food vacuoles 7–10 µm across, contain bacteria. Swims rather rapidly.

Ciliary rows meridionally and equidistantly arranged, except for slightly more closely spaced postoral kineties, of which the anterior, dikinetidal portion of kinety 2 is sharply (~90°) bent rightwards extending close above and along nassulid organelle 3. Dorsal and lateral ciliary

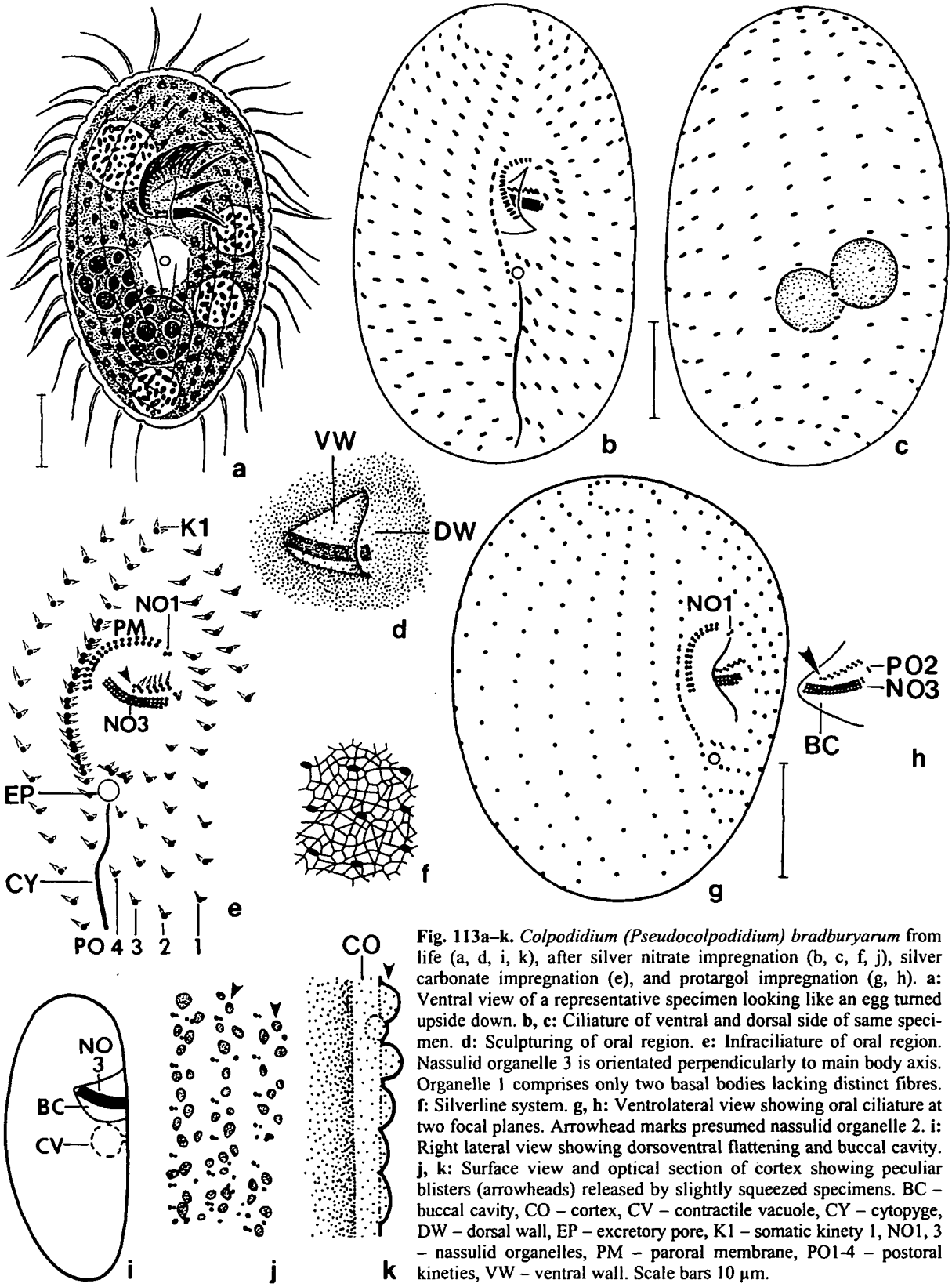


Fig. 113a–k. *Colpodidium (Pseudocolpodidium) bradburyarum* from life (a, d, i, k), after silver nitrate impregnation (b, c, f, j), silver carbonate impregnation (e), and protargol impregnation (g, h). **a:** Ventral view of a representative specimen looking like an egg turned upside down. **b, c:** Ciliature of ventral and dorsal side of same specimen. **d:** Sculpturing of oral region. **e:** Infraciliature of oral region. Nassulid organelle 3 is orientated perpendicularly to main body axis. Organelle 1 comprises only two basal bodies lacking distinct fibres. **f:** Silverline system. **g, h:** Ventrolateral view showing oral ciliature at two focal planes. Arrowhead marks presumed nassulid organelle 2. **i:** Right lateral view showing dorsoventral flattening and buccal cavity. **j, k:** Surface view and optical section of cortex showing peculiar blisters (arrowheads) released by slightly squeezed specimens. BC – buccal cavity, CO – cortex, CV – contractile vacuole, CY – cytopyge, DW – dorsal wall, EP – excretory pore, K1 – somatic kinety 1, NO1, 3 – nassulid organelles, PM – paroral membrane, PO1-4 – postoral kineties, VW – ventral wall. Scale bars 10 μm.

rows bipolar. Preoral suture short because formed by only three to four shortened ciliary rows left of midline and one shortened row at right; nonetheless, rather conspicuous because fairly wide and merging into comparatively large, ovate, unciliated anterior pole area. Kinety 1 (first right of paroral) commences subapically with ordinarily spaced monokinetids, extends along oral apparatus with closely spaced, ciliated dikinetids, and abuts on cytopyge with short (~3 kinetids), monokinetidal tail (Fig. 113e, g; 364d–j; Table 92). Four postoral kineties: kinety 1 commences left of left end of paroral membrane, monokinetidal throughout; kinety 2 commences in proximal portion of buccal cavity, dikinetidal and orientated perpendicularly to main body axis in anterior half, monokinetidal and orientated parallel to main body axis in posterior half; kineties 3 and 4 commence at level of excretory pore of contractile vacuole leaving blank a square area underneath oral apparatus, monokinetidal throughout (Fig. 113e, g; 364d, f, i, j).

Somatic cilia 8–10 µm long in vivo, single except for eight to thirteen dikinetids in kinety 1 at level of oral apparatus, about two dikinetids around excretory pore, and six to eight dikinetids in anterior portion of postoral kinety 2. Ciliature loosened in posterior pole area because distances between cilia increase slightly from anterior to posterior. Fibrillar (?) associates of somatic kinetids as described in → *C. horribile* and shown in figures 113e and figures 364d–

Table 92. Morphometric data on *Colpodidium (Pseudocolpodidium) bradburyarum.*

Characteristics [a]	Me [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	CHL	51.1	50.0	5.6	1.4	10.9	43.0	68.0	15
Body, width in ventral view	CHL	30.8	30.0	4.0	1.0	12.9	24.0	39.0	15
Body length:width, ratio in ventral view	CHL	1.7	1.7	0.1	0.0	7.0	1.5	1.9	15
Anterior end to anterior macronuclear nodule, distance	CHL	24.7	25.0	4.1	1.1	16.6	16.0	31.0	15
Anterior body end to excretory pore, distance	CHL	27.1	28.0	3.0	0.8	11.0	21.0	34.0	15
Anterior body end to somatic kinety 1, distance	CHL	7.8	9.0	1.8	0.5	22.8	3.0	9.0	15
Anterior body end to cytostome (right end of nassulid organelle), distance	CHL	18.4	19.0	1.7	0.4	9.1	15.0	21.0	15
Anterior body end to left end of paroral, distance	CHL	15.0	15.0	2.0	0.5	13.3	11.0	20.0	15
Macronuclei, length	PA	8.8	9.0	1.1	0.3	12.4	7.5	11.5	15
Macronuclei, width	PA	7.6	7.5	1.0	0.3	13.4	6.0	10.0	15
Macronuclei, number [b]	PA	2.0	2.0	0.3	0.1	16.6	1.0	3.0	29
Somatic ciliary rows, number	CHL	23.3	23.5	1.3	0.5	5.5	21.0	25.0	8
Kinetids in a dorsal kinety, number	CHL	18.5	18.0	2.1	0.5	11.4	16.0	23.0	15
Postoral kinety 2, number of dikinetids	PA	7.5	8.0	0.8	0.3	10.1	6.0	8.0	8
Nassulid organelle 3, number of ciliary rows	PA	16.8	17.0	1.0	0.4	6.2	15.0	18.0	8
Paroral membrane, number of dikinetids	PA	16.5	16.0	1.5	0.4	9.1	14.0	19.0	15

[a] Data based on silver-impregnated, mounted, and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Me – methods, Min – minimum, n – number of individuals investigated, PA – protargol impregnation (FOISSNER's method), SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Of 29 specimens investigated, 2 have one macronuclear nodule, 26 have two nodules, and 1 has three nodules.

f, i. Special features are: (i) kinetodesmal fibres not elongated in anterior portion of postoral kineties; (ii) transverse fibres not elongated in preoral portion of kineties 1–3.

Buccal cavity in second quarter of cell, pocket-shaped, that is, extends dorsally and rightwards almost parallel to cell surface, contains (large) nassulid organelle 3 and anterior, dikinetidal portion of postoral kinety 2. Buccal entrance an obclavate slit, ventral buccal wall with sharp, L-shaped margin, dorsal gradually deepening from left to right (Fig. 113a, b, d, e, g–i; 364a–c; Table 92). Nassulid organelles without distinct fibres, details difficult to recognize due to their small size (Fig. 113e, h; 364f). Nassulid organelle 1 between left end of paroral and anterior end of postoral kinety 1, minute because consisting of only two basal bodies. Nassulid organelle 2 probably near proximal end of postoral kinety 2, where a few faintly impregnated and thus hardly recognizable basal bodies occur. Nassulid organelle 3 extends on dorsal wall of buccal cavity to cytostome, orientated perpendicularly to main body axis, slightly concave, composed of 15–18 ciliary rows with three basal bodies each, except for leftmost row comprising only two basal bodies. Paroral membrane conspicuous, even in vivo, because composed of closely spaced cilia, extends along right and upper margin of buccal entrance, distinctly curved, composed of 14–19 dikinetids orientated perpendicularly to kinety axis. Pharyngeal basket commences at upper right vertex of buccal cavity and extends anteriad, very delicate, only the distal portion could be recognized in vivo and silver carbonate preparations (Fig. 364b, c, f).

Silverline system as in *C. caudatum* (FOISSNER 1995), that is, irregularly meshed producing 3–4 minute polygons between each two ciliary rows (Fig. 113f).

Occurrence and ecology: To date found only at type location. The sample was a mixture of litter and moist, loamy, dark-brown soil (pH 6.7) inhabited by a highly diverse ciliate community comprising 62 species.

Comparison with related species: *Colpodidium (Pseudocolpodidium) bradburyarum* is easily distinguished from most (all?) nassulids by the two macronuclear nodules and by the obovoidal body shape from all described Colpodidiidae, except for → *Apocolpodidium* (*Phagoon*) *macrostoma*, which, however, has a large oral apparatus with a long, C-shaped paroral membrane. Furthermore, it differs from the other Colpodidiidae by the main subgeneric features, viz., the pocket-shaped buccal cavity and horizontal orientation of nassulid organelle 3.

Apocolpodidium nov. gen.

Diagnosis: Colpodidiidae FOISSNER, 1995 with keyhole-shaped, small and slightly concave or large and rather deep buccal cavity. Paroral membrane short and slightly curved or long and C-shaped. Nassulid organelle 3 orientated obliquely to main body axis. Postoral kineties basically monokinetidal. Trichocysts simply fusiform or composed of fusiform shaft and quadripartited head structure.

Type species: *Apocolpodidium* (*Apocolpodidium*) *etoschense* nov. spec.

Etymology: Composite of *apo* (Greek prefix; derived from) and *Colpodidium*. Neuter gender.

Classification and comparison with related genera: *Apocolpodidium* belongs to the Colpodidiidae, according to the features discussed in the family classification. It differs from → *Colpodidium* WILBERT, 1982 in the shape of the buccal cavity (keyhole-shaped vs. horn- or pocket-shaped) and the lack of dikinetidal postoral kineties. In the latter feature, *Apocolpodidium* is similar to → *Pedohymena* FOISSNER, 1995, which, however, has a unique, loop-shaped paroral membrane and a broadly conical buccal cavity. As concerns separation from *Parafurgasonia* spp., see "comparison with similar species" below.

Remarks: We discovered two colpodidiids, which look rather different at first glance due to the distinctly different size of the oral apparatus. Furthermore, they have different extrusomes. However, their infraciliature is very similar. Thus, we separate these new species not at genus but subgenus level.

Apocolpodidium nov. subgen.

Diagnosis: Oral apparatus comparatively inconspicuous, that is, with small, flat buccal cavity and short, slightly curved paroral membrane. Trichocysts fusiform.

Apocolpodidium (*Apocolpodidium*) *etoschense* nov. spec. (Fig. 114a–o; 279–282, 365a–y; Table 93)

Diagnosis: Size about 65 × 30 µm in vivo; ellipsoidal. Trichocysts about 7 µm long. On average 19 somatic ciliary rows and 17 paroral dikinetids. Buccal cavity in second quarter of cell. Nassulid organelle 3 composed of about 4 ciliary rows.

Type location: Highly saline soil from margin of Etosha Pan, Namibia, 18°45'S 16°45'E (site 70 in figures 2, 3 and chapter 2.1.2).

Etymology: Named after the site discovered.

Description: Size 55–75 × 25–35 µm in vivo. Lateral view ellipsoidal with ventral margin flattened and dorsal distinctly vaulted, anteriorly occasionally slightly broader rounded than posteriorly; flattened up to 2:1, ventral and dorsal view thus elongate ellipsoidal with slightly projecting preoral suture forming some sort of frontal plate (Fig. 114a, l, m; 365a, b, e, f; Table 93). Macronucleus usually in posterior half of cell, globular, with comparatively large, irregularly shaped nucleoli. Micronucleus usually attached to macronucleus, globular. Contractile vacuole in second quarter of cell, surrounded by contributory vesicles during diastole; excretory pore underneath paroral membrane, about 1.5 µm in diameter, distinct even in vivo. Cytopyge slit in line with excretory pore, extends in posterior body third. Resting trichocysts attached almost perpendicularly to cortex close to left posterior side of kinetids in anterior half of cell and to left anterior side in posterior half of cell, rarely between kineties; protrude slightly from body proper in Austrian and distinctly so in Namibian specimens making the latter somewhat spiny at middle and high magnification; form distinct fringe, fusiform, in vivo about 7 × 0.8 µm in Namibian and 8–10 × 1 µm in

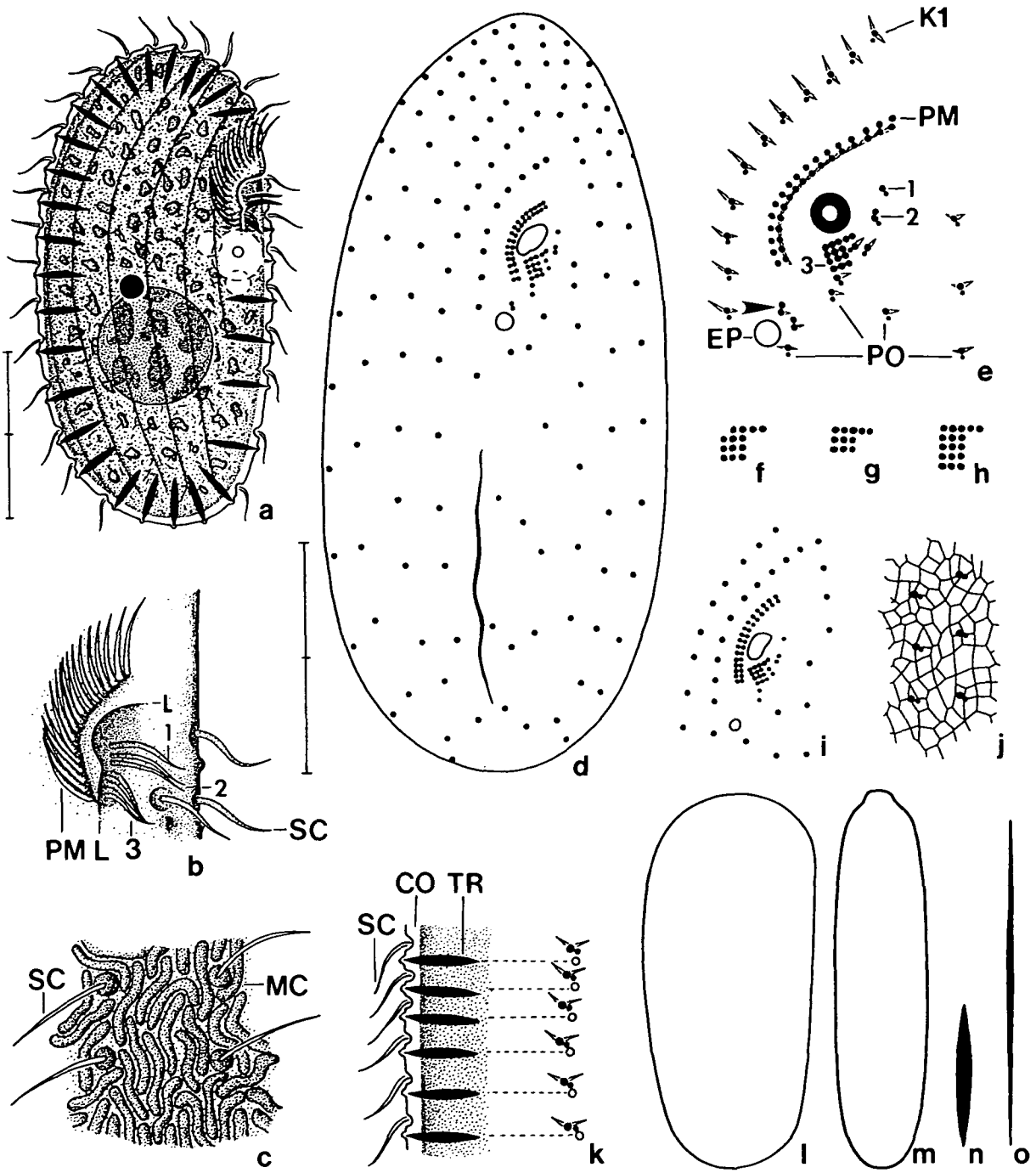


Fig. 114a–o. *Apocolpodidium (Apocolpodidium) etoschense* from life (a–c, l–o), after silver nitrate impregnation (d, i, j), and silver carbonate impregnation (e–h). **a, b:** Right lateral view and oral area of a representative specimen. **c:** Surface view showing the about 5 µm long mitochondria and the deep ciliary pits. **d, i:** Ciliary pattern of ventral side and oral area (combined silver carbonate and silver nitrate preparations). **e:** Infraciliature of oral area. The somatic ciliature consists of monokinetids (large granule is ciliated, small unciliated), except for some dikinetids (arrowhead) around the excretory pore. The nassulid organelles 1 and 2 differ from somatic kinetids in the lack of fibrillar (?) associates. The black ring marks the oral opening. **f–h:** Variability of nassulid organelle 3. **j:** Silverline system. **k:** Schematized optical and tangential section of cortex in anterior body half. **l, m:** Shape variant and ventral view. **n, o:** Resting (7–10 µm long) and exploded (60 µm) trichocyst. 1-3 – nassulid organelles, CO – cortex, EP – excretory pore, K1 – somatic kinety 1, L – lip, MC – mitochondria, PM – paroral membrane, PO – postoral kineties, SC – somatic cilium, TR – trichocyst. Scale bar division 10 µm.

Austrian specimens; fusiform and up to 60 × 1.3 µm when exploded (Fig. 114a, k, n, o; 279–282, 365a–d, g–j). Cortex up to 1 µm thick and bright, distinctly punctated by trichocysts and large ciliary pits; mitochondria close underneath cortex, conspicuous because serpentine and about 5 µm long (Fig. 114c; 365a–c). Cytoplasm colourless and very hyaline, contains 1–5 µm-sized, bright, angular inclusions (possibly compacted spirilli) and, in Austrian specimens, 6–9 µm-sized vacuoles with fine content, possibly remnants of flagellates. Glides moderately rapidly on microscope slide, jerky when trichocysts are extruded.

Somatic cilia only about 5 µm long in vivo, loosened in posterior pole area and underneath paroral membrane; distances between individual cilia increase from anterior to posterior, especially in ciliary rows right of oral opening. Ciliary rows meridionally and equidistantly arranged, abut on frontal plate forming distinct preoral suture. Four basically monokinetidal postoral kineties (Fig. 114d, e, i; 279–282, 365k, l): kinety 1 commences at level and left of oral opening; kinety 2 commences, possibly with two dikinetids, at left side of nassulid organelle 3; kinety 3 commences at distal end of nassulid organelle 3; kinety 4 commences at level of excretory pore of contractile vacuole. Somatic infraciliature composed of monokinetids, except for some dikinetids usually found around the excretory pore of the contractile vacuole. Silver carbonate preparations reveal kinetids to be composed of (i) an irregular (possibly due to attached parasomal sac and/or alveolocyst and/or trichocyst) granule bearing the cilium; (ii) a short structure (kinetodesmal fibre?) extending obliquely anteriad at right side; and (iii) a short structure (transverse fibre?) extending almost perpendicularly to the kinety axis at left side of basal body (Fig. 114e; 365k, l).

Oral apparatus in second quarter of cell. Oral opening marked by heavily argyrophilic ring in silver carbonate preparations, pharyngeal basket, however, recognizable neither in vivo nor in silver preparations. Buccal cavity flatter than in → *Colpodidium* and → *Pedohymena*, conspicuously keyhole-shaped not only due to the sculpturing of the oral cortex but also due to the roughly E-shaped, hyaline lip at right merging into oral cortex anteriorly and into somatic cortex posteriorly (Fig. 114a, b; 279–282, 365a, p; Table 93). Nassulid organelles without distinct fibres, details difficult to recognize, even in excellent preparations (Fig. 114d–i; 279–282, 365i, k, l), due to their small size. Organelle 1 left of buccal entrance, very likely composed of a single basal body. Organelle 2 in buccal cavity, probably comprising two basal bodies. Organelle 3 underneath oral opening in rather deep indentation, orientated obliquely to main body axis, composed of about four ciliary rows, anteriormost row with five basal bodies[16], other rows with three basal bodies each; some variations occur (Fig. 114f–h). Paroral membrane conspicuous even in vivo because of the closely spaced, 5 µm long cilia originating from the right basal body of the dikinetids, extends in flat bow along buccal cavity at base of buccal lip, distinctly set off from somatic ciliary rows, composed of 13–17 dikinetids arranged perpendicularly to kinety axis; left (unciliated) basal body of dikinetids associated with short argyrophilic structure (postciliary microtubule ribbon?) extending parallel to kinety axis posteriad (Fig. 114a, b, d, e, i; 279–282, 365a, b, k–u).

Silverline system as in *Colpodidium caudatum* (FOISSNER 1995), that is, irregularly meshed in somatic and oral cortex producing 2–3 minute polygons between each two ciliary rows; meshes often filled with argyrophilic substance in suboptimal preparations (Fig. 114j).

Ontogenesis: A middle divider was found in the preparations of the Austrian population

[16] The two leftmost basal bodies rather distinctly set off and thus possibly belonging to postoral kinety 2.

(Fig. 365y). It highly resembles middle dividers of → *Colpodidium* and → *Pedohymena* (FOISSNER 1995). A reorganization of the proter's oral apparatus is indicated by the absence of the heavily impregnated ring marking the oral opening and the zigzagging basal bodies in the slightly straightened and shortened paroral membrane. The opisthe's oral apparatus looks very similar to that of the proter, and in both are the three nassulid organelles now clearly recognizable.

Occurrence and ecology: *Apocolpodidium (Apocolpodidium) etoschense* was discovered in highly saline soil from Namibian site (70) and later found in a moderately saline grassland soil (pH 7.9) from the littoral of the Neusiedlersee, a soda lake in the "hell" region near Illmitz, Burgenland, Austria (47°45'N 16°48'E). It was rather abundant at both sites. In spite of the great spatial distance, the Austrian and Namibian specimens match so well that not a single different feature could be found (Fig. 365q, s–y). There are some morphometrical differences which, however, are minute and fall into the range usually encountered in different populations (Table 93). Obviously, *A. etoschense* is a euryhaline cosmopolitan with great morphological stability.

Table 93. Morphometric data on two populations of *Apocolpodidium* (*Apocolpodidium*) *etoschense*: NA – Namibian population, AA – Austrian population.

Characteristics [a]	Pop [a]	Me [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	NA	CHL	61.9	63.0	3.7	1.0	6.0	56.0	69.0	15
	AA	CHL	57.2	58.0	5.1	1.2	8.9	46.0	66.0	19
Body, width in lateral view	NA	CHL	29.9	30.0	3.3	0.9	11.1	25.0	36.0	15
	AA	CHL	25.9	26.0	2.9	0.8	11.3	20.0	31.0	15
Body, width in ventral view	NA	CHL	21.3	21.0	3.5	0.9	16.4	15.0	28.0	15
	AA	CHL	22.5	22.0	1.9	1.0	8.5	21.0	25.0	4
Body length:width, ratio in lateral view	NA	CHL	2.1	2.1	0.2	0.1	8.8	1.8	2.4	15
	AA	CHL	2.2	2.2	0.2	0.1	7.8	1.8	2.4	15
Body length:width, ratio in ventral view	NA	CHL	3.0	2.9	0.5	0.1	18.1	2.1	4.3	15
	AA	CHL	2.6	2.6	0.1	0.1	2.8	2.6	2.7	4
Anterior body end to macronucleus, distance	NA	CHL	30.4	31.0	2.6	0.7	8.4	25.0	34.0	15
	AA	CHL	28.4	28.0	3.9	1.0	13.6	21.0	36.0	16
Anterior body end to excretory pore, distance	NA	CHL	24.1	23.0	2.3	0.6	9.6	20.0	28.0	15
	AA	CHL	21.4	22.0	2.9	1.0	13.7	16.0	24.0	8
Anterior body end to oral opening, distance	NA	CHL	16.5	16.0	1.9	0.5	11.6	13.0	19.0	15
Anterior end to proximal end of paroral, distance [b]	AA	CHL	19.3	20.0	2.9	0.7	15.0	14.0	23.0	19
Macronucleus, length	NA	CHL	9.6	9.0	0.8	0.2	8.6	9.0	11.0	15
	AA	CHL	10.1	10.0	1.6	0.4	16.0	8.0	14.0	16
Macronucleus, width	NA	CHL	7.8	8.0	1.0	0.3	13.0	6.0	10.0	15
	AA	CHL	10.1	10.0	1.6	0.4	16.0	8.0	14.0	16
Micronucleus, diameter	NA	CHL	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
	AA	CHL				no data				
Paroral membrane, length (measured as chord of organelle)	NA	CHL	9.9	10.0	0.5	0.1	4.6	9.0	11.0	15
	AA	CHL	8.7	9.0	1.0	0.2	11.3	6.0	10.0	17
Macronucleus, number	NA	SC	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	AA	SC	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11

(continued)

Characteristics [a]	Pop [a]	Me [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Micronucleus, number	NA	SC	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	AA	SC	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
Somatic ciliary rows, number [c]	NA	SC	17.3	17.0	0.6	0.2	3.4	16.0	18.0	15
	AA	SC	18.9	19.0	–	–	–	18.0	19.0	11
Kinetids in a dorsal kinety, number	NA	SC	14.8	15.0	1.4	0.4	9.6	12.0	17.0	15
	AA	SC	13.6	13.0	1.6	0.5	11.9	11.0	17.0	11
Nassulid organelles, number	NA	SC	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
	AA	SC	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
Large nassulid organelle, number	NA	CHL	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	AA	SC	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
Small nassulid organelles, number	NA	SC	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15
	AA	SC	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
Paroral membrane, number of kinetids	NA	SC	15.9	16.0	1.4	0.4	8.9	13.0	17.0	15
	AA	SC	17.3	17.0	0.9	0.3	5.2	16.0	19.0	11

[a] Data based on silver-impregnated, randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Me – methods, Min – minimum, n – number of individuals investigated, Pop – population, SC – silver carbonate impregnation, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Oral opening not impregnated.

[c] Of 11 Austrian specimens investigated, only one has 18 somatic ciliary rows.

Comparison with similar species: Easily confused, especially in vivo, with other small nassulids because the familial and generic features are difficult to recognize. In silver carbonate preparations most features are recognizable making identification rather easy, except for some small *Parafurgasonia* species, especially *P. protectissima*, as redescribed by FOISSNER (1999b). Indeed, *Parafurgasonia protectissima* and *A. etoschense* are so similar in most respects that it is only the pharyngeal basket (a conspicuous funnel extending posteriorly vs. invisible likely extending anteriorly) which separates them unequivocally in vivo and protargol slides. In vivo, *A. etoschense* differs from *P. protectissima* also by the deeper and more richly structured buccal cavity, especially by the pit containing nassulid organelle 3. *Parafurgasonia terricola* FOISSNER, 1999b lacks trichocysts.

Phagoon nov. subgen.

Diagnosis: Oral apparatus conspicuous, that is, with large, rather deep buccal cavity and long, C-shaped paroral membrane. Trichocysts composed of fusiform shaft and quadripartited head structure.

Type species: *Apocolpodidium* (*Phagoon*) *macrostoma* nov. spec.

Etymology: *Phagoon* is a composite of the Greek substantives *phagon* (feed) and *oon*

(egg), referring to the large mouth and obovoidal body shape of the organism. Actually, the name means a "feeding egg" in analogy of, for instance, a phagocyte. Neuter gender.

Comparison with related genera: *Phagoon* is easily distinguished, even in vivo, from → *Apocolpodidium*, → *Pedohymena*, and → *Colpodidium* by the main subgeneric feature, namely, the very large buccal cavity bordered at right and upper margin by a long, C-shaped paroral membrane.

The compound resting trichocysts of *Apocolpodidium* (*Phagoon*) *macrostoma* are highly remarkable and regarded as a subgeneric feature (Fig. 115k–m; 366a, b, g, i, j). As yet, compound trichocysts were mainly reported from the nassuline order Microthoracida (HAUSMANN 1978). In the exploded state, however, the trichocysts of *Apocolpodidium* (*Phagoon*) *macrostoma* are likely simple spindle trichocysts (Fig. 115n), and thus differ from those of the microthoracids by the lack of the four highly characteristic, spread head structures. However, we cannot exclude to have overlooked small appendages.

Apocolpodidium (*Phagoon*) *macrostoma* nov. spec. (Fig. 115a–o; 286, 366a–m; Table 94)

Diagnosis: Size about 45 × 25 µm in vivo; conspicuously obovoidal. Trichocysts approximately 7 µm long. About 15–17 somatic ciliary rows and 33 paroral dikinetids. Buccal cavity in anterior half of cell. Nassulid organelle 3 composed of about four ciliary rows.

Type location: Soil from the Everglades in Florida, USA, 26°N 81°W.

Etymology: Greek substantive in apposition, referring to the large oral apparatus occupying one third of body length and half of body width.

Description: Size 40–60 × 20–30 µm in vivo. Shape fairly constant and conspicuous, namely, ventral and dorsal view obovoidal with slightly pointed anterior and distinctly tapered posterior end; lateral view ellipsoidal to obovoidal with ventral side usually flattened and dorsal distinctly vaulted (Fig. 115a–d, h; 366a, b; Table 94). Macronucleus uniquely in anterior third of cell, about 13 µm across in vivo and with lobate nucleoli. Micronucleus usually adjacent to macronucleus, globular (Fig. 115a; 366c, d, m). Contractile vacuole underneath mid-body in midline of cell, surrounded by contributory vesicles during diastole; excretory pore in line but distinctly apart from paroral membrane, recognizable also in vivo (Fig. 115a, b; 366a, b). Cytopyge slit underneath excretory pore, extends in posterior body third. Resting trichocysts attached almost perpendicularly to cortex close to left posterior margin of some somatic kinetids in anterior half of cell and to left anterior margin of some kinetids in posterior half of cell; although sparse conspicuous because 7 × 1.0–1.3 µm and thus large compared to size of cell (Fig. 115a; 366a, b, g); shape highly remarkable, that is, composed of fusiform shaft plugging in quadripartited head structure; very slenderly fusiform, 50–70 µm long, and likely lacking appendages (see genus comparison) when exploded (Fig. 115k–n; 366a, b, i, j). Trichocysts do not impregnate with protargol, but their quadripartited head stains, occasionally, intensely with silver carbonate or silver nitrate, producing a peculiar, spotted appearance of impregnated specimens (Fig. 286, 366d, k). Cortex up

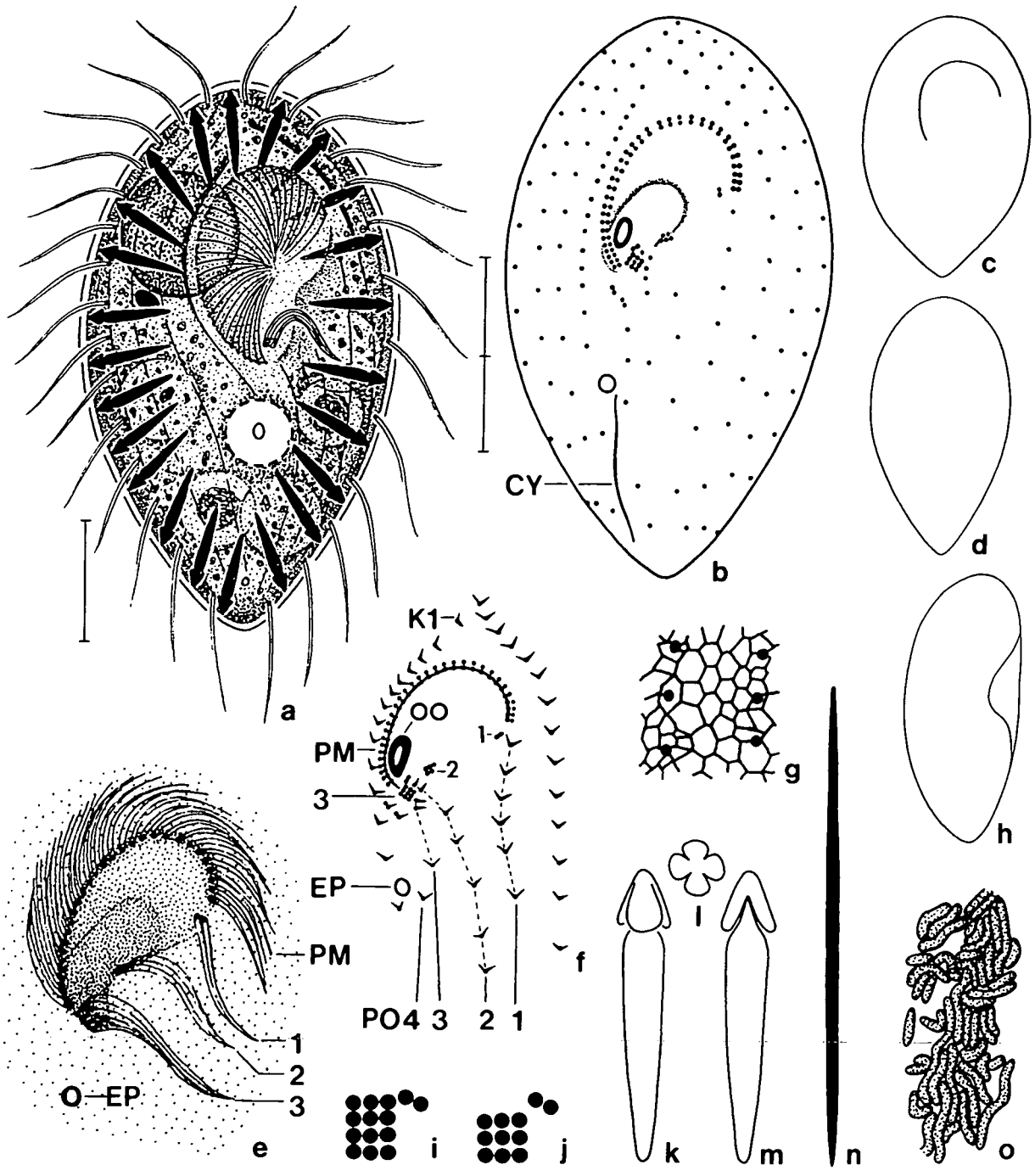


Fig. 115a–o. *Apocolpodidium (Phagoon) macrostoma* from life (a, c–e, h, k–o), after silver nitrate impregnation (b), and silver carbonate/protargol impregnation (b, f, g, i, j). **a:** Ventral view showing the large oral apparatus. **b:** Ciliary pattern of ventral side, composite from various methods. **c, d:** Stout and slender shape variant. **e:** The keyhole-shaped buccal cavity is bordered by the C-shaped paroral and contains the nassulid organelles; whether organelles 1 and 2 are ciliated or barren, has not been observed. **f:** Infraciliature of oral area. **g:** Cortical alveoli (silverline pattern?). **h:** Lateral view showing rather deep buccal cavity. **i, j:** Variability of nassulid organelle 3. **k–m:** Lateral view (k), top view (l), and optical section (m) of 7 µm-long resting trichocysts. **n:** Exploded trichocysts are 50–70 µm long and possibly lack appendages. **o:** Surface view showing serpentine mitochondria. 1-3 – nassulid organelles, CY – cytopyge, EP – excretory pore, K1 – somatic kinety 1, OO – oral opening, PM – paroral membrane, PO1-4 – postoral kineties. Scale bar divisions 10 µm.

to 1 µm thick and bright; mitochondria underneath cortex conspicuous because numerous, serpentine, and up to 10 µm long (Fig. 115o; 366a, g, h). Cells rather dark at low magnification due to countless, 2–3 µm-sized, angular fat inclusions. Food vacuoles 6–10 µm across, appear usually almost empty. Movement without peculiarities.

Somatic cilia about 9 µm long in vivo, not elongated but loosened in posterior pole area because distances between individual cilia increase from anterior to posterior, especially in somatic kinety 1. Ciliary rows meridionally and equidistantly arranged, almost of same length, preoral suture thus indistinct. Four monokinetidal postoral kineties (Fig. 115b, f; 286, 366d, k, l; Table 94): kinety 1 commences underneath left end of paroral membrane; kinety 2 commences, possibly with two dikinetids, at left side of nassulid organelle 3; kinety 3 commences at distal end of nassulid organelle 3; and kinety 4 commences usually underneath dikinetids below right end of paroral membrane. Somatic ciliature composed of monokinetids, except for some dikinetids underneath right end of paroral membrane. Silver carbonate preparations reveal each somatic kinetid to be composed of (i) an irregular (possibly due to attached parasomal sac and/or alveolocyst and/or trichocyst) granule bearing the cilium; (ii) a short structure (kinetodesmal fibre?) extending obliquely anteriad at right side of basal body; and (iii) a short structure (transverse fibre?) extending obliquely anteriad at left side of basal body (Fig. 115f; 286, 366f, l, m).

Oral apparatus in anterior half of cell, conspicuously large, that is, occupies about one third of body length and half of body width. Oral opening near right posterior end of paroral, that is, in right corner of buccal cavity, marked by heavily argyrophilic ring in silver carbonate preparations; pharyngeal basket, however, recognizable neither in vivo nor in silver preparations. Buccal cavity conspicuous because large compared to size of cell and key-hole shaped, that is, broadened anteriorly and narrowed posteriorly; consists of a flat portion extending wedge-like from right to left end of paroral and a smaller, ellipsoidal, rather abruptly deepened part containing nassulid organelle 3 and oral opening in right corner (Fig. 115a, e; 286, 366a, b, d, g; Table 94). Nassulid organelles without distinct fibres, details difficult to recognize due to their small size (Fig. 115b, f, i, j; 286, 366d–f, k, l). Nassulid organelle 1 at left slope of buccal entrance underneath left end of paroral membrane, minute because consisting of only two granules lighter impregnated than paroral and somatic kinetids. Nassulid organelle 2 at posterior slope of buccal cavity, close to organelle 3, appears as heavily impregnated, obliquely orientated, rectangular structure in silver carbonate preparations, probably composed of about five basal bodies. Nassulid organelle 3 underneath oral opening in rather deep and narrow indentation, orientated obliquely to main body axis, composed of four ciliary rows, anteriormost row with five basal bodies[17], other rows with three basal bodies each; occasionally, the three rightmost basal bodies of the anteriormost row apparently lacking (Fig. 115i, j). Paroral membrane very conspicuous because long and C-shaped, extends along upper and right slope of buccal entrance, composed of about 31–35 dikinetids orientated perpendicularly to kinety axis and having only one basal body ciliated; left (unciliated) basal body of dikinetids associated with short argyrophilic structure (postciliary microtubule ribbon?) extending parallel to kinety axis posteriad; distances between dikinetids increase slightly from right to left (Fig. 115a, f; 286, 366d–g).

Silverline system as in *Colpodidium caudatum* (FOISSNER 1995), that is, irregularly meshed in

[17] The two leftmost basal bodies are rather distinctly set off and thus possibly belong to postoral kinety 2.

somatic and oral cortex, producing about four polygons between each two ciliary rows (Fig. 115g; 366k, m).

Occurrence and ecology: To date found only in a sample collected by Miss Gerlinde FISCHER near the "Pine Trail" in the Everglades of Florida (USA) in 1990. The sample, in which the species was rather rare, was a mixture of conifer needles, mosses, lichens, and soil particles. As this is a conspicuous species, it is unlikely that we overlooked it in any of the 1000 other soil samples studied, suggesting that it is either extremely rare and/or has a restricted geographic distribution.

Comparison with related species: *Apocolpodidium* (*Phagoon*) *macrostoma* is easily distinguished from all other colpodidiids and furgasoniids by the large oral apparatus and the location of the nuclear apparatus in the anterior third of the cell. Its obovoidal body shape is similar to that of → *Colpodidium* (*Pseudocolpodidium*) *bradburyarum* and → *Wolfkosia loeffleri*: the former lacks trichocysts and has a distinctly smaller oral apparatus with a pocket-shaped buccal cavity; the latter has a comparatively inconspicuous oral apparatus with a rather distinct pharyngeal basket.

Table 94. Morphometric data on *Apocolpodidium* (*Phagoon*) *macrostoma*.

Characteristics [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	CHL	45.4	45.0	5.4	1.4	11.9	39.0	60.0	15
Body, width	CHL	24.1	24.0	3.3	0.8	13.6	19.0	33.0	15
Body length:width, ratio	CHL	1.9	1.9	0.1	0.0	6.9	1.7	2.1	15
Anterior body end to macronucleus, distance	CHL	6.5	6.0	1.5	0.4	22.5	4.0	9.0	15
Anterior body end to excretory pore, distance	CHL	27.3	28.0	2.6	0.7	9.3	21.0	31.0	15
Anterior body end to nassulid organelle 3, distance	CHL	19.2	19.0	1.2	0.3	6.3	16.0	21.0	15
Anterior body end to summit of paroral, distance	CHL	8.1	8.0	1.1	0.3	13.0	6.0	10.0	15
Macronucleus, length	PA	9.2	9.0	0.8	0.2	8.4	8.0	10.0	15
Macronucleus, width	PA	8.1	8.0	0.6	0.2	7.9	7.0	9.0	15
Micronucleus, length	PA	2.2	2.0	–	–	–	2.0	3.0	15
Micronucleus, width	PA	2.1	2.0	0.5	0.1	22.1	1.0	3.0	15
Paroral membrane, length (≅ chord of bow)	CHL	13.9	14.0	0.7	0.2	5.1	13.0	15.0	15
Macronucleus, number	PA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Micronucleus, number	PA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Somatic ciliary rows, number	SC	16.3	16.5	1.0	0.5	5.9	15.0	17.0	4
Kinetids in a dorsal kinety, number	SC	10.4	11.0	0.9	0.4	8.6	9.0	11.0	5
Paroral membrane, number of dikinetids	SC	32.6	31.0	2.0	0.8	6.1	31.0	35.0	7

[a] Data based on silver-impregnated, randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, PA – protargol impregnation (FOISSNER's method), SC – silver carbonate impregnation, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

HYMENOSTOMATA

Frontonia EHRENBERG, 1838

Four *Frontonia* species or subspecies occur in the Etosha Pan region. At first glance, three of them look rather similar, especially because they have several excretory pores. However, more detailed investigations provide sufficient features for a reliable separation (Table 95). *Frontonia depressa*, which is very common in many soils world-wide, occurs in Namibia only at site 66 (Table 4). *Frontonia depressa* and its junior synonym, *F. parvula*, are easily distinguished from the other species by the single excretory pore (Fig. 116a, b; FOISSNER 1987b, GIL & PÉREZ-SILVA 1964b, KAHL 1931, ROQUE 1961a). We introduce the shape of the postoral suture in alpha-taxonomy of *Frontonia*. With this simple and easy-to-use feature, → *F. terricola* can be clearly distinguished from the other species mentioned in table 95 (Fig. 116b, d, 117i, 118o; 367a–l). The shape of the preoral suture, in contrast, varies only slightly and its orientation is influenced by the angle the cell is viewed. Furthermore, details of the oral structures, which are increasingly used in species definitions of *Frontonia*, are doubtful in our experience because highly dependent on the methods used and at the limits of microscope resolution (Fig. 368h).

Table 95. Comparison of main features of → *Frontonia angusta solea*, → *F. angusta obovata*, → *F. terricola*, and *F. depressa*.

Characteristics [a]	*Frontonia angusta solea*	*Frontonia angusta obovata*	*Frontonia terricola*	*Frontonia depressa* [b]
Body size, range	74–100 x 31–58	99–146 x 46–104	64–98 x 33–54	74–93 x 25–40
Body length, mean	86	122	82	83
Body shape, in vivo	elongate obovoidal with rounded anterior end, distinctly flattened	obovoidal with truncate anterior end, unflattened	obovoidal with truncate anterior end, slightly flattened	ellipsoidal with rounded anterior end, slightly flattened
Buccal cavity, length	16–20 ($\bar{x}$ = 18)	24–29 ($\bar{x}$ = 26)	33–39 ($\bar{x}$ = 36)	16–18 ($\bar{x}$ = 17)
Buccal cavity, mean length in % of mean body length	21	26	43	21
Postoral suture, dorsal portion	distinct, obliquely orientated stripe	distinct, obliquely orientated stripe	indistinct line parallel to main body axis merging into small, blank, area	distinct, obliquely orientated stripe
Somatic ciliary rows, number	56–66 ($\bar{x}$ = 62)	83–101 ($\bar{x}$ = 92)	64–78 ($\bar{x}$ = 68)	57–62 ($\bar{x}$ = 60)
Excretory pores, number	2–4 ($\bar{x}$ = 3)	3–6 ($\bar{x}$ = 5)	2–5 ($\bar{x}$ = 4)	1

[a] Data based, if not otherwise stated, on mounted, CHATTON-LWOFF silver nitrate-impregnated, and randomly selected specimens from non-flooded Petri dish cultures of Namibian soils. Measurements in µm. Further morphometrics, see tables 98, 99, 100.

[b] Austrian population investigated by FOISSNER (1987b).

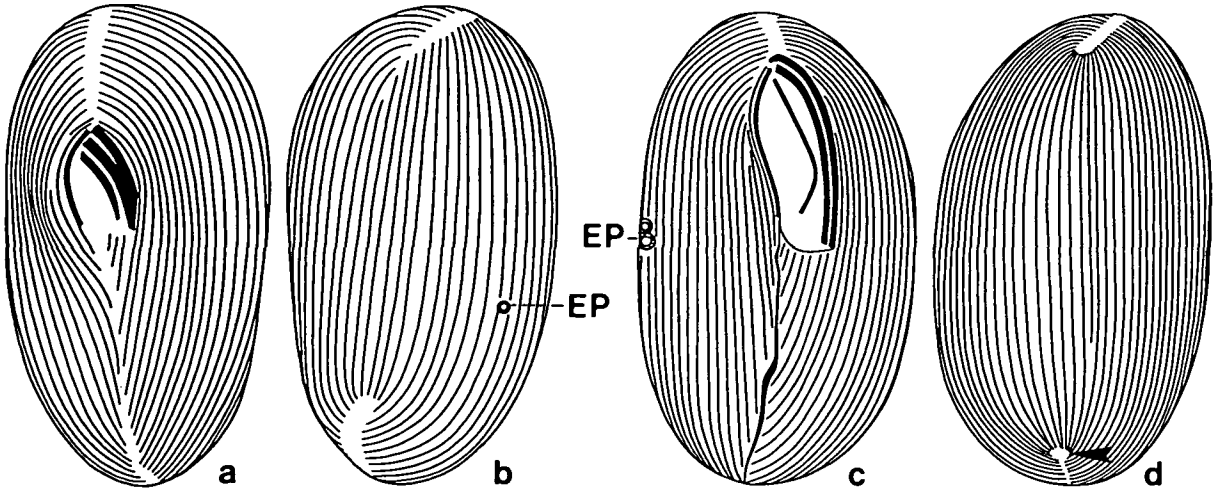


Fig. 116a–d. Features distinguishing *Frontonia* species occurring in Namibia. **a, b:** *Frontonia depressa* (original from Austrian population) is easily distinguished from the other species by the single excretory pore. **c, d:** *Frontonia terricola* (original from Namibian specimen) has several excretory pores and a disproportionally large oral apparatus occupying about 40% of body length. Furthermore, it is the sole species where the dorsal portion of the postoral suture (arrowhead) is very inconspicuous because it ends in the posterior pole area. EP – excretory pores.

Frontonia angusta KAHL, 1931

1922 *Frontonia acuminata* (EHRENB.) BÜTSCHLI 1889 — PENARD, Études Infusoires: 139 (partim, Fig. 9).

1931 *Frontonia acuminata* var. *angusta* KAHL, Tierwelt Dtl., 21: 320.

1994 *Frontonia angusta* KAHL, 1931 — FOISSNER, BERGER & KOHMANN, Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft, 1/94: 160 (raised to species status and redescribed).

Improved diagnosis: Size about 80–150 × 35–110 µm in vivo. Shape obovoidal with rounded or truncate anterior end, or elongate obovoidal with rounded anterior end; unflattened with buccal cavity in midline, or more or less distinctly (up to 4:1) flattened with buccal cavity near body margin in gliding specimens. Single contractile vacuole with 2–6 excretory pores. 56–105 ciliary rows including 2–5 postoral kineties. Dorsal portion of postoral suture a distinct, oblique stripe. Usually 4 vestibular kineties. Peniculus 3 slightly curved.

Remarks: We split *F. angusta* into three subspecies with similar main features (several excretory pores, same pattern of postoral suture, similar size of body and oral apparatus), but

distinctly different details (Fig. 367d–l; Table 96). The most important of these is body shape, which is so different that the subspecies are rather easily distinguished. We are aware that this is a problematic feature, often highly dependent on nutrition. However, the general appearance of, for instance, → *F. angusta solea* and → *F. angusta obovata* is so different in vivo that they look like different species, although it is mainly body flattening which produces this appearance. Certainly, there are also quite a lot of morphometric differences, some of which do not even overlap, between these subspecies (Table 96). However, they must be handled with care because *Frontonia* species, for instance, *F. leucas*, are highly variable (FOISSNER et al. 1994).

Frontonia acuminata differs from its former variety *angusta* by the pigment patch in the anterior dorsal side and the cap-shaped transverse body outline (FOISSNER et al. 1994, KAHL 1931b). The pigment patch, an accumulation of highly refractive granules, and the acuminate posterior body end are highly characteristic features found in all "typical" *F. acuminata* populations. Thus, *F. acuminata* and *F. acuminata angusta*, which lacks these characteristics, should be separated at species level.

FOISSNER et al. (1994) suppose *Frontonia bullingtoni* DRAGESCO, 1960 and *F. roqueae* DRAGESCO, 1970 (nom. corr. for *F. roquei* DRAGESCO, 1970) to be synonyms of *F. angusta*. Synonymy, however, need to be substantiated by more detailed investigations.

Table 96. Main morphometrics of → *Frontonia angusta angusta* (from FOISSNER et al. 1994 and unpubl.), → *F. angusta solea* (Namibian population), and → *F. angusta obovata* nov. sspec.

Characteristics [a]	*F. angusta angusta*	*F. angusta solea*	*F. angusta obovata*
Body size, range	90–135 x 40–77	74–100 x 31–58	99–146 x 46–104
Body length, mean	115	86	122
Body, mean length:width ratio	1.9:1	2.1:1	1.8:1
Body shape, in vivo	obovoidal with rounded anterior end, slightly to distinctly flattened	elongate obovoidal with rounded anterior end, distinctly flattened	obovoidal with truncate anterior end, unflattened
Somatic ciliary rows, number	80–105 ($\bar{x}$ = 94)	56–66 ($\bar{x}$ = 62)	83–101 ($\bar{x}$ = 92)
Postoral kineties, number	4–5 ($\bar{x}$ = 4)	3–4 ($\bar{x}$ = 3)	2–4 ($\bar{x}$ = 2)
Vestibular kineties, number	4	4	4
Postoral suture, length of dorsal portion	long, extending to posterior fifth of cell	short, extending to posterior eighth of cell	long, extending to posterior fifth of cell
Buccal cavity, length	21–42 ($\bar{x}$ = 27)	16–20 ($\bar{x}$ = 18)	24–29 ($\bar{x}$ = 26)
Buccal cavity, mean length in % of mean body length	23	21	26
Excretory pores, number	2–4 ($\bar{x}$ = 3)	2–4 ($\bar{x}$ = 3)	3–6 ($\bar{x}$ = 5)

[a] Data based, if not otherwise stated, on mounted, CHATTON-LWOFF silver nitrate-impregnated, and randomly selected specimens from non-flooded Petri dish cultures of Namibian soils. Measurements in µm. Further morphometrics, see tables 97, 98, 99.

Frontonia angusta angusta KAHL, 1931 **nov. stat.** (Fig. 118p, q; 367j–l; Tables 96, 97)

Neotype material: Neotypified from a population of an ephemeral meadow puddle in the surroundings of Salzburg, Austria (47°N 13°E), according to reasons 1, 3, 4, 6 given in chapter 2.4.2.

Improved diagnosis: Size about 125 × 65 µm in vivo. Obovoidal with rounded anterior end, flattened up to 2:1. On average 3 excretory pores and 94 ciliary rows. Buccal cavity near body margin in gliding specimens, in vivo about 30 µm long occupying about one fourth of body length.

Table 97. Morphometric data on *Frontonia angusta angusta* (from FOISSNER et al. 1994 and unpubl.).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	115.7	117.0	12.1	2.2	10.4	90.0	135.0	29
Body, width in lateral view	61.0	60.0	9.8	1.8	16.1	40.0	77.0	29
Body length:width, ratio in lateral view	1.9	1.9	0.3	0.0	13.1	1.5	2.6	29
Anterior body end to anteriormost excretory pore, distance	56.0	56.0	6.2	1.4	11.1	45.0	68.0	19
Anterior body end to buccal cavity, distance	22.0	21.0	2.9	0.7	13.2	18.0	28.0	19
Buccal cavity, length	26.9	27.0	4.7	1.1	17.3	21.0	42.0	19
Posterior body end to proximal dorsal end of postoral suture, distance	22.2	21.0	7.7	2.0	34.5	14.0	39.0	15
Macronucleus, length	23.7	23.5	5.6	1.1	23.4	15.0	34.0	26
Macronucleus, width	17.7	17.0	4.7	0.9	26.5	8.0	29.0	26
Micronucleus, length	4.2	4.0	0.6	0.2	15.1	3.0	5.0	10
Micronucleus, width	3.6	3.5	0.7	0.2	19.4	3.0	5.0	10
Peniculus 1, length (chord of organelle)	26.8	27.0	1.5	0.4	5.5	24.0	28.0	14
Peniculus 2, length (chord of organelle)	24.9	25.0	1.7	0.5	6.9	21.0	28.0	14
Peniculus 3, length (chord of organelle)	20.1	20.5	1.5	0.4	7.5	17.0	22.0	14
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	25
Micronuclei, number	1.1	1.0	–	–	–	1.0	2.0	16
Excretory pores, number	2.8	3.0	0.6	0.1	22.6	2.0	4.0	26
Somatic ciliary rows, number [b]	94.1	96.0	8.3	2.1	8.8	80.0	105.0	15
Postoral kineties, number	4.1	4.0	–	–	–	4.0	5.0	14
Vestibular kineties, number	3.9	4.0	–	–	–	3.0	4.0	15
Peniculus 1, number of ciliary rows	4.7	5.0	0.6	0.2	13.0	4.0	6.0	14
Peniculus 2, number of ciliary rows	4.6	4.5	0.6	0.2	14.1	4.0	6.0	14
Peniculus 3, number of ciliary rows	4.2	4.0	–	–	–	4.0	5.0	14

[a] Data based on mounted, CHATTON-LWOFF silver nitrate-impregnated, and randomly selected specimens from a culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Including postoral kineties but without vestibular kineties.

Locus classicus: Außenalster, Hamburg (Germany), where KAHL (1931b) discovered *F. angusta angusta* in mud.

Remarks: Redescribed by FOISSNER et al. (1994). Here, we provide the complete morphometry and some additional observations of a cultivated population from a meadow puddle in the surroundings of Salzburg, Austria. These specimens are in fact rather similar to → *Frontonia angusta obovata*. However, the body is usually less obovate and wide, and the anterior region is never as truncate as in → *F. angusta obovata*. Furthermore, the cells are slightly to strongly flattened, shifting the oral apparatus to the body margin in gliding specimens (Fig. 118p, q; 367j–l).

Frontonia angusta solea FOISSNER, 1987 **nov. stat.** (Fig. 117a–p; 367g–i, 368a–g; Tables 96, 98)

1987 *Frontonia solea* FOISSNER, Sber. Akad. Wiss. Wien, 195: 257.

Improved diagnosis (original data plus Namibian population): Size about 100 × 45 µm in vivo. Elongate obovoidal with rounded anterior end, flattened up to 4:1. On average 3 excretory pores and 60 ciliary rows. Buccal cavity near body margin in gliding specimen, in vivo about 20 µm long occupying about one fifth of body length.

Locus classicus: Elisabethfelsen in Carinthia (Austria), where FOISSNER (1987b) discovered *F. angusta solea* in mosses surrounding puddle 72 in FOISSNER (1980a).

Redescription: Size about 90–130 × 35–60 µm in live cells from Austria (FOISSNER 1987[18]) and 74–100 × 31–58 µm in silver nitrate-impregnated specimens from Namibia. In vivo obovoidal with narrowly rounded posterior and broadly rounded, never truncate anterior end; distinctly (up to 4:1) flattened laterally, flattening, as is usual, rarely preserved in silver preparations, where shape is rather variable: obovoidal to elongate obovoidal or ellipsoidal to elongate ellipsoidal; length:width ratio 1.6–2.5:1, usually 2.1:1 in lateral view (Fig. 117a–c, g–i, m, n; 367g–i, 368a, b, e–g; Table 98). Nuclear apparatus usually in anterior body half. Macronucleus ellipsoidal, about 35 × 18 µm in live specimens from Austria, 21 × 12 µm in prepared Namibian specimens; nucleoli approximately 3 µm across. Micronucleus in anterior or lateral indentation of macronucleus, about 7 µm across in live cells from Austria, while only 3 × 2 µm in silver nitrate-impregnated specimens from Namibia. Contractile vacuole with 2–4 excretory pores slightly underneath mid-body in Austrian and slightly above mid-body in Namibian specimens; surrounded by contributory vesicles during diastole, but without collecting canals. Cytopyge extends in ventral portion of postoral suture. Resting extrusomes form conspicuous fringe because attached almost perpendicularly to cortex between each two kinetids of a ciliary row (see also below), fusiform and about 7 µm long; occasionally impregnate with protargol, where they are broadly fusiform. Exploded extru-

[18] Scale bar of figure 35a in FOISSNER (1987b) not 50 µm, as stated in the figure explanation, but 35 µm.

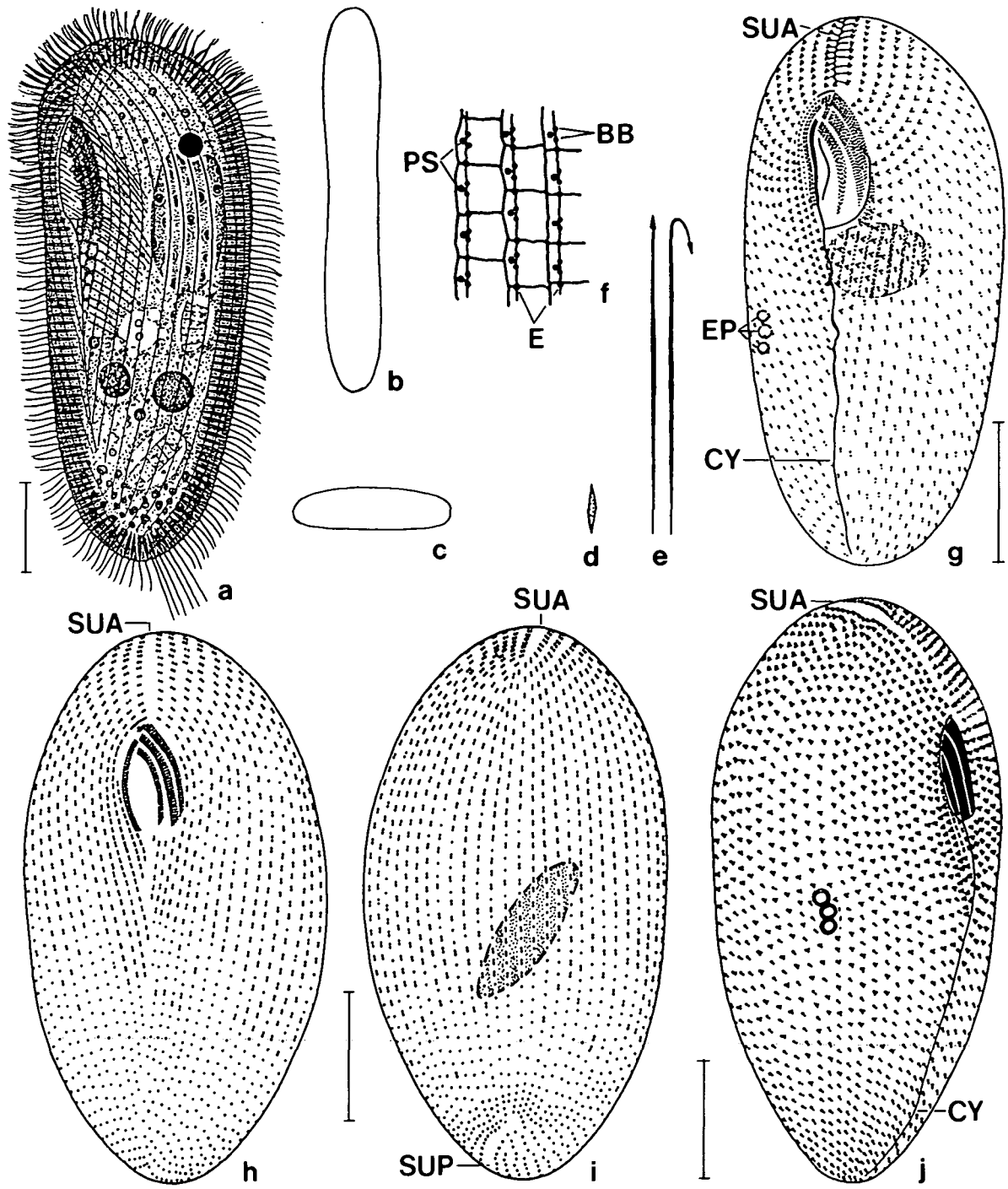


Fig. 117a–j. *Frontonia angusta solea* from life (a–e), after KLEIN-FOISSNER (f) and CHATTON-LWOFF (g, j) silver nitrate impregnation, and protargol impregnation (h, i). Austrian type (a–g; from FOISSNER 1987b) and Namibian (h–j) population. **a–c:** Ventrolateral, dorsal, and transverse view. Note the slightly elongated caudal cilia (a). **d, e:** Resting (d) and exploded (f) extrusomes. **f:** Silverline system. **g:** Ciliary pattern of ventral side showing (dorso) laterally situated excretory pores. Note the herring-bone pattern of the silverlines in the preoral suture. **h, i:** Ciliary pattern of ventral and dorsal side of same specimen. Note the variegated appearance due to the mixed occurrence of monokinetids and dikinetids. **j:** Right side view showing ciliary pattern and excretory pores. BB – basal bodies, CY – cytopyge, E – extrusome attachment sites, EP – excretory pores, PS – parasomal sacs, SUA – preoral suture, SUP – postoral suture. Scale bars 20 µm.

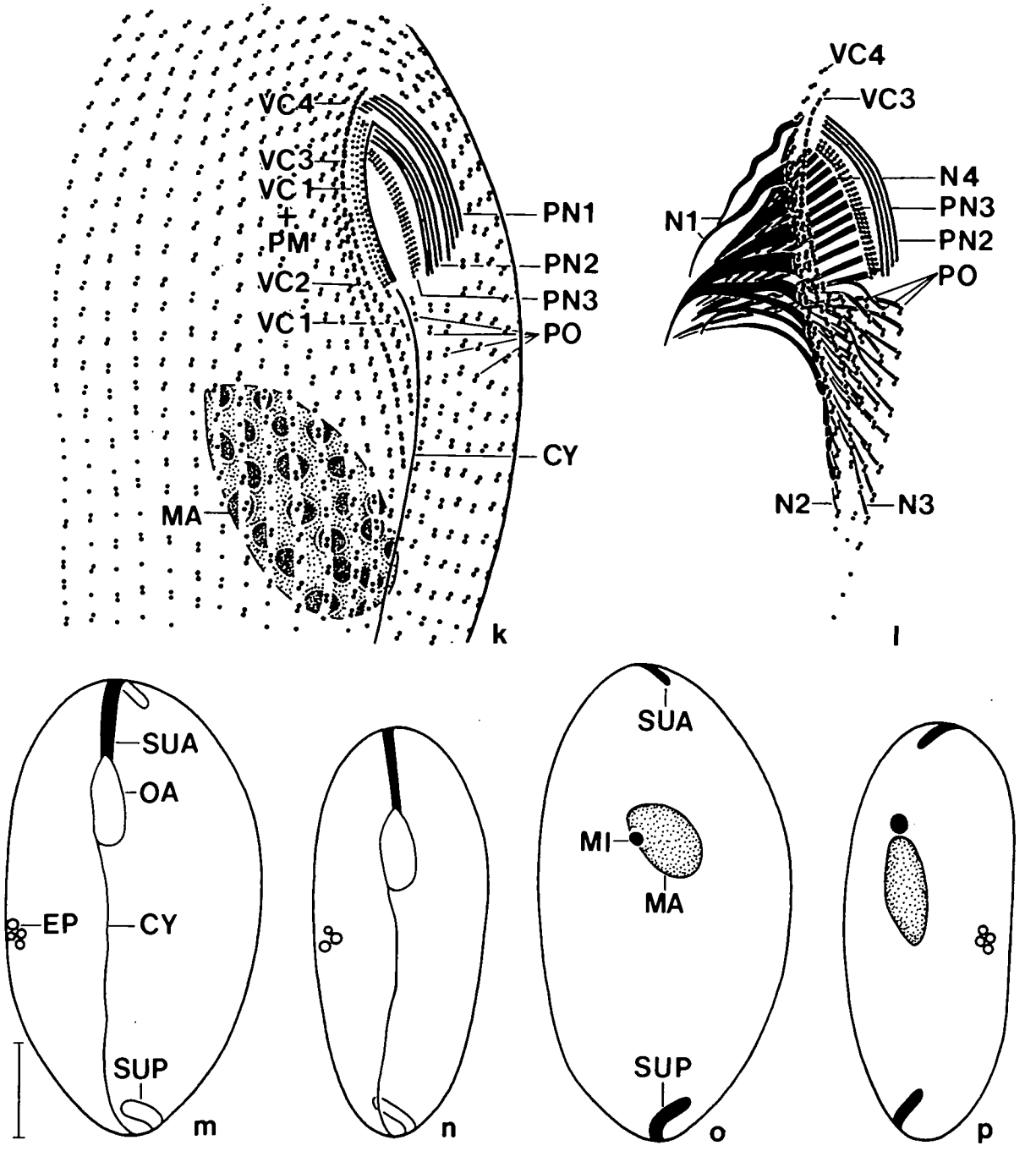


Fig. 117k–p. *Frontonia angusta solea*, Namibian specimens after protargol (k, l) and silver nitrate (m–p) impregnation. **k, l:** Oral infraciliature at two focal planes showing thick nematodesmata commencing underneath vestibular kinety 4 (N1) and peniculus 3 (N4) as well as fine fibre bundles originating from kinetids in posterior portion of vestibular kineties (N2) and anterior portion of postoral kineties (N3). The paroral and anterior portion of vestibular kinety 1 were removed from figure (l) to show the nematodesmata of peniculus 3 more clearly. **m–p:** Ventral (m, n), left lateral (o), and right lateral (p) views showing variability of body shape and sutures as well as location of main cell organelles. CY – cytopyge, EP – excretory pores, MA – macronucleus, MI – micronucleus, N1-4 – nematodesmata, OA – oral apparatus, PM – paroral, PN1-3 – peniculi, PO – postoral kineties, SUA – preoral suture, SUP – postoral suture, VC1-4 – vestibular kineties. Scale bar 20 µm.

somes filiform, about 50 µm long, with small, conical tip; occasionally bent hook-like in anterior portion (Fig. 117d, e). Cortex bright and rigid, except for postoral region, where cells easily rupture under cover glass pressure. Cytoplasm without special inclusions, contains yellow-green granules mainly in posterior portion and some large fat globules. Feeds on filamentous cyanobacteria, in Namibia also on pennate diatoms up to 31 µm long and testate amoebae. Movement without peculiarities.

Somatic cilia about 8 µm long in vivo, except for slightly elongated caudal cilia. 50–66 meridional, equidistant ciliary rows form a suture in ventral midline of cell (Fig. 117g–j, m–p; Table 98). Preoral suture commences at vertex of buccal cavity and extends straight ahead across anterior pole terminating subapically on dorsal side, about 2–2.5 µm wide. Postoral suture extends as a line from right posterior corner of buccal cavity to rear end, where it widens to 2–2.5 µm, passes the pole, and ends subterminally as counter-clockwise inclined stripe. Ventral kineties shorten gradually from both cell ends to oral apparatus, abut obliquely on both sutures, except for three or four postoral kineties commencing underneath buccal cavity. Dorsal ciliary rows almost bipolar, except for those extending between sutures. Cilia paired in oral body portion, some pairs also postorally, as revealed by protargol impregnation and scanning electron microscopy (Fig. 117h, i; 368a, b). Silver carbonate impregnations show (Fig. 368c): (i) a curious impregnation attribute of the dikinetids, viz., only the basal body with the kinetodesmal fibre impregnates, although both are ciliferous; (ii) distinct kinetodesmal fibres decreasing in length from anterior to posterior; (iii) vestibular and postoral kinetids more heavily impregnated than ordinary kinetids, possibly because associated with unstained nematodesmata; and (iv) fine fibres originating from the peniculi.

Oral apparatus about 17% back from anterior body end and near body margin in gliding specimens due to distinct body flattening, about 25 µm long in live specimens from Austria, about 20 µm long in Namibian population. Buccal cavity pointed arch-shaped, symmetrical, with three almost parallel, slightly curved peniculi (adoral membranelles, ophryokineties) on left wall and paroral and vestibular kineties on right. Peniculus 1 about 18 µm long, anteriorly curved hook-like to right side of cavity, composed of four or five rows of basal bodies posteriorly gradually shortened from right to left. Peniculus 2 about 15 µm long, composed of five kineties in Austrian and three or four in Namibian specimens, posteriorly gradually shortened from right to left; slightly separated anterior portion recognizable only in two out of eight Namibian specimens. Peniculus 3 about 13 µm long, composed of three or four kineties gradually shortened from right to left. Paroral membrane commences ahead of peniculus 3 and extends along right margin of buccal cavity, composed of two rows of very closely spaced basal bodies (Fig. 117g, h, k; 368a–d; Table 98).

Vestibular kineties posteriorly gradually shortened from right to left and thus obliquely abutting on postoral suture, composed of rather closely spaced dikinetids, except for distal portion of kineties 3 and 4, where dikinetids are usually very densely, respectively, normally (as in somatic kineties) spaced (Fig. 117g, h, j, k; 368c). Orientation of dikinetids (oblique or parallel to kinety axis) was studied very carefully and proved to be highly variable for unknown reasons (Fig. 117h, k). Parasomal sacs recognizable only in kinety 4 and proximal portion of other vestibular kineties. First kinety easily overlooked because, as in many congeners (BERAN 1990, GIL & PÉREZ-SILVA 1964a, b, ROQUE 1961a, b, c, ROQUE & PUYTORAC 1972), very close to paroral membrane, longer than paroral by 2–5 kinetids and thus terminating about 38% back from anterior body end. Second kinety commences in five of nine Namibian specimens near distal end of peniculus 1 and terminates about 44% back

Table 98. Morphometric data on *Frontonia angusta solea* from Namibian site (65).

Characteristics [a]	Me [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	CHL	86.5	86.0	6.0	1.1	7.0	74.0	100.0	30
Body, width in lateral view	CHL	42.4	41.0	7.4	1.9	17.5	31.0	58.0	15
Body, width in ventral view	CHL	43.2	40.0	5.5	1.4	12.7	36.0	56.0	15
Body length:width, ratio in lateral view	CHL	2.1	2.2	0.2	0.1	11.7	1.7	2.5	15
Body length:width, ratio in ventral view	CHL	2.0	2.0	0.2	0.1	11.3	1.6	2.3	15
Anterior end to anteriormost excretory pore, distance	CHL	41.9	43.0	2.4	0.6	5.8	36.0	45.0	15
Anterior end to macronucleus, distance	CHL	26.4	25.0	7.8	2.0	29.4	16.0	45.0	15
Anterior end to buccal cavity, distance	CHL	14.3	14.0	1.5	0.4	10.4	10.0	16.0	15
Anterior end to posterior end of vestibular kinety 1, distance	CHL	33.3	33.0	1.4	0.4	4.3	31.0	35.0	15
Anterior end to posterior end of vestibular kinety 2, distance	CHL	38.0	38.0	1.5	0.4	3.9	35.0	40.0	15
Anterior end to posterior end of vestibular kinety 3, distance	CHL	43.1	43.0	1.4	0.4	3.3	40.0	45.0	15
Anterior end to posterior end of vestibular kinety 4, distance	CHL	46.5	46.0	1.6	0.4	3.3	44.0	49.0	15
Buccal cavity, length	CHL	17.9	18.0	1.2	0.3	6.6	16.0	20.0	15
Posterior body end to posterior dorsal end of postoral suture, distance	CHL	10.7	11.0	1.7	0.4	15.7	8.0	14.0	15
Macronucleus, length	PA	20.8	20.0	3.3	0.9	16.1	16.0	28.0	15
Macronucleus, width	PA	11.7	11.0	1.6	0.4	13.8	10.0	15.0	15
Micronucleus, length	PA	2.7	3.0	0.6	0.2	21.7	2.0	4.0	15
Micronuclei, width	PA	2.1	2.0	1.1	0.3	53.2	1.0	4.0	15
Peniculus 1, length (chord of organelle)	CHL	17.8	18.0	1.1	0.3	6.4	16.0	20.0	15
Peniculus 2, length (chord of organelle)	CHL	15.3	15.0	0.9	0.2	5.9	14.0	17.0	15
Peniculus 3, length (chord of organelle)	CHL	13.4	13.0	0.6	0.2	4.7	13.0	15.0	15
Macronucleus, number	PA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Micronucleus, number	PA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Excretory pores, number	CHL	3.4	3.0	0.6	0.2	18.6	2.0	4.0	15
Somatic ciliary rows, number [b]	CHL	61.7	62.0	3.0	0.8	4.8	56.0	66.0	15
Postoral kineties, number	CHL	3.3	3.0	–	–	–	3.0	4.0	15
Vestibular kineties, number	CHL	4.0	4.0	0.0	0.0	0.0	4.0	4.0	15
Peniculus 1, number of ciliary rows [c]	CHL	4.4	4.0	–	–	–	4.0	5.0	5
Peniculus 2, number of ciliary rows [c]	CHL	3.8	4.0	–	–	–	3.0	4.0	5
Peniculus 3, number of ciliary rows [c]	CHL	3.4	3.0	–	–	–	3.0	4.0	5

[a] Data based on mounted, silver-impregnated, and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Me – methods, Min – minimum, n – number of individuals investigated, PA – protargol impregnation (FOISSNER's method), SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Including postoral kineties but without vestibular kineties.

[c] Only five properly orientated and well-impregnated specimens were found.

from anterior body end; in other specimens probably anteriorly shortened commencing near level of mid-buccal cavity (Fig. 117h, k). Third kinety commences above buccal vertex and terminates at about mid-body. Fourth kinety commences above buccal vertex and usually terminates 54% back from anterior body end (Table 98).

Fibrillar apparatus associated with oral and postoral ciliature after protargol impregnation similar as described by DIDIER (1970), that is, consists of (i) very thick nematodesmata separated from proximal end of basal bodies of vestibular kinety 4 by a minute unstained gap; (ii) thick nematodesmata separated from proximal end of basal bodies of peniculus 3 by a minute unstained gap; and (iii) rather fine fibre bundles associated with kinetids of at least anterior portion of postoral kineties and posterior portion of vestibular kineties (Fig. 117k, l). Kinetids of postoral and vestibular kineties contribute to oral basket, and are thus oralized somatic kinetids in the sense of FOISSNER & FOISSNER (1988).

Silverline system only recognizable in dry silver nitrate impregnations of Austrian population, composed of (i) silverlines in cortical ridges forming longitudinal rows of tetra- to polygonal meshes and (ii) longitudinal silverlines connecting the regularly alternating kinetids and extrusome attachment sites, dividing each mesh into a small right and a broad left portion (Fig. 117f).

Occurrence and ecology: *Frontonia angusta solea* was discovered in wet mosses from Austria. In Namibia, it occurred at sites (65) and (70), that is, in highly saline, alkaline, occasionally flooded soils. The species is obviously rare but euryhaline and cosmopolitan.

Comparison with related species: The original description of *Frontonia solea* bases mainly on live observations of an Austrian population and does not provide detailed morphometrics (FOISSNER 1987b). When this species was established, FOISSNER (1987b) definitely stated the similarity to *F. angusta* KAHL, 1931b, which, however, was still poorly known at that time. With the new data available (Table 98 and FOISSNER et al. 1994), it turns out that *F. solea* is best considered as a subspecies of → *F. angusta*. In vivo, *F. angusta solea* is rather easily distinguished from → *F. angusta angusta* and → *F. angusta obovata* by the elongate, distinctly flattened body, a feature unfortunately often lost in preparations. Furthermore, *solea* is the smallest of the three subspecies and thus has distinctly fewer ciliary rows (< 70 vs. > 90; Table 96).

Frontonia angusta obovata **nov. sspec.** (Fig. 118a–k, m–o; 367d–f, 369a–i; Tables 96, 99)

Diagnosis: Size about 125 × 70 µm in vivo. Obovoidal with truncate anterior region. On average 5 excretory pores and 92 ciliary rows. Buccal cavity in body midline in gliding specimens, in vivo approximately 30 µm long occupying about one fourth of body length.

Type location: Slightly saline soil from Etosha National Park, Namibia, 19°S 15°40'E (site 56 in figures 2, 3 and chapter 2.1.2).

Etymology: The Latin adjective *obovatus* refers to the inverted egg-shaped outline.

Description: Shape and size were studied in specimens from raw (non-flooded Petri dish) and pure cultures. The other morphometrical data base on cells from a pure culture.

Size 99–146 × 46–104 µm in silver nitrate-impregnated specimens from raw culture, while slightly smaller and less variable (85–140 × 44–78 µm) in specimens from pure culture (Table 99). Shape obovoidal with truncate anterior body region, providing cells with a conspicuous, obovoidal outline; in detail, however, highly variable, especially in the non-flooded Petri dish culture, that is, in 70% of 20 silver nitrate-impregnated specimens obovoidal, in 10% elongate obovoidal, in 15% broadly ellipsoidal, and in 5% elongate ellipsoidal (Fig. 118a, g–k, m; 367d–f). Truncate anterior region very conspicuous in vivo, less so in silver preparations although at least recognizable in about 75% of specimens. Cells slightly flattened laterally in raw culture; length:width ratio thus about 1.7:1 in ventral and 1.6:1 in lateral view, where shape is broadly obovoidal, broadly ellipsoidal or ellipsoidal with indistinctly flattened ventral and convex dorsal side. Specimens from pure cultures slightly dorsoventrally flattened and thus more slender than those from raw culture in lateral view (length:width ratio 1.9:1 vs. 1.6:1). Location of nuclear apparatus rather variable, that is, in anterior or middle third of cell, on average slightly above mid-body. Macronucleus usually broadly ellipsoidal, in three out of 15 specimens investigated elongate ellipsoidal, in three specimens globular (possibly because seen from short axis); nucleoli numerous and 1–2 µm across. Probably only one micronucleus attached to macronucleus, in vivo about 3 µm across and surrounded by a distinct membrane. Contractile vacuole dorsolateral, with 3–6, usually 5 excretory pores slightly above mid-body (Table 99); no collecting canals. Cytopyge extends in ventral portion of postoral suture. Resting extrusomes form conspicuous fringe because attached almost perpendicularly to cortex between each two kinetids of a ciliary row (see also below). Shape peculiar, that is, composed of an about 4.5 µm long and 0.8 µm wide, cuneate, slightly inflated shaft and an about 1.5 µm long, conical tip; exploded organelles elongate fusiform, about 50 µm long and with refractive tip, anterior portion occasionally curved as in congeners (Fig. 118b, c; FOISSNER 1987b). Cortex weak in postoral region, where cells rupture easily under cover glass pressure. Cytoplasm colourless, that is, without any granule patch, contains numerous crystals 2–4 µm in size (Fig. 118e). Food vacuoles contain green algae from various taxa, one specimen had a diatom almost as long as its body ingested. Movement without peculiarities. Resting cysts observed but not studied in detail.

Somatic cilia about 10 µm long in vivo, rather stiff and closely spaced; no caudal cilia. 83–101 meridional, equidistant ciliary rows form a suture in ventral midline of cell (Fig. 118m, o). Preoral suture commences at vertex of buccal cavity and extends straight ahead across anterior pole to first eighth of dorsal side, 2–2.5 µm wide. Postoral suture extends as a line from right posterior corner of buccal cavity to rear end, where it widens to 2–2.5 µm, passes the pole, and ends subterminally as counter-clockwise inclined stripe. Ventral kineties shorten gradually from both cell ends to oral apparatus, abut obliquely on postoral suture and almost perpendicularly on preoral suture, except for 2–4 postoral kineties commencing underneath buccal cavity. Dorsal ciliary rows almost bipolar, except those extending between sutures. Silver carbonate and silver nitrate preparations reveal kineties to be composed of irregularly alternating pairs and triplets of granules, very likely monokinetids and dikinetids with a parasomal sac (ALLEN 1971; Fig. 118m, o; 369a). A kinetodesmal fibre extends obliquely anteriad on right side of kinetids.

Oral apparatus about 20% back from anterior end, of ordinary size, that is, occupies about 1/4 of body length and 1/7 of body width (Table 99; FOISSNER et al. 1994). Buccal cavity pointed

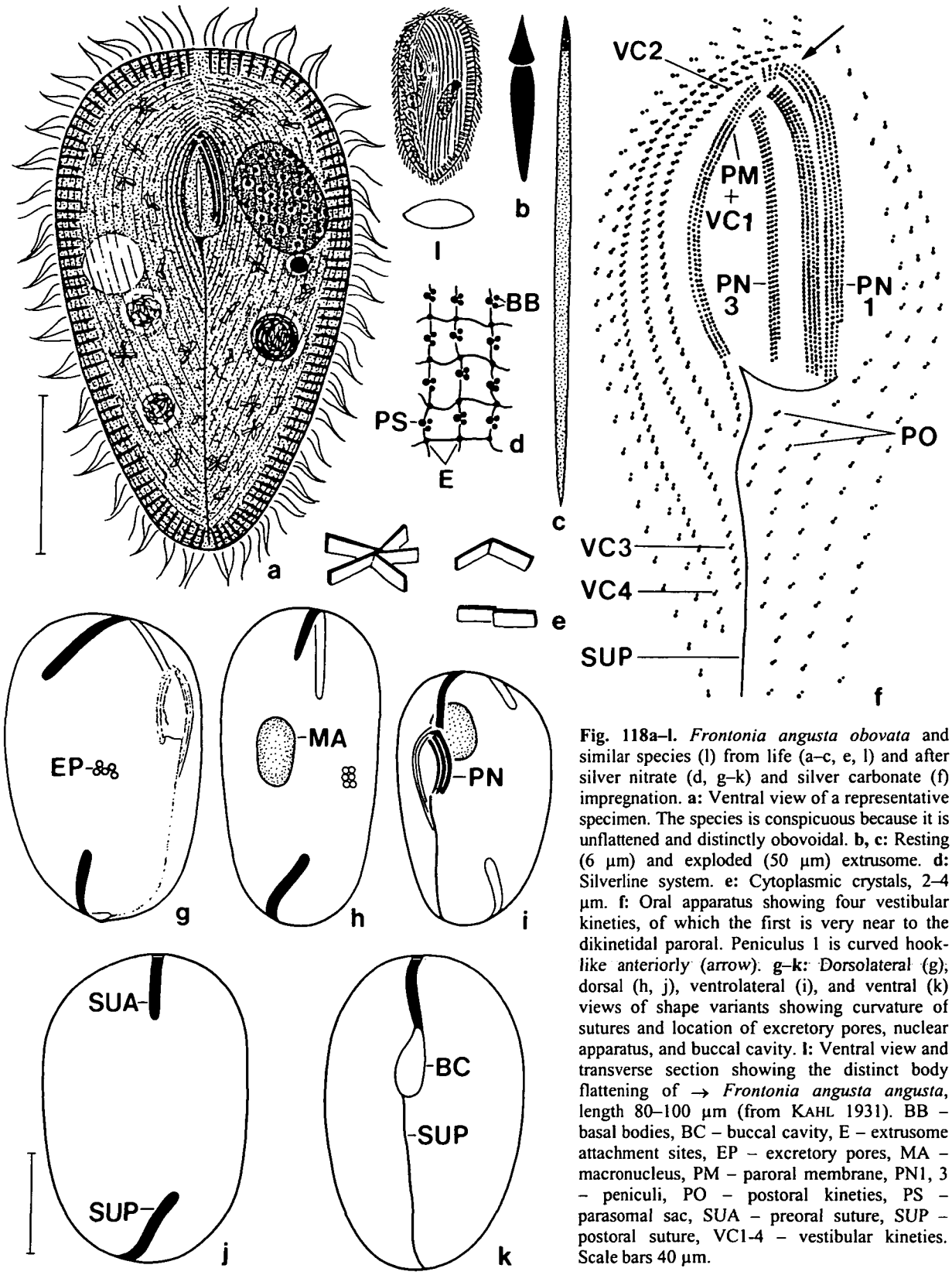
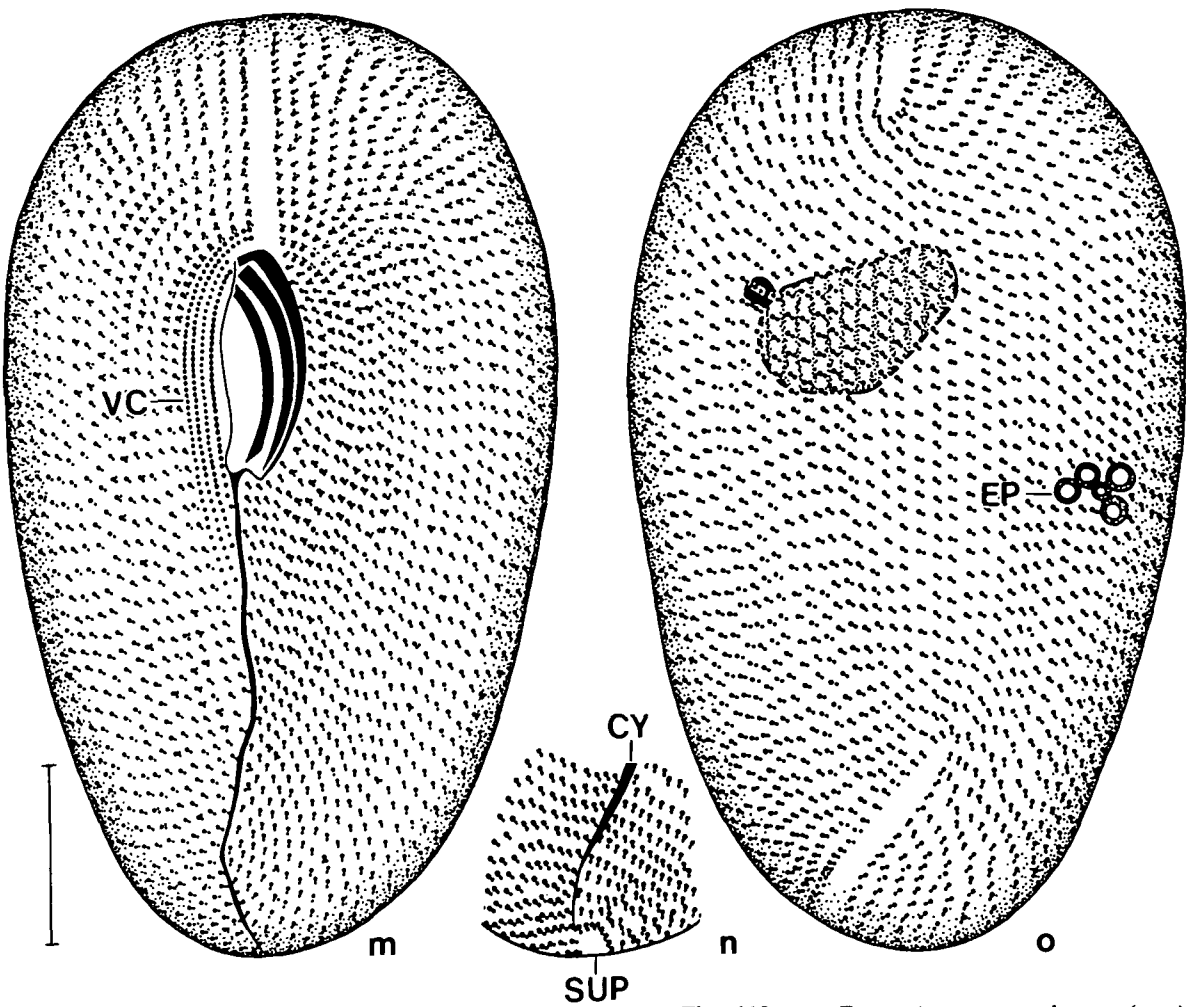


Fig. 118a–l. *Frontonia angusta obovata* and similar species (l) from life (a–c, e, l) and after silver nitrate (d, g–k) and silver carbonate (f) impregnation. **a:** Ventral view of a representative specimen. The species is conspicuous because it is unflattened and distinctly obovoidal. **b, c:** Resting (6 µm) and exploded (50 µm) extrusome. **d:** Silverline system. **e:** Cytoplasmic crystals, 2–4 µm. **f:** Oral apparatus showing four vestibular kineties, of which the first is very near to the dikinetidal paroral. Peniculus 1 is curved hook-like anteriorly (arrow). **g–k:** Dorsolateral (g), dorsal (h, j), ventrolateral (i), and ventral (k) views of shape variants showing curvature of sutures and location of excretory pores, nuclear apparatus, and buccal cavity. **l:** Ventral view and transverse section showing the distinct body flattening of → *Frontonia angusta angusta*, length 80–100 µm (from KAHL 1931). BB – basal bodies, BC – buccal cavity, E – extrusome attachment sites, EP – excretory pores, MA – macronucleus, PM – paroral membrane, PN1, 3 – peniculi, PO – postoral kineties, PS – parasomal sac, SUA – preoral suture, SUP – postoral suture, VC1-4 – vestibular kineties. Scale bars 40 µm.



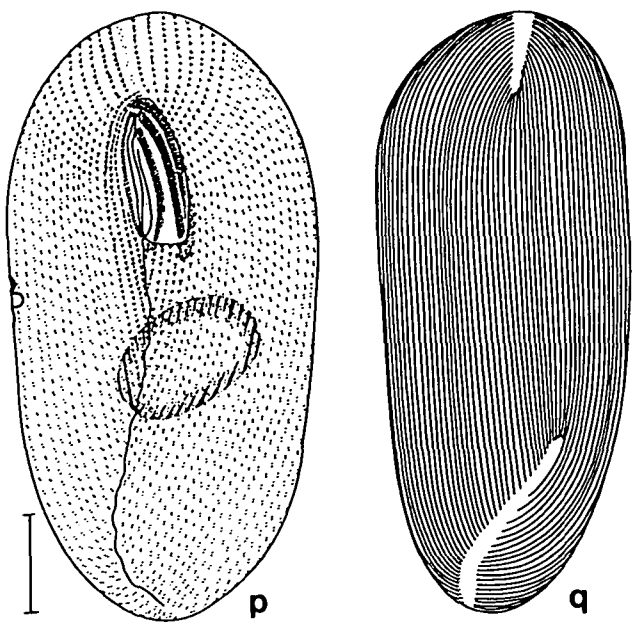


Fig. 118m–q. *Frontonia angusta obovata* (m–o) and → *F. angusta angusta* (p, q) after silver nitrate impregnation. **m, o:** Ciliary pattern of ventral and dorsal side of same specimen. *Frontonia angusta obovata* has four vestibular kineties and a paroral membrane at the right side of the oral opening. Vestibular kinety 1 is very near or on the paroral and thus not recognizable in the drawing; however, it can be clearly seen in silver carbonate stains (Fig. 369a–i). **n:** Posterior polar view. The narrow ventral portion of the postoral suture merges into a broad, blank stripe ending subterminally on dorsal side. **p, q:** Ciliary pattern of ventral and dorsal side of two different specimens from the Austrian population investigated by FOISSNER et al. (1994). *Frontonia angusta angusta* has very similar morphometrics to *F. angusta obovata*; they differ, however, in body flattening, which is rather distinct in the former and lacking in the latter. Furthermore, the anterior end of *F. angusta angusta* is never as truncate as in *F. angusta obovata*. CY – cytopyge in ventral portion of postoral suture, EP – excretory pores, SUP – postoral suture, VC – vestibular kineties. Scale bars 20 µm.

Table 99. Morphometric data on *Frontonia angusta obovata* from a raw (R, non-flooded Petri dish) and a pure (P) culture.

Characteristics [a]	Culture	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	R	121.6	121.5	10.3	1.9	8.5	99.0	146.0	30
	P	100.8	100.0	11.0	2.0	10.9	85.0	140.0	30
Body, width in ventral view	R	68.3	66.0	14.6	3.8	21.4	46.0	104.0	15
	P	57.9	55.0	8.3	2.1	14.3	44.0	78.0	15
Body, width in lateral view	R	75.1	75.0	12.1	3.1	16.1	58.0	93.0	15
	P	54.0	54.0	4.2	1.1	7.7	46.0	61.0	15
Body length:width, ratio in ventral view	R	1.8	1.7	0.3	0.1	15.9	1.3	2.3	15
	P	1.7	1.7	0.1	0.0	8.3	1.4	1.9	15
Body length:width, ratio in lateral view	R	1.7	1.6	0.2	0.1	13.8	1.3	2.1	15
	P	1.9	1.9	0.1	0.0	6.1	1.7	2.1	15
Anterior body end to anteriormost excretory pore, distance	P	43.1	43.0	6.6	1.7	15.4	34.0	53.0	15
Anterior body end to macronucleus, distance	P	23.2	20.0	8.6	2.2	36.9	10.0	38.0	15
Anterior body end to buccal cavity, distance	P	19.5	20.0	3.2	0.8	16.7	14.0	25.0	15
Anterior body end to posterior end of vestibular kinety 1, distance	P	52.6	52.0	6.1	1.8	11.5	45.0	66.0	11
Anterior body end to posterior end of vestibular kinety 2, distance	P	57.6	56.0	7.0	2.1	12.2	46.0	69.0	11
Anterior body end to posterior end of vestibular kinety 3, distance	P	62.5	61.0	5.9	1.8	9.5	52.0	74.0	11
Anterior body end to posterior end of vestibular kinety 4, distance	P	66.9	66.0	5.2	1.6	7.8	58.0	78.0	11
Buccal cavity, length	P	26.4	26.0	1.5	0.4	5.9	24.0	29.0	15
Posterior body end to posterior dorsal end of postoral suture, distance	P	18.7	18.0	3.2	0.8	16.9	14.0	24.0	15
Macronucleus, length	P	24.6	24.0	3.6	0.9	14.7	19.0	31.0	15
Macronucleus, width	P	16.8	16.0	2.7	0.7	16.3	12.0	20.0	15
Peniculus 1, length (chord of organelle)	P	26.3	26.0	1.8	0.5	6.7	24.0	29.0	15
Peniculus 2, length (chord of organelle)	P	23.1	24.0	2.0	0.5	8.5	21.0	26.0	15
Peniculus 3, length (chord of organelle)	P	19.3	19.0	2.6	0.7	13.6	16.0	25.0	15
Macronucleus, number	P	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Excretory pores, number	P	4.7	5.0	0.7	0.1	13.8	3.0	6.0	19
Somatic ciliary rows, number [b]	P	92.1	92.0	5.3	1.4	5.7	83.0	101.0	15
Postoral kineties, number	P	2.5	2.0	0.7	0.2	29.3	2.0	4.0	15
Vestibular kineties, number	P	3.9	4.0	–	–	–	3.0	4.0	31
Peniculus 1, number of ciliary rows	P	4.6	5.0	–	–	–	4.0	5.0	15
Peniculus 2, number of ciliary rows	P	4.1	4.0	–	–	–	4.0	5.0	15
Peniculus 3, number of ciliary rows	P	3.3	3.0	–	–	–	3.0	4.0	15

[a] Data based on mounted, CHATTON-LWOFF silver nitrate-impregnated, and randomly selected specimens. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Including postoral kineties but without vestibular kineties.

arch-shaped, symmetrical, with three almost parallel, slightly curved peniculi (adoral membranelles, ophryokineties) on left wall and paroral and vestibular kineties on right (Fig. 118f, m; 369a–i). Peniculus 1 about 26 µm long, anteriorly curved hook-like to right wall of cavity, composed of four or five kineties; marginal kineties irregular, that is, shortened anteriorly or posteriorly or comprising only a few scattered basal bodies. Peniculus 2 about 24 µm long, composed of four kineties posteriorly gradually shortened from right to left; occasionally, a fifth kinety occurs on left, but is inconspicuous because comprising only a few, usually scattered basal bodies. Peniculus 3 about 19 µm long, composed of three kineties posteriorly gradually shortened from right to left; a fourth kinety usually occurs on left, but is inconspicuous because comprising only a few scattered basal bodies (Table 99). Paroral membrane commences anteriorly of peniculus 3 and extends along right margin of buccal cavity, composed of two rows of very closely spaced basal bodies.

Vestibular kineties posteriorly gradually shortened from right to left and thus obliquely abutting on postoral suture, composed of very closely spaced granules; fine structure highly depending on impregnation conditions (Fig. 118f; 369a–i). Very likely, they basically consist of dikinetids (BERAN 1990) each with a parasomal sac, which impregnates more lightly or not at all. Of 31 specimens analyzed in silver nitrate preparations or photographed after silver carbonate impregnation, 29 had four vestibular kineties and 2 had three (Fig. 369f). First kinety easily overlooked because, as in most congeners (BERAN 1990, GIL & PÉREZ-SILVA 1964a, b, ROQUE 1961a, b, c, ROQUE & PUYTORAC 1972), very close to paroral membrane; longer than paroral by 4–14 kinetids and thus terminating about 52% back from anterior body end. Second kinety commences, like paroral membrane, near distal end of peniculus 1 and usually terminates 57% back from anterior body end. Third and fourth kinety commence above buccal vertex, that is, roof over all peniculi and usually terminate 62%, respectively, 66% back from anterior body end (Table 99).

Silverline system recognizable only in heavily impregnated specimens, composed of rectangular, longitudinally orientated meshes (about 2 × 2.5 µm) and thus similar to that of most congeners (FOISSNER 1987b, KLEIN 1930, ROQUE 1961a, b, c); forms herring-bone pattern in preoral suture and rectangular, obliquely or perpendicularly orientated meshes in dorsal portion of postoral suture. Kinetids connected by longitudinal silverlines and not within meshes; extrusome attachment sites marked by a granule at vertices of longitudinal and horizontal silverlines, that is, between each two kinetids (Fig. 118d). Silver carbonate occasionally impregnates the infraciliary lattice (Fig. 369a).

Occurrence and ecology: *Frontonia angusta obovata* was discovered in a Moringa forest soil of the Etosha National Park (site 56). The sample was a mixture of slightly saline, circumneutral (pH 7.8), powder-like soil and grass roots. However, we found the species also in a highly alkaline (pH 9.7) and saline soil of this area (site 67). Furthermore, *F. angusta obovata* occurred in a circumneutral (pH 6.5) soil sample from the dry bed of the Mlambane River in the Kruger National Park (24°S 32°E), Republic of South Africa (collected in 1992 by Mag. Eric STROBL, Salzburg). Obviously, *F. angusta obovata* is euryhaline and widespread in subtropical Africa.

Comparison with related species: *Frontonia angusta obovata* is a really conspicuous ciliate because it is so voluminous, has the oral apparatus in body midline, and often has a broadly truncate anterior body end (Fig. 118a, m, o). This and the basically identical oral structures make *F. angusta obovata* highly similar to *Disematostoma buetschlii*, which, however,

has an elongate reniform macronucleus and a very long postoral suture ending at the excretory pore of the contractile vacuole, that is, near mid-body of dorsal side (for a brief review, see FOISSNER et al. 1994). Accordingly, *Disematostoma* might be considered as a junior synonym of *Frontonia*. It is beyond the present monograph to discuss this problem in more detail. *Frontonia angusta obovata* also shows some similarities with → *Frontonia terricola*, especially in having an obovoidal body shape and several excretory pores (Table 95). However, → *F. terricola* has a much larger oral apparatus and the postoral suture hardly extends onto the dorsal side (Fig. 116c, d; 367b; Table 95). Furthermore, → *F. terricola* is usually smaller (< 90 µm vs. > 90 µm) than *F. angusta obovata* and thus has fewer ciliary rows (60–78 vs. 83–101). Accordingly, both are distinct taxa rather easily distinguished. Another species, which shows similarities to *F. angusta obovata* is *F. minuta* DRAGESCO, 1970. This species has symbiotic green algae and a conspicuously crescentic peniculus 3; furthermore, it is considerably smaller (70 µm vs. 125 µm) and thus has fewer ciliary rows (50–56 vs. 83–101; DRAGESCO 1970, DRAGESCO & DRAGESCO-KERNÉIS 1986).

The arrow-like resting extrusomes of *F. angusta obovata* are unique because those of the congeners are simply fusiform (FOISSNER 1987b, FOISSNER et al. 1994, KRÜGER 1936). However, this difference must not be over-interpreted because such details frequently have not been studied thoroughly. Similarly, the silverline pattern is highly dependent on the method used and the quality of the preparation. The pattern of *F. angusta obovata* is similar to that of → *F. angusta solea* as described by FOISSNER (1987b; Fig. 117f). Other authors obviously could not impregnate the longitudinal silverline connecting the kinetids but only the silverlines in the cortical ridges (e.g. ROQUE 1961a, DRAGESCO & DRAGESCO-KERNÉIS 1986); thus, the kinetids are in the centre of the meshes.

Frontonia terricola FOISSNER, 1987b (Fig. 116c, d; 367a–c, 370a–d; Tables 95, 100)

The Namibian specimens of *Frontonia terricola* match the Austrian populations in most respects, especially the disproportionally large oral apparatus (Fig. 370a, c). But the number of vestibular kineties is different: three in the Austrian populations, four in the Namibian specimens. However, this difference must not be over-interpreted because the vestibular kineties of *F. terricola* are comparatively inconspicuous and very close together. Thus, their number is difficult to ascertain and subject to various interpretations. The point is that, in *F. terricola*, vestibular kineties 2–4 are gradually shortened anteriorly – an unusual pattern found in both the Austrian type specimens and the Namibian population, where it is also clearly recognizable in SEM micrographs (Fig. 116c; 370a–d). Furthermore, the Namibian population differs from the Austrian type population in the number of distinct kineties composing peniculus 3 (invariably 2 vs. 3); however, there are one or two very short rows left of the distinct ones in the Namibian specimens. The SEM investigation of a few well-preserved and/or deciliated specimens showed and/or confirmed some further details: (i) the cilia of the vestibular kineties are distinctly shorter than those of the peniculi and the ordinary somatic kinetids; (ii) the paroral dikinetids and the first vestibular kinety form three distinct rows of basal bodies at the right oral margin, where the oral ribs produce a ladder-like structure; (iii) minute tubercles (basal bodies?) are right of the peniculi, whose basal bodies

are highly ordered; (iv) peniculi 1 and 2 extend side by side close together and are widely separate from the ends of the distinctly curved peniculus 3; (v) peniculus 3 consists of a right row of long cilia and a left row of short cilia (Fig. 370b, c). Likewise, the other peniculi obviously do not have all rows ciliated, at least not with long cilia.

Table 100. Morphometric data on *Frontonia terricola* from Namibian site (70).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	82.1	82.0	7.6	1.4	9.3	64.0	98.0	30
Body, width in lateral view	43.5	44.0	6.2	1.6	14.3	33.0	54.0	15
Body, width in ventral view	38.5	38.0	8.2	2.1	21.3	20.0	54.0	15
Body length:width, ratio in lateral view	2.0	1.9	0.2	0.1	11.4	1.6	2.4	15
Body length:width, ratio in ventral view	2.1	2.0	0.5	0.1	23.5	1.6	3.8	15
Anterior body end to anteriormost excretory pore, distance	37.5	35.0	6.8	1.8	18.2	31.0	59.0	15
Anterior body end to macronucleus, distance	32.5	34.0	10.7	2.8	33.1	8.0	48.0	15
Anterior body end to buccal cavity, distance	6.9	6.0	2.4	0.6	35.1	4.0	13.0	15
Buccal cavity, length	35.5	35.0	1.8	0.5	5.1	33.0	39.0	15
Macronucleus, length	25.9	26.0	3.8	1.0	14.7	18.0	31.0	15
Macronucleus, width	12.4	13.0	2.4	0.6	19.7	9.0	18.0	15
Peniculus 1, length (chord of organelle)	35.5	35.0	1.8	0.5	5.1	33.0	39.0	15
Peniculus 2, length (chord of organelle)	33.9	34.0	1.8	0.5	5.5	30.0	38.0	15
Peniculus 3, length (chord of organelle)	27.6	28.0	1.2	0.3	4.5	25.0	29.0	15
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Excretory pores, number	3.9	4.0	0.8	0.2	21.6	2.0	5.0	15
Somatic ciliary rows, number [b]	68.3	67.0	4.0	1.0	5.8	64.0	78.0	15
Postoral kineties, number	6.0	6.0	0.9	0.2	15.4	5.0	8.0	15
Vestibular kineties, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	15
Peniculus 1, number of ciliary rows	4.0	4.0	0.0	0.0	0.0	4.0	4.0	7
Peniculus 2, number of ciliary rows	4.0	4.0	0.0	0.0	0.0	4.0	4.0	7
Peniculus 3, number of ciliary rows	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15

[a] Data based on mounted, CHATTON-LWOFF silver nitrate-impregnated, and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Including postoral kineties but without vestibular kineties.

Apocyclidium nov. gen.

Diagnosis: Cyclidiidae, as defined by PUYTORAC (1994), with a secondary silverline meridian between each two continuous ciliary rows (primary meridians).

Type species: *Cyclidium obliquum* KAHL, 1926.

Etymology: Composite of the Greek prefix *apo* (derived from) and the generic name *Cyclidium*.

Comparison with related genera: In vivo, *Apocyclidium obliquum* is distinguished from *Cyclidium* only by the twisted ciliary rows; a feature too weak for establishing a distinct genus (KAHL 1926, 1931b). However, KLEIN-FOISSNER silver nitrate impregnation reveals a further conspicuous difference, viz., the silverline pattern. *Cyclidium* species, including the type *C. glaucoma*, have only primary silverline meridians connecting the kinetids of each kinety (CZAPIK 1963, FOISSNER et al. 1994, KLEIN 1926, POMP & WILBERT 1988, WILBERT 1986), while *Apocyclidium* additionally has a secondary meridian between each two primary meridians (Fig. 119j, k; 371d–f, i–n). In this respect, *A. obliquum* differs also from most (all?) other pleuronematid and philasterid genera (Fig. 371g, h; CZAPIK & WILBERT 1986, FOISSNER & WILBERT 1981, FOISSNER et al. 1982, 1994, PÉREZ-UZ & SONG 1995, PUYTORAC et al. 1974, SONG 1991, SONG & WILBERT 2000, THOMPSON & EVANS 1968, WILBERT 1986, WILBERT & FOISSNER 1980). However, a similar pattern is found in many tetrahymenid ciliates, for instance, *Dexiostoma campylum*, *Glaucoma scintillans*, *Colpidium kleini*, and some populations of *Tetrahymena pyriformis* (FOISSNER et al. 1994, GELEI & HORVÁTH 1931). The indirect-connecting silverline system of *A. obliquum* forms a mesh around each kinetid, as in many other scuticociliates (FOISSNER et al. 1994, WILBERT & BUITKAMP 1973, WILBERT & FOISSNER 1980).

In *Apocyclidium obliquum*, extrusomes occur not only within the ciliary rows, as in *Cyclidium glaucoma* (BARDELE 1983), but also in a row each between the kineties. Apparently, the occurrence of extrusomes between the kineties is combined with the occurrence of secondary silverline meridians or branches of primary meridians, as in *Dexiostoma campylum*, *Colpidium colpoda*, and *Colpidium kleini* and several other tetrahymenids, such as *Glaucoma* and *Tetrahymena* (FOISSNER et al. 1994).

The silverline pattern is not known for most of the following genera and thus cannot be compared with that of *Apocyclidium*. Fortunately, these genera differ from *Apocyclidium* by other features (PUYTORAC 1994). *Paracyclidium* GROLIÈRE et al., 1980, *Isocyclidium* ESTEBAN et al., 1993, and *Paurotricha* DRAGESCO & DRAGESCO-KERNÉIS, 1991 are distinguished from *Apocyclidium* mainly by the discontinuous ciliary rows leaving blank mid-body, where a short, curved kinety extends horizontally in *Paurotricha*[19]. *Pseudocyclidium* SMALL & LYNN, 1985 differs from *Apocyclidium* in the shape and arrangement of the adoral membranelles: membranelles 1 and 2 each composed of two long ciliary rows extending parallel to the paroral vs. *Cyclidium* pattern. *Cristigera* ROUX, 1899, as characterized by FOISSNER et al. (1982), is distinguished from *Apocyclidium* not only by a different silverline pattern (see above), but also by a conspicuous ventral furrow. *Echinocyclidium* JANKOWSKI in SMALL & LYNN, 1985, as characterized by PUYTORAC (1994), differs from *Apocyclidium* mainly by membranelle 1 comprising two short, posteriorly diverging ciliary rows and the habitat, namely, the digestive tract of sea urchins. In → *Protocyclidium* ALEKPEROV, 1993, the adoral ciliature is not differentiated into distinct membranelles.

[19] ESTEBAN & OLMO (1997) synonymize *Paurotricha cyclidiformis* with *Cristigera pleuronemoides*, although the latter lacks the short, transverse kinety on the right side of cell, emphasized by DRAGESCO & DRAGESCO-KERNÉIS (1991) in the diagnosis of *Paurotricha*.

Apocyclidium obliquum (KAHL, 1926) **nov. comb.** (Fig. 119a–m; 371a–r, 372a–i; Table 101)

1926 *Cyclidium obliquum* KAHL, Arch. Protistenk., 55: 371.
1926 *Cyclidium spirale* KAHL, Arch. Protistenk., 55: 370.
1931 *Cyclidium obliquum* KAHL, 1926 — KAHL, Tierwelt Dtl., 21: 375 (revision and redescription).

Neotype material: Neotypified from Namibian site (37) population, according to reasons 1, 3, 6 given in chapter 2.4.2.

Improved diagnosis: Size about 30–35 × 15–20 µm in vivo; ellipsoidal. Usually 2 macronuclear nodules. Contractile vacuole terminal, excretory pore underneath kineties 1 and 2. Extrusomes about 2.5 µm long, curved rods. 8 sinistrally twisted ciliary rows composed of monokinetids and 1–3 dikinetids anteriorly. Oral apparatus occupies anterior ventral body half. Adoral membranelles at right connected by a row of basal bodies, membranelle 1 rhomboid, membranelles 2 and 3 rectangular.

Redescription: Several populations of this species have been investigated (see "occurrence and ecology"). They match the original description in most features, especially the twisted ciliary rows. The improved diagnosis and the redescription are based on the original description and the Namibian site (37) population.

Size in vivo 35 µm in German type (KAHL 1926) and 20–30 × 8–15 µm in Namibian neotype population, 35–45 µm according to first redescription (KAHL 1931b). Shape ellipsoidal to slightly ovoidal in lateral view, ellipsoidal to elongate ellipsoidal in ventral and dorsal view because slightly (Italian specimens) to up to 2:1 (Namibian and Saudi Arabian specimens) laterally flattened. Anterior end with inconspicuous frontal plate, posterior broadly to narrowly rounded, never indented at caudal cilium (Fig. 119a, b, d–g; 372a, c, g–i; Table 101). Nuclear apparatus in anterior two thirds of cell. Usually, two abutting macronuclear nodules each about 2.5 µm across (93% of specimens, n = 200); in 6% of specimens one macronuclear nodule about 4 µm across; and in 1% three abutting nodules each about 2 µm across. Nucleoli apparently only in periphery of nodules and lobate. Micronuclei in indentations of macronuclear nodules, about 1 µm across and only occasionally impregnated; thus, their number (up to 3?) is difficult to ascertain. Contractile vacuole subterminal in German, invariably terminal and slightly shifted to ventral side in Namibian, Italian, and Saudi Arabian specimens, surrounded by contributory vesicles during diastole. Excretory pore underneath and between kineties 1 and 2 right of oral apparatus; distinct only in some properly orientated silver carbonate and KLEIN-FOISSNER silver nitrate-impregnated cells (Fig. 119a, b, j; 371i, p, r, 372a, e, g). Cytopyge slit extends between scutica and posterior fifth of cell. Cortex distinctly ribbed right of ciliary rows. Extrusomes (mucocysts?) about 2.5 µm long and slightly curved in vivo, appear as bright dots in surface view, form conspicuous fringe, usually obliquely attached to cortex between each two kinetids of a kinety and in a longitudinal, anteriorly slightly shortened row between kineties; not protruding from body proper in European populations, but slightly so in Namibian and distinctly so in Saudi Arabian specimens, where they form bundles and give cells a spiny appearance (Fig. 119a, b; 372b, e, f, i). Attachment sites well-impregnated in CHATTON-LWOFF silver nitrate preparations, producing a distinct pattern totally different from that of related genera, especially *Cyclidium*,

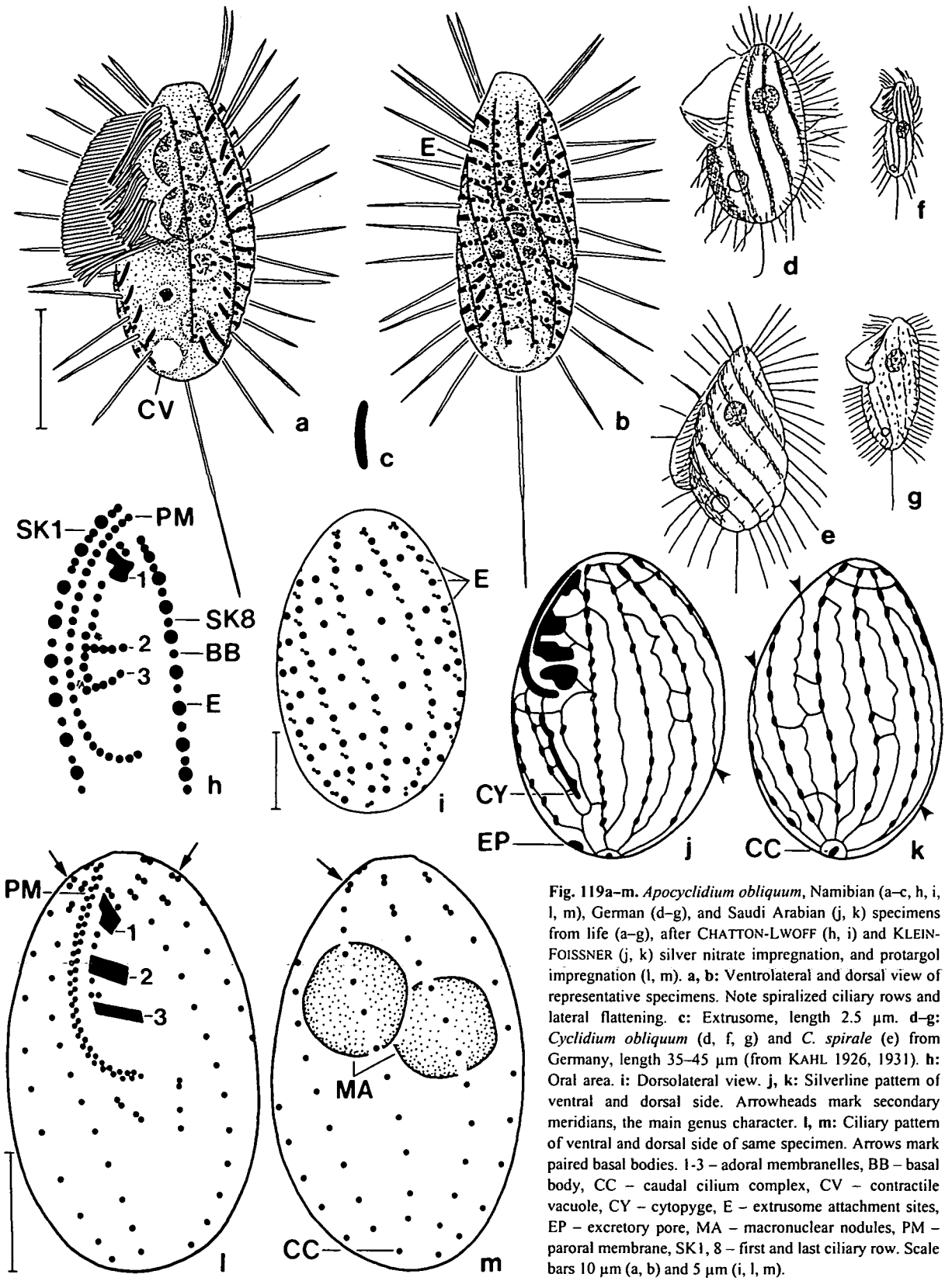


Fig. 119a–m. *Apocyclidium obliquum*, Namibian (a–c, h, i, l, m), German (d–g), and Saudi Arabian (j, k) specimens from life (a–g), after CHATTON-LWOFF (h, i) and KLEIN-FOISSNER (j, k) silver nitrate impregnation, and protargol impregnation (l, m). **a, b:** Ventrolateral and dorsal view of representative specimens. Note spiralized ciliary rows and lateral flattening. **c:** Extrusome, length 2.5 µm. **d–g:** *Cyclidium obliquum* (d, f, g) and *C. spirale* (e) from Germany, length 35–45 µm (from KAHL 1926, 1931). **h:** Oral area. **i:** Dorsolateral view. **j, k:** Silverline pattern of ventral and dorsal side. Arrowheads mark secondary meridians, the main genus character. **l, m:** Ciliary pattern of ventral and dorsal side of same specimen. Arrows mark paired basal bodies. 1-3 – adoral membranelles, BB – basal body, CC – caudal cilium complex, CV – contractile vacuole, CY – cytopyge, E – extrusome attachment sites, EP – excretory pore, MA – macronuclear nodules, PM – paroral membrane, SK1, 8 – first and last ciliary row. Scale bars 10 µm (a, b) and 5 µm (i, l, m).

where they occur exclusively within the ciliary rows (Fig. 119i; BARDELE 1983, DIDIER & WILBERT 1981, FOISSNER et al. 1994, POMP & WILBERT 1988, WILBERT 1986). Cytoplasm colourless, contains some food vacuoles 2–3 µm across with remnants of bacteria. Moves like *Cyclidium glaucoma* (TAMAR 1979), that is, jumps hastily to and fro interrupted by short rests; when resting and feeding, somatic cilia somewhat disorderly spread and paroral spread to a conspicuous velum.

Somatic cilia in vivo about 10 µm long in German and 8 µm in Namibian population, rather stiff, single, except for (i) three pairs at anterior end of ciliary row left of oral opening; (ii) one pair at anterior end of ciliary row right of oral opening; and (iii) two pairs each at anterior end of other ciliary rows. Kinetids equidistantly arranged, that is, not locally condensed as in some other species (FOISSNER 1995, 1996a). All ciliary rows of almost body length leaving blank frontal plate and posterior pole area, equidistant and uniquely sinistrally twisted. Spiralling very conspicuous in vivo, less so in silver preparations (Fig. 119b, d–g, i–m; 371b, j–l, q, 372a, f–h; Table 101). Caudal cilium conspicuous because about 15 µm long in vivo, slightly inclined to dorsal side; proximal portion of ordinary thickness, distal very fine and straight. Scutica underneath oral apparatus, arranged in two short, converging rows on both sides of cytopyge; right row usually composed of two kinetids, left of three. Silver carbonate preparations reveal each kinetid to be composed of an irregular granule (mono- or dikinetid plus parasomal sac) and a short structure (kinetodesmal fibre?) extending almost parallel to kinety axis anteriad at right side of kinetid; scutica apparently without parasomal sac and fibrillar (?) associates, lighter impregnated than ordinary kinetids, probably because unciliated as is usual (Fig. 371a–c, p–r).

Oral apparatus extends from frontal plate to mid-body (Table 101), mid-portion covered by a very hyaline cortical process (seen only in Saudi Arabian specimens but likely present also in the other populations). Adoral membranelles (oral polykinetids) distinct in vivo, details difficult to recognize due to their small size, at right connected by a row of (ciliated?) basal bodies (Fig. 119h, l; 371c, p). Membranelle 1 left of anterior end of paroral, rhomboid. Membranelles 2 and 3 roughly rectangular and more or less horizontally orientated; both apparently composed of about five aligned basal bodies in CHATTON-LWOFF silver nitrate preparations, while apparently composed of more than one ciliary row in protargol, silver carbonate, and KLEIN-FOISSNER silver nitrate preparations. Paroral membrane L-shaped, entirely composed of zigzagging basal bodies as recognizable in properly orientated and impregnated cells, that is, not single-rowed in anterior portion, as in *Cyclidium glaucoma* and probably *C. plouneouri* (Fig. 119 l; 371c; FOISSNER 1996a, WILBERT 1986).

Silverline system best revealed by KLEIN-FOISSNER silver nitrate impregnation, basically as in *Cyclidium glaucoma* (FOISSNER 1996a), that is, composed of primary meridians connecting the kinetids and some transverse commissures anteriorly and posteriorly; furthermore, an indirect-connecting system, which rarely impregnates, forms a mesh around each kinetid. *Apocyclidium obliquum* is unique in having a secondary silverline meridian between each two primary meridians (ciliary rows). Secondary meridians curve right to meet primary meridians between second and third or third and fourth kinetid anteriorly and underneath last kinetid posteriorly; usually contain some granules, very likely attachment sites of extrusomes (Fig. 119j, k; 371i–n).

A few divisional stages were found in the preparations; they resemble those of *Cyclidium bonneti* (Fig. 371o; GROLIÈRE 1980).

Table 101. Morphometric data on a Namibian population of *Apocyclidium obliquum*.

Characteristics [a]	Me [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	CHL	19.5	19.0	1.3	0.2	6.8	16.0	23.0	30
Body, width in ventral view	CHL	7.1	7.0	0.8	0.2	11.1	6.0	9.0	21
Body, width in lateral view	CHL	11.0	11.0	0.8	0.2	6.9	10.0	12.0	15
Anterior end to proximal end of membranelle 3, distance	CHL	6.6	7.0	0.6	0.2	9.6	6.0	8.0	15
Anterior end to vertex of paroral membrane, distance	CHL	9.9	10.0	–	–	–	9.0	10.0	15
Macronucleus, length	PA	2.8	2.5	0.5	0.1	16.5	2.5	4.0	15
Macronucleus, width	PA	2.7	2.5	0.3	0.1	11.7	2.5	3.5	15
Macronuclear nodules, number	PA	2.0	2.0	–	–	–	1.0	3.0	220
Somatic ciliary rows, number	PA	8.0	8.0	0.0	0.0	0.0	8.0	8.0	15
Kinetids in a dorsal ciliary row, number	PA	12.0	12.0	0.8	0.2	7.0	11.0	13.0	15

[a] Data based on mounted, silver-impregnated, and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Me – methods, Min – minimum, n – number of individuals investigated, PA – protargol impregnation (FOISSNER's method), SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Occurrence and ecology: KAHL (1926, 1931b) discovered *A. obliquum* in freshwater mud, probably in the surroundings of Hamburg, Germany. We found it at several sites in Namibia (8, 16, 28, 37, 48), Saudi Arabia, and Italy. The Namibian samples were slightly to highly saline soil and bark from a succulent Vitaceae. The sample from the Al-Hassa Oasis in Saudi Arabia (25°30'N 49°40'E) was a mixture of litter (mainly from legumes planted for desalinization) and highly saline (8‰), slightly acidic (pH 6.0), yellowish sand with many roots and patches of iron concretions. The second Saudi Arabian sample was collected in an irrigated grove of date-palms near the centre of the ancient town of Riyadh (24°N 46°E). It consisted of litter and yellow-brown, slightly acidic (pH 6.2), saline sand with some grass roots. The sample taken from the littoral of a lagoon near Venice, Italy (45°N 12°E) was a mixture of slightly saline and alkaline (pH 8.0) soil and roots from halophytes. Obviously, *A. obliquum* is a cosmopolitan preferring saline habitats.

Comparison with original description and similar species: KAHL (1926) described two *Cyclidium* species with twisted ciliary rows, namely, *C. obliquum* and *C. spirale* (Fig. 119d, e). The descriptions were based on live observations. Later, KAHL (1931b) synonymized *C. spirale* with *C. obliquum* assuming that the former was only a modification with more distinctly twisted kineties (Fig. 119f, g). Our populations match *C. obliquum* in this unique feature; thus, the few minor differences, such as body size (35–45 µm vs. 20–30 µm) and location of the contractile vacuole (slightly subterminal vs. terminal) are insufficient for separating the populations. The number of macronuclear nodules is difficult to ascertain, especially in vivo, because they usually abut. Furthermore, this feature seems to be highly variable in scuticociliates (Table 101).

According to FOISSNER (1998a), two *Cyclidium* and one → *Protocyclidium* species have been reported from soil and moss, namely, *Cyclidium glaucoma*, *C. muscicola*, and → *Protocyclidium terricola*. In vivo, they can be easily distinguished from *A. obliquum* by the straight

course of the ciliary rows. Furthermore, *C. glaucoma* and *A. obliquum* have the contractile vacuole in the posterior end (Fig. 119a, j; 371i, p, r, 372a, e, g; FOISSNER 1996a), while it is distinctly subterminal near the peristomial vertex in *C. muscicola* (FOISSNER 1995) and → *P. terricola*.

Protocyclidium ALEKPEROV, 1993

Improved diagnosis: Cyclidiidae, as defined by PUYTORAC (1994), with continuous ciliary rows. Adoral membranelle 1 a patch of cilia, membranelles 2 and 3 hardly separated from each other, forming a cuneate ciliary field composed of almost equidistant, horizontally orientated rectangles (kineties) increasing in width from anterior to posterior.

Remarks: An improved diagnosis of *Protocyclidium* is necessary because ALEKPEROV (1993) included several species-specific features, such as the number of ciliary rows and the location of the macronucleus. The poorly described type species, *P. terrenum*, is very likely a junior synonym of *C. muscicola* KAHL, as redescribed by FOISSNER (1995), because all main features match. A literature search showed that at least four *Cyclidium* species should be transferred to *Protocyclidium* because they have the same oral pattern: *P. sphagnetorum* (ŠRÁMEK-HUŠEK, 1949) nov. comb., as redescribed by GROLIÈRE (1973); *P. citrullus* (COHN, 1866) nov. comb., as redescribed by CZAPIK (1963), WILBERT (1995), and ESTEBAN et al. (2000)[20]; → *P. terricola* (KAHL, 1931b) nov. comb., as redescribed below; and *P. muscicola* (KAHL, 1931b) nov. comb., as redescribed by FOISSNER (1995). As concerns the last mentioned species, we reinvestigated the type material and found scattered basal bodies between membranelles 2 and 3, which are thus not as distinctly separate as illustrated by FOISSNER (1995). This was confirmed by a study on another Austrian population (Fig. 373t, u).

Comparison with related genera: In vivo, *Protocyclidium* is hardly distinguishable from other Cyclidiidae with continuous ciliary rows, while silver impregnation shows a different oral pattern as diagnosed by ALEKPEROV (1993) and above (Fig. 120h, i, l; 373g–j, o, p, r). GROLIÈRE (1973), who investigated several such species, suggests that the posteriormost rectangle of the cuneate field corresponds to adoral membranelle 3, while the other rectangles between membranelles 1 and 3 correspond to membranelle 2. In the absence of detailed ontogenetic data, we accept this interpretation. *Protocyclidium* has a *Cyclidium*-like silverline pattern and thus lacks the secondary meridians characterizing → *Apocyclidium* (Fig. 120h; 373m–q). *Cristigera* ROUX, 1899, as characterized by FOISSNER et al. (1982), is distinguished from *Protocyclidium* by the bipolar ventral furrow. *Echinocyclidium* JANKOWSKI in SMALL & LYNN, 1985, as characterized by PUYTORAC (1994), differs from *Protocyclidium* by the structure of adoral membranelles 1 and 2 and the habitat (digestive tract of sea urchins vs. soil and soil mosses).

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[20] The recent redescription of *C. citrullus* by BUITKAMP (2000) from a freshwater habitat in Germany does not match the redescriptions by CZAPIK (1963) and WILBERT (1995); likely, it is another species.

Protocyclidium terricola (KAHL, 1931) **nov. comb.** (Fig. 120a–p; 373a–s; Table 102)

Neotype material: Neotypified from a meadow soil population of Salzburg, Austria (48°N 13°E), according to reasons 1, 2, 4, 6 given in chapter 2.4.2.

Improved diagnosis: Size about 35 × 18 µm in vivo; broadly ellipsoidal to slightly ovoidal. Contractile vacuole distinctly subterminal, excretory pore usually near posterior quarter of cell left of kinety 2. Extrusomes about 4 µm long and cuneate. Usually 12–14 ciliary rows composed of dikinetids in anterior body half and monokinetids in posterior. Oral apparatus occupies about 50% of body length. Adoral membranelle 1 rhomboid, cuneate membranellar field composed of 8 rectangles.

Description of Austrian neotype population: Size in vivo 30–40 µm in German type and 28–35 × 15–20 µm in Austrian neotype population. In lateral view broadly ellipsoidal to slightly ovoidal, dorsal side convex, ventral slightly flattened and without longitudinal groove; elongate ellipsoidal in ventral and dorsal view because laterally flattened up to 2:1 in vivo, less so in CHATTON-LWOFF silver nitrate preparations (Table 102). Anterior end with rather distinct, circular to elliptical frontal plate, posterior widely rounded or slightly truncate, never indented at caudal cilium (Fig. 120a, h–j, k, m–p; 373a–d). Macronucleus in anterior half of cell, about 7 µm across in vivo; nucleoli very small and globular. Micronucleus usually adjacent to anterior end of macronucleus, globular. Contractile vacuole distinctly subterminal underneath and right of peristomial vertex, small, surrounded by contributory vesicles during diastole; excretory pore slightly underneath posterior quarter of cell at left end of posteriorly shortened kinety 2. Cytopyge slit extends between scutica and posterior fifth of cell. Extrusomes (mucocysts?) of Austrian specimens hardly recognizable in vivo because of similar light refraction as cytoplasm, while conspicuous in German, Namibian, and Costa Rican specimens, where they appear as bright dots in surface view and form a distinct fringe; 4–5 × 0.4–0.5 µm and cuneate with thicker end attached to cortex between each two kinetids slightly left of ciliary rows, rarely between kineties and in peristomial area; attachment sites usually impregnate in CHATTON-LWOFF silver nitrate preparations, while organelles only rarely do so (Fig. 120d–f, h, i; 373e–j, s). Cytoplasm colourless, packed with 1 µm-sized granules and some food vacuoles 5–7 µm across partially containing a compact mass, likely bacterial remnants; Namibian site (66) specimens ingest also small green algae. Jumps inconspicuously, compared to *Cyclidium glaucoma*, but swims rapidly in Austrian population, and crawls jerkily in German; cilia and paroral membrane spread when resting and feeding.

Somatic cilia long compared to size of cell, namely, about 13 µm in vivo, stiff, paired in anterior body half, single in posterior; proximal portion of ordinary thickness, distal thin. Distances between individual kinetids increases slightly from anterior to posterior, no local cilia condensations as in some other species and Costa Rican specimens (see below). Ciliary rows meridionally and equidistantly arranged, of almost body length, leave frontal plate and posterior pole area blank; second kinety usually shortened by two to three kinetids and thus terminating near posterior quarter of cell at excretory pore, last kinety shortened by one kinetid each anteriorly and posteriorly. Caudal cilium inconspicuous because only about 20 µm

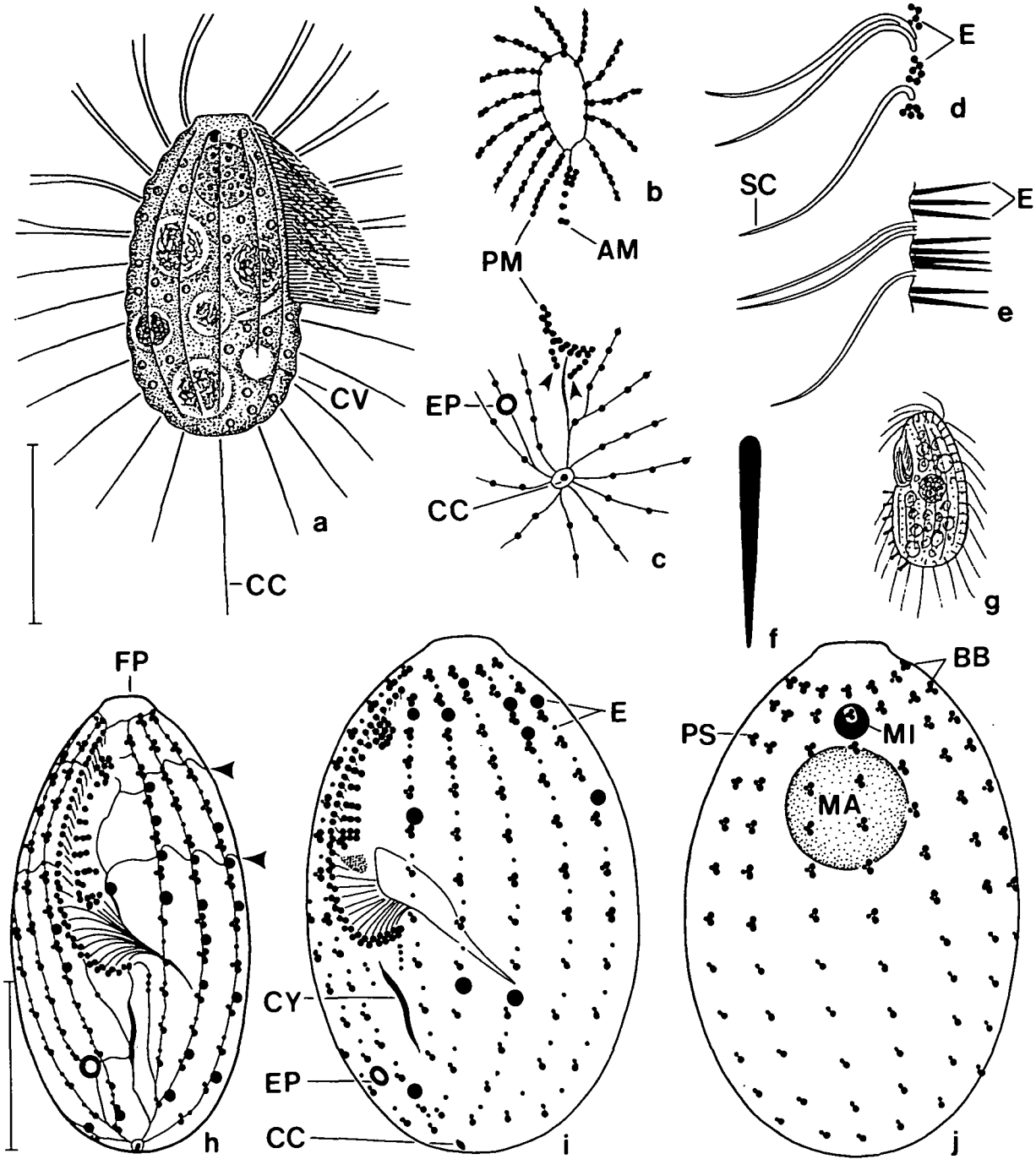
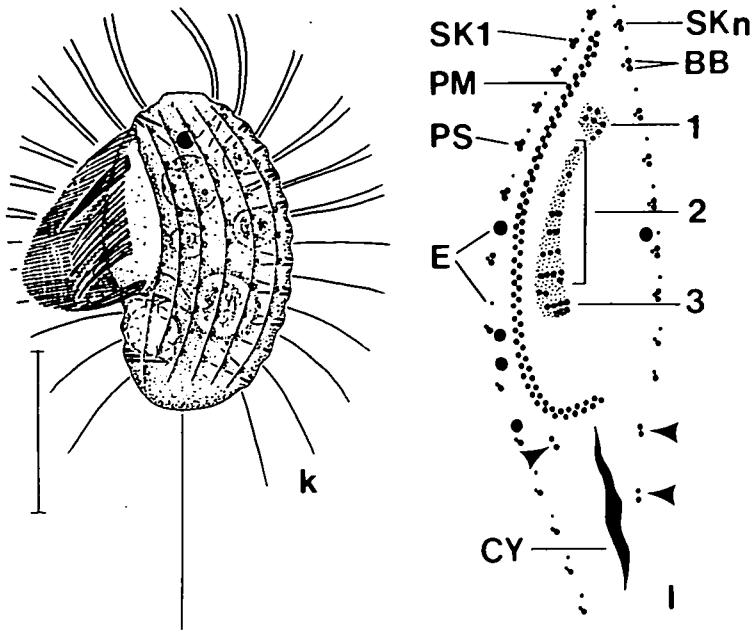


Fig. 120a–j. *Protocyclidium terricola*, Austrian (a–c, h–j), Namibian (d–f), and German (g) specimens from life (a, d–g) and combined after protargol and CHATTON-LWOFF silver nitrate impregnation (b, c, h–j). **a:** Lateral view of a representative specimen from Austrian neotype population. Note the subterminal location of the contractile vacuole. **b, c:** Anterior and posterior polar view. Arrowheads mark scutica. **d, e:** Surface view and optical section showing arrangement of extrusomes. **f:** Extrusome, length 4–5 µm. **g:** German type specimen, length 30–40 µm (from KAHL 1931b). **h:** Ciliary and silverline pattern of ventral side showing primary meridians and some transverse commissures (arrowheads). **i, j:** Ventrolateral- and dorsolateral view of same specimen. AM – adoral membranelles, BB – basal bodies, CC – caudal cilium, CV – contractile vacuole, CY – cytopyge, E – extrusomes, EP – excretory pore, FP – frontal plate, MA – macronucleus, MI – micronucleus, PM – paroral membrane, PS – parasomal sac, SC – somatic cilium. Scale bars 20 µm (a) and 10 µm (h–j).



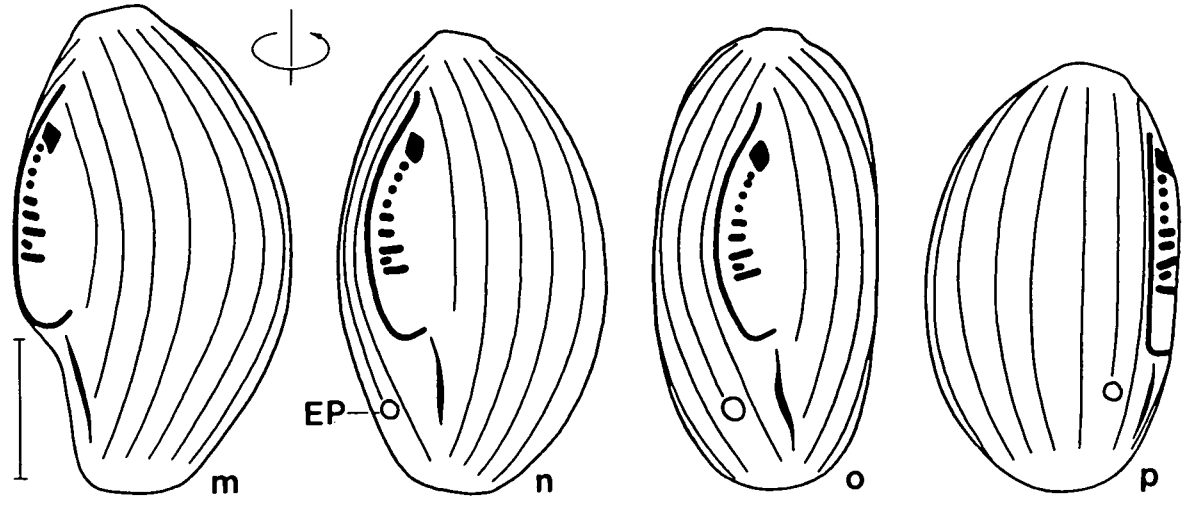


Fig. 120k–p. *Protocyclidium terricola*, Namibian specimens from life (k) and after CHATTON-LWOFF silver nitrate impregnation (l–p). k: Ventrolateral view showing the slightly obovoidal body shape and the distinct extrusomes. l: Ciliary pattern of oral area showing the zigzagging basal bodies comprising the paroral membrane. Adoral membranelle 1 is roughly rhomboid, membranelles 2 and 3 are hardly distinguishable and form a cuneate field of eight transverse rectangles. The extrusomes are attached to the cortex between each two kinetids of a ciliary row. Arrowheads mark scutica. m–p: Slightly schematized specimens showing shapes during an about 180° counter-clockwise rotation about main body axis. 1-3 – adoral membranelles, BB – basal bodies, CY – cytopyge, E – extrusome attachment sites, EP – excretory pore, PM – paroral membrane, PS – parasomal sac, SK1, n – first and last ciliary row. Scale bars 20 μm (k) and 10 μm (m–p).

long in vivo, extends parallel to main body axis, proximal portion of ordinary thickness, distal very fine; easily shed. Scutica underneath oral apparatus on both sides of cytopyge, usually lighter impregnated than ordinary somatic and oral kinetids, probably because unciliated as is usual; left portion probably composed of three or four basal bodies forming an oblique row, right likely comprises one to three basal bodies (Fig. 120h–j, m–p; 373a, g, h, k–o, s).

Oral apparatus extends to second fifth of cell in German type and to third fifth in Austrian neotype population (Table 102). Adoral ciliature rather conspicuous because composed of a series of nine groups of strongly impregnated basal bodies forming a peculiar pattern, viz., an upside down exclamation mark; details of individual groups difficult to recognize due to their small size (Fig. 120h, i, l; 373g–j, o, p, r). Membranelle 1 left and slightly underneath distal end of paroral membrane, rhomboid. Membranelles 2 and 3 hardly distinguishable, form a cuneate field composed of eight almost equidistant, horizontally orientated rectangles increasing

Table 102. Morphometric data on an Austrian (upper line) and Namibian (lower line) population of *Protocyclidium terricola*.

Characteristics [a]	Me [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	CHL	28.6	28.0	1.7	0.4	6.0	26.0	31.0	15
	CHL	33.2	33.0	3.0	0.5	8.9	29.0	39.0	30
Body, width in ventral view	CHL	13.8	14.0	1.1	0.3	7.8	11.0	16.0	15
	CHL	12.8	13.0	2.0	0.5	15.4	9.0	16.0	15
Body, width in lateral view	CHL	16.4	17.0	1.5	0.4	8.9	14.0	18.0	15
	CHL	18.3	19.0	2.0	0.5	11.0	15.0	23.0	15
Body length:width, ratio in ventral view				no data					
	CHL	2.5	2.4	0.4	0.1	14.2	2.1	3.2	15
Body length:width, ratio in lateral view				no data					
	CHL	1.9	1.9	0.1	0.0	6.2	1.7	2.1	15
Anterior body end to macronucleus, distance	CHL	3.0	3.0	0.3	0.1	10.9	2.5	4.0	15
	CHL	6.3	6.0	1.5	0.4	23.7	4.0	10.0	15
Anterior body end to excretory pore, distance	CHL	22.0	22.0	1.4	0.4	6.4	20.0	25.0	15
	CHL	24.1	25.0	2.9	0.7	11.8	20.0	28.0	15
Anterior body end to paroral membrane, distance	CHL	3.5	3.5	0.6	0.2	17.6	2.0	4.0	15
	CHL	3.7	4.0	0.7	0.2	18.8	3.0	5.0	15
Anterior body end to vertex of paroral membrane, distance	CHL	16.6	17.0	0.9	0.2	5.5	15.0	18.0	15
	CHL	22.0	23.0	1.9	0.5	8.4	18.0	24.0	15
Anterior body end to membranelle 1, distance	CHL	3.5	3.5	0.6	0.2	17.6	2.0	4.0	15
	CHL	6.7	7.0	1.2	0.3	17.3	4.0	9.0	15
Anterior body end to proximal end of membranelle 3, distance	CHL	12.9	13.0	1.0	0.2	7.4	11.0	14.0	15
	CHL	17.3	18.0	1.8	0.5	10.6	14.0	20.0	15
Macronucleus, length	PA	7.1	7.0	0.6	0.2	8.4	6.0	8.0	15
	CHL	7.1	7.0	1.1	0.3	14.9	5.0	9.0	15
Macronucleus, width	PA	6.6	7.0	–	–	–	6.0	7.0	15
	CHL	6.5	7.0	–	–	–	5.0	7.0	15
Micronucleus, diameter	PA	1.4	1.4	–	–	–	1.3	1.5	15
	CHL	1.8	2.0	–	–	–	1.5	2.5	15
Excretory pore, diameter	CHL	1.5	1.5	–	–	–	1.4	1.6	15
	CHL	1.4	1.5	–	–	–	1.0	1.5	15
Macronucleus, number	PA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	CHL	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Micronucleus, number	PA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	CHL	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Somatic ciliary rows, number	CHL	12.0	12.0	0.0	0.0	0.0	12.0	12.0	15
	CHL	13.5	13.0	–	–	–	13.0	15.0	15
Kinetids in a dorsal ciliary row, number	CHL	12.0	12.0	0.0	0.0	0.0	12.0	12.0	15
	CHL	12.3	12.0	–	–	–	12.0	13.0	15
Adoral membranelle 2, number of rectangles (kineties?)	CHL	7.0	7.0	0.0	0.0	0.0	7.0	7.0	15
	CHL	7.0	7.0	0.0	0.0	0.0	7.0	7.0	15

[a] Data based on mounted, silver-impregnated, and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Me – methods, Min – minimum, n – number of individuals investigated, PA – protargol impregnation (FOISSNER's method), SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

in width from anterior to posterior. Rectangles apparently composed of one row of basal bodies each, except for the two posteriormost, each likely consisting of two rows. Membranelle 2 comprises seven rectangles, of which the anteriormost is adjacent to right side of membranelle 1. Membranelle 3 comprises one rectangle connected at right with membranelle 2 by two (?) more or less obliquely arranged basal bodies. Paroral membrane L-shaped, entirely composed of zigzagging basal bodies, as recognizable in properly orientated and impregnated cells, that is, not single-rowed in anterior portion, as in *C. glaucoma* and probably *C. plouneouri* (FOISSNER 1996a, WILBERT 1986); proximal portion associated with distinct oral ribs extending radially to the cytostome.

Silverline system best revealed by KLEIN-FOISSNER silver nitrate impregnation, as in *Cyclidium glaucoma*, that is, composed of primary meridians connecting the kinetids of a ciliary row and some transverse commissures connecting kineties; furthermore, an indirect-connecting system, which rarely impregnates, forms a mesh around each kinetid (Fig. 120b, c, h; 373 l–q).

Other populations: The Namibian population matches the type and neotype population in most morphometrics (Table 102). It differs, however, in body shape because it is postorally slightly narrowed making cells obovoidal (Fig. 120k, m; 373a–d). Furthermore, the Namibian specimens are more slender (length:width ratio 2.5:1 vs. 2:1 in ventral and 1.9:1 vs. 1.7:1 in lateral view) and usually slightly longer (33 µm vs. 29 µm long on average; Table 102) than the Austrian ones. The extrusomes are often clustered and form a distinct fringe and rather conspicuous tubercles recognizable even at low (×150) magnification on the cell surface (Fig. 120d–f, k; 373e, f). The last somatic ciliary row is not only shortened by one kinetid posteriorly, as in the Austrian population, but terminates at the level of the peristomial vertex. Additionally, the oral apparatus is larger than in the Austrian specimens (usually terminating 58% vs. 66% back from anterior body end), the adoral membranelles are more posteriorly located (distance to anterior body end 6.7 µm vs. 3.5 µm), the paroral membrane often forms a small hook distally, and jumping is more pronounced.

The Costa Rican specimens have a similar body shape to the Namibian ones. The excretory pore is even more subterminal (70% back from anterior body end) than in the Austrian (77%) and Namibian (73%) cells and not at end of kinety 2, which is usually shortened by only one kinetid, but between its ultimate and penultimate kinetid (Fig. 373g–l, s). Furthermore, kinety 1 often has about five slightly condensed kinetids anteriorly. The last of the 12–16 ($\bar{x}$ = 14, n = 6) ciliary rows usually commences not near the distal end of the paroral but at level of adoral membranelle 1 and is shortened by one kinetid posteriorly, as in the Austrian specimens.

Occurrence and ecology: KAHL (1931b) discovered *P. terricola* in soil mosses from the surroundings of Hamburg in northern Germany, as well as in alpine mosses from southern Germany. FOISSNER (1998a) recorded it from the Holarctic, Palaeotropical, and Australian regions. The Austrian neotype population is from a meadow in the town of Salzburg. The Namibian population was found at site (66), namely, in mud taken from rock-pools in the dolomite hills at the south margin of the Etosha Pan. In Costa Rica, *P. terricola* occurred in mud from rock-pools at the bank of the Rio Corobici, Central America (10°28'N 85°10'W). A further population was found in red soil from Alice Springs, Australia (24°S 133°E). In Namibia and Costa Rica, *P. terricola* was associated with → *Wolfkosia loeffleri*. Generally, *P. terricola* is a common species in a wide variety of terrestrial habitats, possibly preferring nutrient-rich soils.

Comparison with original description and related species: The original description of *C. terricola* is rather incomplete and confusing because KAHL (1931b) mentions features in the key that are not shown in the illustration, especially the caudal cilium, which is, indeed, not very pronounced in this species (Fig. 120a, g). Another difference, namely, the size of the oral apparatus (40% vs. 60% of body length), could indicate that we are dealing with different species. However, in over 1000 moss and soil samples we found only four *Cyclidium* s.l. species, viz., *Protocyclidium muscicola* (most common), *Cyclidium glaucoma* (very infrequent), → *Apocyclidium obliquum* (mainly in saline soils), and populations like those described here. Thus, it is reasonable to assume that our populations are conspecific with the forgotten *C. terricola* KAHL, 1931b. Generally, this species shows a rather high interpopulation variability (see above), especially in the distinctness and arrangement of the extrusomes, the body shape, the length of the second and last ciliary row, and the occurrence of condensed cilia in the anterior portion of kinety 1. This might indicate that it is a sibling species complex (see also next paragraph).

Protocyclidium terricola highly resembles *P. muscicola*, as redescribed by FOISSNER (1995), especially in the subterminal location of the contractile vacuole. When the following data are taken into account, even main morphometrics overlap slightly. The *P. muscicola* specimens from Namibian site (66) are larger than those from Austria (CHATTON-LWOFF silver nitrate preparation: 18–25 µm vs. 13–17 µm) and are thus rather difficult to separate from small individuals of *P. terricola* (CHATTON-LWOFF silver nitrate preparation: 26–31 µm in Austrian and 29–39 µm in Namibian population). However, they are usually distinguishable by body size (CHATTON-LWOFF silver nitrate preparation: 15 µm in Austrian and 22 µm in Namibian specimens vs. 28 µm in Austrian and 33 µm in Namibian specimens) and number of ciliary rows (9–10 vs. 12–16).

Protocyclidium sphagnetorum (ŠRÁMEK-HUŠEK, 1949) is distinguished from *P. terricola* mainly by the zoochlorellae (present vs. absent). The location of the excretory pore is similar in both species, namely underneath the level of the peristomial vertex near the end of the posteriorly shortened kinety 2 (STRÜDER 1991, WILBERT 1986). Thus, GROLIÈRE (1973) obviously misinterpreted an extrusome attachment site within the peristomial area as excretory pore. *Protocyclidium citrullus* (COHN, 1866) has the same adoral pattern as *P. terricola* because CZAPIK (1963) obviously misinterpreted the left margin of the cytostome as membranelle 3. This is substantiated by the observations of WILBERT (1995) and ESTEBAN et al. (2000). According to these redescriptions and KAHL (1931b), *P. citrullus* and *P. terricola* differ in the number of ciliary rows (14–16 vs. 10–15), the location of the contractile vacuole (terminal vs. distinctly subterminal), and the indentation containing the caudal cilium complex (present vs. lacking).

Pseudocohnilembus binucleatus **nov. spec.** (Fig. 121a–h; Table 103)

Diagnosis: Size about 30 × 15 µm in vivo; lanceolate. 2 macronuclear nodules and 7 somatic kineties. Excretory pore of contractile vacuole at end of kinety 3.

Type location: Highly saline soil from margin of Etosha Pan, Namibia, 19°10'S 15°55'E (site 59 in figures 2, 3 and chapter 2.1.2).

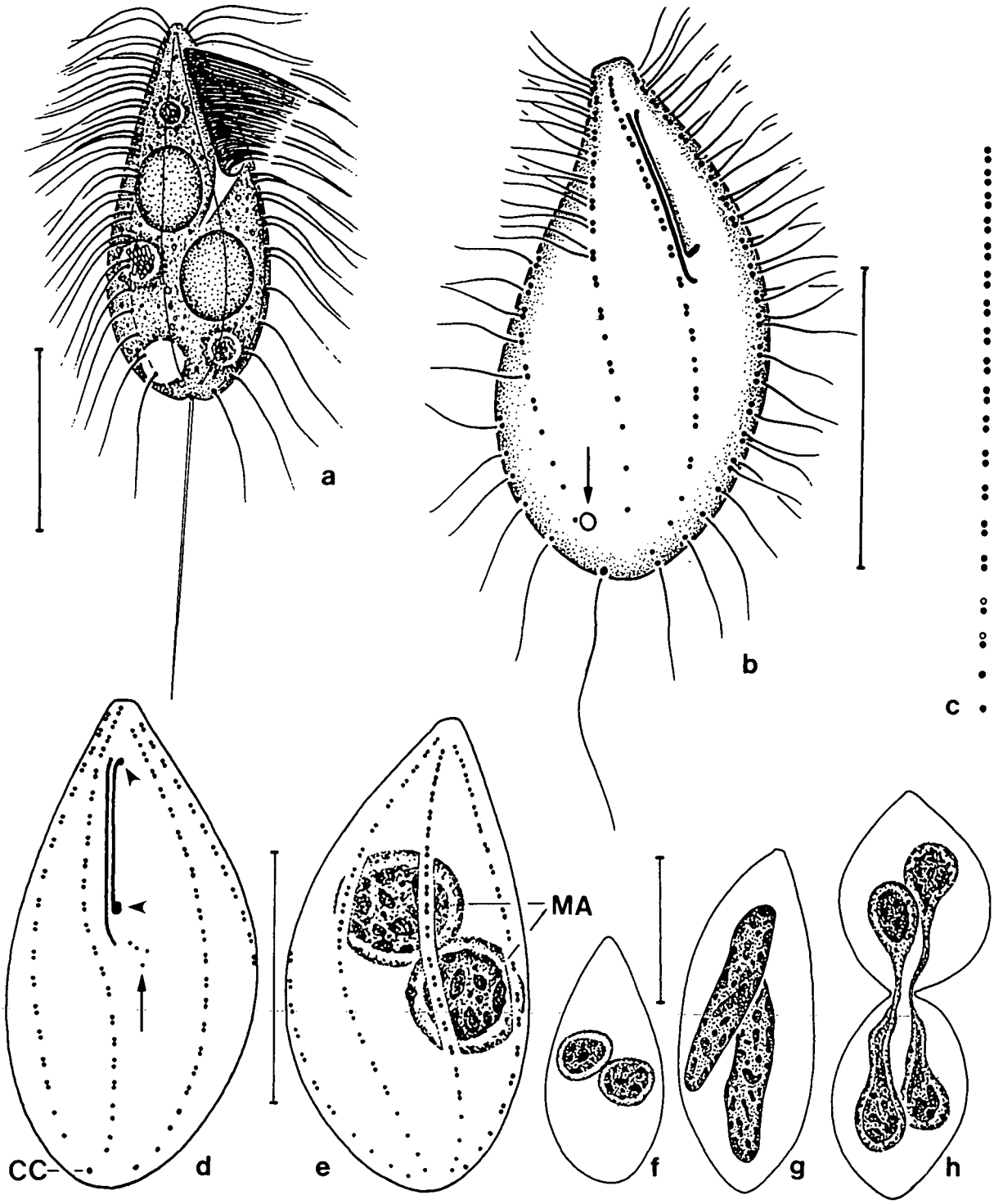


Fig. 121a–h. *Pseudocohnilembus binucleatus* from life (a) and after protargol impregnation (b–h). **a, b:** Ventrolateral views of representative specimens. Arrow marks excretory pore of contractile vacuole at end of kinety 3. **c:** Ciliary pattern of a kinety. Unciliated basal bodies shown by contour. **d, e:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrow marks scutica. Upper arrowhead denotes thickened end of adoral membranelle 2, lower marks membranelle 3 at proximal end of membranelle 2. **f–h:** Morphostatic specimen, middle divider, and very late divider, showing that both nuclei divide. Drawn to scale. CC – caudal cilium, MA – macronuclear nodules. Scale bars 15 µm.

Etymology: The Latin *binucleatus* (two nuclei) refers to the main feature of the species, that is, the two macronuclear nodules.

Description: Size 20–40 x 10–20 µm in vivo. Shape lanceolate to ovate, length:width ratio 1.7–2.6:1, on average 2:1; unflattened. Macronuclear nodules in middle third of cell, slightly ellipsoidal, nuclear membrane more or less distinctly separate from chromatin in prepared specimens (Fig. 121e, f). Of 122 specimens investigated, 2 have one macronucleus, 118 have two nuclei, 1 has three nuclei, and 1 even has four. Very likely amicronucleate because micronuclei recognizable neither in morphostatic nor dividing specimens (Fig. 121f–h). Contractile vacuole in rear end, excretory pore at end of kinety 3 (Fig. 121a, b). Cortex bright, flexible. No extrusomes recognizable. Feeds on bacteria. Swims rather rapidly by rotation about main body axis.

Somatic cilia about 8 µm long in vivo, invariably arranged in 7 slightly spiralling rows, distances between kinetids increase slightly from anterior to posterior. All kineties composed of dikinetids, except near posterior end, where some monokinetids occur; furthermore, some posterior dikinetids have only the posterior basal body ciliated. Caudal cilium in centre of posterior pole, about as long as cell (Fig. 121a–c).

Oral apparatus as in other members of genus (FOISSNER et al. 1994, POMP & WILBERT 1988), extends to mid-body. Buccal field triangular and very flat. Cilia of adoral membranelles and paroral membrane about 8 µm long, decrease in length proximally, form conspicuous velum in vivo. Adoral membranelle 2 slightly thickened anteriorly, membranelle 3 at proximal end of membranelle 2, rectangular, minute. Scutica at buccal vertex, usually recognizable only in early dividers (Fig. 121a, b, d).

Table 103. Morphometric data on *Pseudocohnilembus binucleatus*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	26.1	25.0	3.5	0.8	13.2	20.0	32.0	21
Body, width	13.1	13.0	2.5	0.5	17.2	10.0	17.0	21
Anterior body end to membranelle 2, distance	2.4	2.5	–	–	–	2.0	3.0	21
Anterior body end to membranelle 3, distance	11.2	11.0	1.0	0.2	8.8	10.0	13.0	21
Anterior body end to macronuclei, distance	8.3	8.0	1.6	0.3	18.8	5.0	12.0	21
Macronuclei, length	7.0	7.0	1.2	0.3	17.5	5.0	9.0	21
Macronuclei, width	6.2	6.0	1.0	0.2	15.8	5.0	8.0	21
Macronuclei, number [b]	2.0	2.0	–	–	–	1.0	4.0	122
Macronuclei, number in dividers	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Somatic ciliary rows, number	7.0	7.0	0.0	0.0	0.0	7.0	7.0	21
Kinetids in a dorsal kinety, number [c]	19.4	19.0	1.9	0.4	9.8	16.0	22.0	21

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a wheat grain culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Of the 122 specimens investigated, 2 have one macronucleus, 118 have two macronuclei, 1 has three nuclei, and 1 has four nuclei.

[c] Dikinetids counted as 1 kinetid!

Occurrence and ecology: To date found only at margin of Etosha Pan (site 59). Obviously euryhaline, as are all other species of the genus.

Comparison with related species: All congeners have a single macronucleus (for reviews, see FERNANDEZ-LEBORANS & NOVILLO 1994, FOISSNER & WILBERT 1981, FOISSNER et al. 1994), distinctly setting off the binucleate Namibian population; very rarely specimens occur with 1, 3 or 4 nuclei (Table 103). Both nuclei divide and are thus not a certain stage of the life cycle (Fig. 121f–h). Two macronuclear nodules are unusual for this kind of scuticociliates. However, SONG (1993) described a similar exception in the genus *Homalogastra*.

A second feature separating *P. binucleatus* from all described species (but see → *P. persalinus hexakineta*, described below) is the possession of only 7 ciliary rows, while the other species have 8–14. However, the number of ciliary rows is not entirely constant in different populations of the same species and must thus be used cautiously (FOISSNER et al. 1994, THOMPSON 1965).

Recently, we studied a *Pseudocohnilembus* from a saline soil in the USA. It has 6–8 ($\bar{x}$ = 7) ciliary rows and one (57%) or two (43%) macronuclei, casting doubts on the species status of the Namibian population.

Pseudocohnilembus persalinus hexakineta **nov. sspec.** (Fig. 122a–i ; Table 104)

Diagnosis: *Pseudocohnilembus persalinus* with 6 or 7 ciliary rows, depending on population.

Type location: Sedge girdle at margin of Etosha Pan, Namibia, 19°10'S 15°55'E (site 61 in figures 2, 3 and chapter 2.1.2).

Etymology: Greek apposition composed of *hexa* (six) and *kinetes* (~ ciliary row), referring to the main feature of the subspecies, viz., six ciliary rows.

Description and comparison with literature data and related species (for literature, see FERNANDEZ-LEBORANS & NOVILLO 1994, FOISSNER & WILBERT 1981, and SONG 2000): SONG (2000) considerably amended and excellently reviewed the data available on various *P. persalinus* populations and concluded: "(i) the structure of the buccal apparatus of all *Pseudocohnilembus* species is extremely similar; (ii) many diagnostic characters (e.g. body size, number and position of contractile vacuole pores) appear to be population-dependent and overlap among species; and (iii) most species have been described from silver-impregnated specimens with little information about the living morphology". We fully agree with SONG's conclusions and would like to supplement them with a fourth one, viz., that the fine details of the oral structures and silverline pattern are highly dependent on the quality of the preparations and the methods used.

SONG (2000) suggests *P. marinus* and *P. longisetus* as junior synonyms of *P. persalinus*, while FOISSNER & WILBERT (1981) synonymize *P. persalinus* and *P. longisetus* with *P. pusillus*. Although we still hold this view, we follow SONG (2000) at the present state of knowledge.

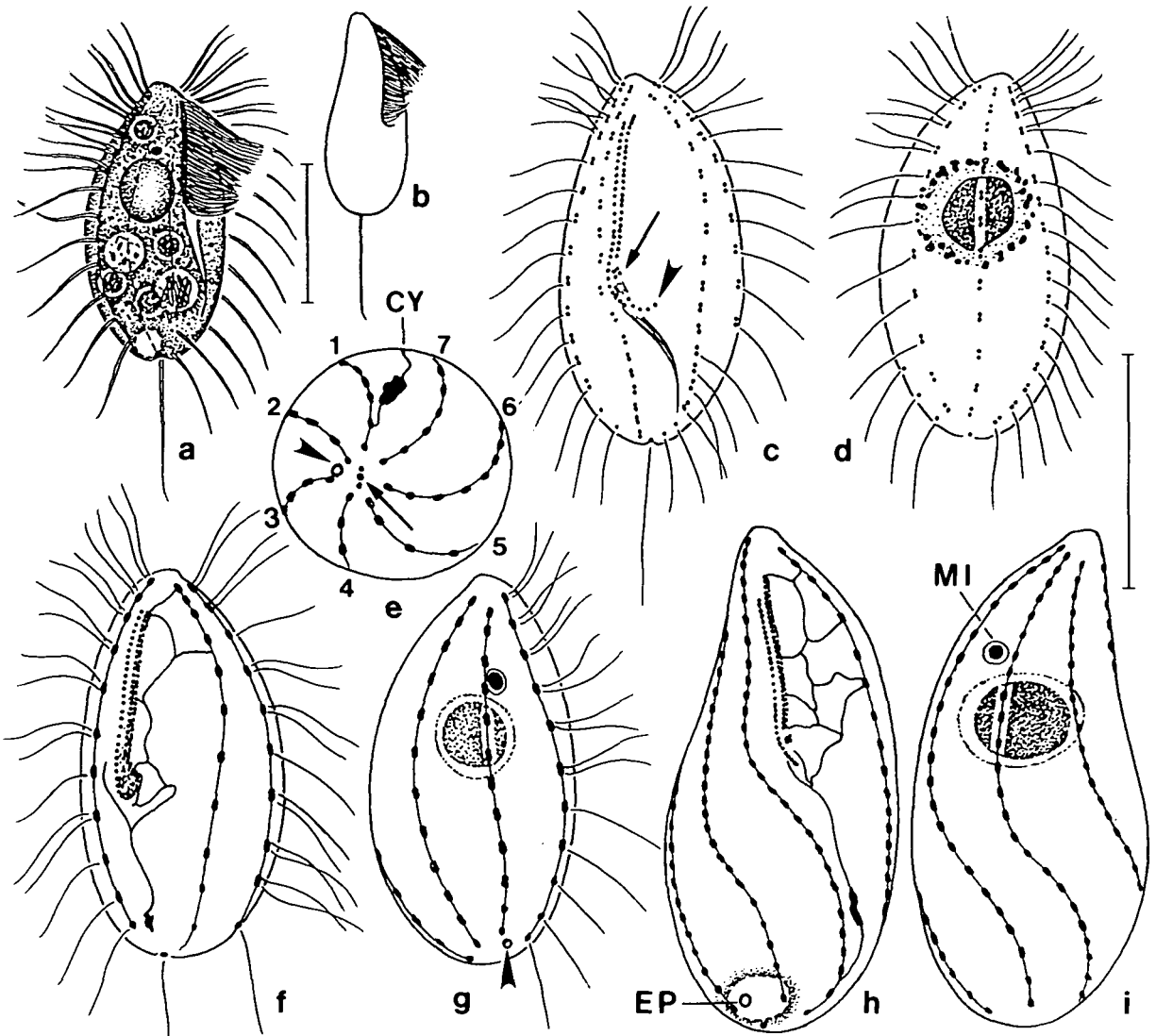


Fig. 122a–i. *Pseudocohnilembus persalinus hexakineta* from life (a, b) and after protargol (c, d) and CHATTON-LWOFF silver nitrate (e–i) impregnation. **a, b:** Ventrolateral view of representative specimens from sites (61) and (14), length 30 µm and 40 µm. **c, d:** Ciliary pattern of ventral and dorsal side and nuclear apparatus of holotype specimen from site (61). Arrow marks adoral membranelle 3. Arrowhead denotes part (?) of scutia. The macronucleus is enveloped by loose granules. **e–g:** Posterior polar and ventral and dorsal view of specimens from site (39). Arrow marks the caudal cilium complex. Arrowheads denote excretory pore of contractile vacuole at end of kinety 3. Numbers mark ciliary rows. **h–i:** Ciliary pattern of ventral and dorsal side and nuclear apparatus of a large specimen with six, distinctly spiralled ciliary rows from site (14). Note excretory pore at end of kinety 3. CY – cytopyge, EP – excretory pore, MI – micronucleus. Scale bars 30 µm (a, c–i).

Most Namibian *Pseudocohnilembus* populations are unique in having only six or seven ciliary rows, even the new species → *P. binucleatus*; typical *P. persalinus* populations with eight or nine kineties occur only at sites (31, 32). We separate the six and seven-rowed Namibian populations at subspecies level because all described *Pseudocohnilembus* species (about 10) and populations (about 20) have eight or more ciliary rows. All other features are highly similar to *P. persalinus*, as described by EVANS & THOMPSON (1964) and redescribed by

SONG (2000). The populations from sites (39) and (61) are ovoidal and thus look like a *Cyclidium* (Fig. 122a, c–g), while the large cells from site (14) are lanceolate and thus look like a typical *Pseudocohnilembus* (Fig. 122b, h, i), but have distinctly spiralled kineties. However, the site (14) population also contains small individuals very similar to those from sites (39) and (61), that is, with straight or only slightly spiralled ciliary rows; possibly, the large cells are some sort of giants, although the oral apparatus is not enlarged (Table 104).

Occurrence and ecology: This species was found at thirteen sites (Table 4). All are saline, most highly saline, showing that *Pseudocohnilembus persalinus hexakineta* is a eurytopic and euryhaline species. It also confirms FOISSNER (1987d) that *Pseudocohnilembus* spp. indicate soil salinity.

Table 104. Morphometric data on *Pseudocohnilembus persalinus hexakineta* from Namibian sites 61 (type; upper line), 39 (middle line), and 14 (lower line).

Characteristics [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	PA	26.0	25.0	2.7	0.6	10.4	21.0	33.0	21
	CHL	26.2	26.0	2.2	0.5	8.5	23.0	30.0	21
	CHL	33.4	33.0	2.7	0.6	8.2	28.0	38.0	21
Body, width	PA	13.2	13.0	1.5	0.3	11.4	11.0	16.0	21
	CHL	13.7	14.0	1.5	0.3	11.2	10.0	16.0	21
	CHL	16.5	17.0	2.4	0.5	14.4	12.0	20.0	21
Body length:width, ratio	PA	2.0	1.9	0.2	0.1	9.8	1.7	2.4	21
	CHL	1.9	1.9	0.2	0.1	10.2	1.7	2.5	21
	CHL	2.1	2.0	0.3	0.1	14.8	1.6	2.8	21
Anterior body end to distal end of adoral membranelles, distance	PA	1.8	2.0	–	–	–	1.0	3.0	21
	CHL	2.4	2.0	–	–	–	2.0	3.0	21
	CHL	3.1	3.0	–	–	–	2.5	5.0	21
Anterior body end to proximal end of adoral membranelles, distance	PA	14.1	14.0	1.1	0.2	8.0	12.0	16.0	21
	CHL	15.3	15.0	0.8	0.2	5.2	14.0	17.0	21
	CHL	17.8	18.0	2.1	0.5	12.1	14.0	21.0	21
Body length:distance to proximal end of adoral membranelles, ratio	PA	1.9	1.8	0.2	0.1	9.5	1.5	2.2	21
	CHL	1.7	1.7	0.1	0.1	8.0	1.5	2.0	21
	CHL	1.9	1.9	0.2	0.1	9.4	1.7	2.4	21
Buccal cavity, width at broadest site	PA	4.8	5.0	0.5	0.1	11.3	4.0	6.0	21
	CHL	4.7	5.0	0.7	0.2	15.7	3.0	6.0	21
	CHL	4.6	5.0	–	–	–	4.0	5.0	21
Anterior body end to macronucleus, distance	PA	7.0	7.0	1.2	0.3	17.3	4.0	9.0	21
	CHL	7.4	7.0	1.5	0.3	20.3	5.0	11.0	21
	CHL	8.7	9.0	1.1	0.2	12.8	6.0	11.0	21
Macronucleus, length [b]	PA	5.7	6.0	0.7	0.2	12.6	5.0	7.0	21
	CHL	6.2	6.0	0.9	0.2	14.3	5.9	9.0	21
	CHL	8.3	9.0	1.0	0.2	12.2	7.0	10.0	21
Macronucleus, width [b]	PA	5.0	5.0	0.6	0.1	11.9	4.0	6.0	21
	CHL	5.9	6.0	0.8	0.2	13.0	4.0	7.0	21
	CHL	8.0	8.0	1.0	0.2	12.9	6.0	10.0	21
Ciliary rows, number	PA	7.0	7.0	0.0	0.0	0.0	7.0	7.0	21
	CHL	6.1	6.0	–	–	–	6.0	7.0	21

(continued)

Characteristics [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	CHL	6.2	6.0	0.5	0.1	8.3	6.0	8.0	21
Kinetids in kinety 1, number [c]	PA	17.2	17.0	1.6	0.4	9.3	13.0	21.0	21
	CHL	13.6	14.0	1.1	0.2	8.2	12.0	15.0	21
	CHL	20.7	20.0	3.8	0.8	18.3	14.0	29.0	21
Kinetids in kinety 4, number [c]	PA	13.7	14.0	1.3	0.3	9.4	12.0	17.0	21
	CHL	12.2	12.0	1.1	0.2	8.9	10.0	15.0	21
	CHL	19.7	20.0	3.2	0.7	16.1	14.0	26.0	21
Excretory pore attached to kinety	PA	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	CHL	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	CHL	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21

[a] Data based on mounted and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CHL – silver nitrate after CHATTON-LWOFF, CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, PA – protargol (FOISSNER's method), SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Only the central, compact part was measured.

[c] Dikinetids counted as 1 kinetid!

PROSTOMATIDA

Holophrya salinarum nov. spec. (Fig. 123a–f; Table 105)

Diagnosis: Size about 220 × 130 µm in vivo; broadly ellipsoidal. On average 17 globular macronuclear nodules forming a transverse ring in mid-body. Oral extrusomes rod-shaped and approximately 35 × 0.5 µm in size, body extrusomes slightly fusiform and approximately 4 µm long. About 250 somatic ciliary rows, 3 anteriorly differentiated to dorsal brush.

Type location: Highly saline pan soil from the Etosha National Park, Namibia, 18°55'S 16°25'E (site 65 in figures 2, 3 and chapter 2.1.2).

Etymology: The Latin plural noun *salinarum* (saline environments) refers to the saline habitat the species was discovered.

Description: This conspicuous ciliate was very rare and thus the data are incomplete. However, the main features were observed both in vivo and silver nitrate preparations and are so distinct that it appears justified to describe the organism as a new species.

Size 160–270 × 100–150 µm in vivo, usually near 220 × 130 µm; length:width ratio on average 1.6:1 both in vivo and silver nitrate preparations (Table 105). Shape broadly ellipsoidal to ellipsoidal, slightly narrower anteriorly than posteriorly, that is, indistinctly ovate; unflattened and acontractile (Fig. 123a). Cells brownish under low magnification (≤ ×100) and bright field illumination due to the large size and cytoplasmic inclusions, both making specimens rather refractive and opaque. Macronucleus extraordinary, that is, composed of an average of 17 globular nodules forming a transverse ring in or near mid-body (Fig. 123a, c, f). Micronuclei not seen. Contractile vacuole in posterior body end, about 15–30 excretory pores in posterior pole area. Two types of extrusomes (Fig. 123b–e): oral extrusomes found only in pharyngeal basket, rod-shaped and slightly curved, about 35 × 0.5 µm in size; body extrusomes indistinctly fusiform, approximately 4 µm long, scattered within and among ciliary rows, as indicated by the silverline circles surrounding docked organelles. Cortex thick and moderately flexible, indistinctly furrowed by ciliary rows, has attached extrusomes as described above. Cytoplasm conspicuously vacuolated providing cells with a foamy appearance, contains many concentrically laminated starch grains up to 35 µm across, possibly from small seeds. Swims rather rapidly by rotation about main body axis.

Cilia about 15 µm long in vivo, arranged in about 250 bipolar, very closely spaced (1.5–2 µm) and densely ciliated rows, anterior third of three rows differentiated to dorsal brush, whose details are not recognizable in the silver preparations (Fig. 123f).

Oral basket large, that is, occupies about one third of body diameter, projects distinctly from body proper, composed of many fine rods forming rather distinct bundles; basket anteriorly filled with extrusomes, as described above, and refractive granules producing a dark ribbon under bright field illumination, similar to *Homalozoon* (Fig. 123a, f). Circumoral ciliature not clearly recognizable in the silver nitrate preparations.

Occurrence and ecology: To date found only at the highly saline type location, where

it was very rare. *Holophrya* species are rare in soil, likely due to their clumsy, rather inflexible body (FOISSNER 1998a). Actually, it is possible that *H. salinarum* is not a soil inhabitant but a limnetic species optimally reproducing when the pan is flooded.

Classification and comparison with related species: Previously, species like *Holophrya salinarum* were classified in *Prorodon* because most authors were unaware of the type species fixed by FROMENTEL (1875). See FOISSNER et al. (1994) for a detailed discussion. The Namibian population is classified in *Holophrya* because its general organization matches typical members of that genus, such as *H. ovum* and *H. teres* (see FOISSNER et al. 1994 for a brief review on these species). *Holophrya salinarum* has two unique features, viz., the ring-like arranged macronuclear nodules and the long oral extrusomes, distinguishing it from all congeners. Likewise, the high number of ciliary rows (about 250) is found only in one other species, that is, *H. spirogyrophaga* (LEIPE 1989) nov. comb. (basionym: *Prorodon spirogyrophagus* LEIPE 1989), which has about 230 rows, scattered contractile vacuoles, and a globular macronucleus. Thus, *H. salinarum* is a very distinct species easily to identify both in vivo and in silver preparations.

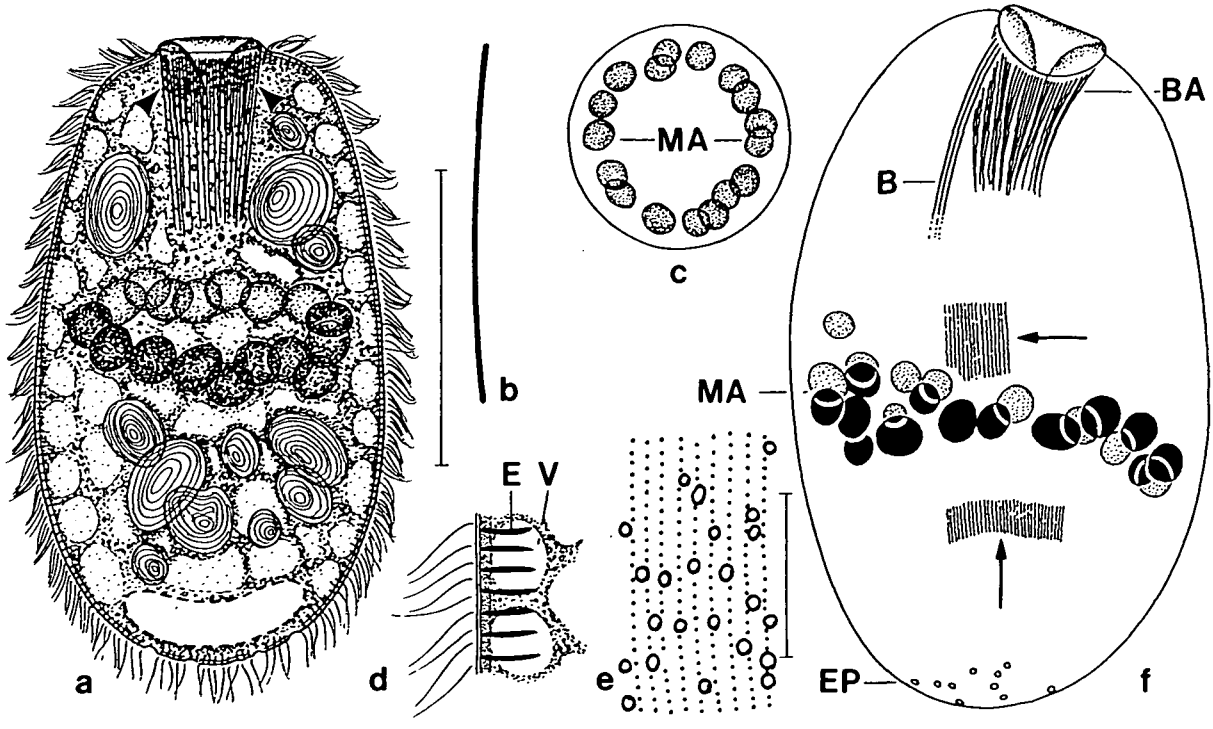


Fig. 123a–f. *Holophrya salinarum* from life (a–d) and after CHATTON-LWOFF silver nitrate impregnation (e, f). **a:** A representative specimen showing the ring of macronuclear nodules in mid-body and the strongly vacuolated cytoplasm containing small and large starch grains. Arrowheads mark zone of refractive granules in oral basket. **b:** Oral extrusome, about 35 × 0.5 µm. **c:** Schematic transverse view showing the ring of macronuclear nodules in mid-body. **d:** Optical section of cortex studded with about 4 µm long, slightly fusiform extrusomes. **e:** Surface view showing ciliary rows and silverline rings surrounding docked extrusomes. **f:** Dorsal view of holotype specimen. Arrows mark areas where the closely spaced ciliary rows are recognizable. B – dorsal brush, BA – oral basket, E – extrusomes, EP – excretory pores of contractile vacuole, MA – macronuclear nodules, V – vacuoles.

Table 105. Morphometric data on *Holophrya salinarum*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	201.0	205.0	35.1	15.7	17.4	145.0	242.0	5
Body, width	126.6	117.0	19.4	8.7	15.3	108.0	150.0	5
Body length:width, ratio	1.6	1.7	0.2	0.1	13.5	1.3	1.8	5
Anterior body end to nuclear figure, distance	94.4	87.0	16.1	7.2	17.1	80.0	120.0	5
Macronuclear nodules, length	14.8	15.0	2.5	1.1	16.8	11.0	17.0	5
Macronuclear nodules, width	13.4	13.0	2.5	1.1	18.7	10.0	17.0	5
Macronuclear nodules, number	17.2	17.0	5.3	2.4	30.6	10.0	24.0	5
Somatic kineties, number [b]	253.8	245.0	58.5	26.2	23.1	169.0	314.0	5
Distances between kineties in mid-body	1.5	1.5	–	–	–	1.5	2.0	5
Oral basket, width at anterior end	37.5	39.0	13.0	5.3	34.8	16.0	55.0	6

[a] Data based on six mounted, CHATTON-LWOFF silver nitrate-impregnated specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Calculated from distances between ciliary rows, assuming a circular transverse section ($2\pi r$).

Family Plagiocampidae KAHL, 1926

FOISSNER (1997b) and FOISSNER & PFISTER (1997) included *Urotricha* in the Plagiocampidae, while SMALL & LYNN (1985) established a new family for *Urotricha* and some related genera with features hardly justifying such a separation (paroral dikinetids as circle vs. semicircle). However, our data from → *Plagiocampa pentadactyla* now support a separation of *Urotricha* and *Plagiocampa* at familial level because the cortical pattern is distinctly different from that of *Urotricha* and highly reminiscent of that found in *Holophrya* (Fig. 124k). Thus, *Plagiocampa* possibly belongs to the holophryids, although its general organisation is very much like that of *Urotricha*.

Plagiocampa pentadactyla nov. spec. (Fig. 124a–l; 374a–e; Table 106)

Diagnosis: Size about 30 × 20 µm in vivo; angular-ellipsoidal due to slight subapical shoulder. Body extrusomes rod-shaped, about 2 µm long. 2 caudal cilia. On average 16 somatic kineties and 4–5 paroral dikinetids (oral flaps).

Type location: Field soil in the surroundings of the town of Cotonou, Benin, Africa, 06°N 02°30'E.

Etymology: The Greek *pentadactyla* (five-fingered) refers to the five, finger-like oral flaps.

Description: We studied five populations of this species (see "occurrence and ecology"). They are very similar, in spite of the large geographical distances. Thus, the diagnosis and description comprise all populations. Morphometric data, however, are kept separate (Table 106).

Size in vivo 25–40 × 15–25 µm (African populations) or 20–35 × 12–25 µm (Chinese and Tenerife populations). Body shape highly characteristic, viz., slightly hexagonal due to a more or less distinct subapical shoulder, usually slightly broadening posteriorly (type and Chinese population, Fig. 124a, f) or anteriorly (South African specimens, Fig. 124g), inconspicuously asymmetrical because laterally up to 1.5:1 flattened and dorsal side usually more distinctly convex than ventral (Fig. 124a; Table 106). Macronucleus in or near body centre, globular, contains small, pale nucleoli. Micronucleus not seen, not impregnated by protargol. Contractile vacuole in posterior end, slightly eccentric, with single excretory pore very near to caudal cilia (Fig. 124a, l). Cortex about 0.8 µm thick, flexible, distinctly furrowed by ciliary rows in anterior third, contains complicated alveolar pattern occasionally recognizable in vivo and in protargol-impregnated specimens (Fig. 124k; 374c); has attached minute (2–2.5 µm long), rod-shaped (Chinese population) to slightly cuneate (African population) extrusomes mainly in anterior two thirds of cell (Fig. 124a, h; 374e); right side of most populations densely covered with about 3 µm long, rod-shaped epipellicular bacteria, many of which contain a bright spore (Fig. 124e; 374a, d, e). Usually rather dark at low (≤ ×100) magnification in posterior half due to many colourless, bright (refractive) lipid droplets 1–3 µm across. Food vacuoles mainly in anterior body half, 5–10 µm across, contain compact material, likely remnants from protozoan prey. Most specimens from type and South African population packed with, very likely parasitic, about 4 µm long bacteria having slightly narrowed ends and bright, ellipsoidal spores (Fig. 124a, d; 374a). Swims rather rapidly by rotation about main body axis jerkily changing direction, but does not jump.

Ordinary somatic cilia 6–7 µm (11 µm in South African specimens) long, arise from deep cortical pits, slightly more closely spaced anteriorly than posteriorly. Caudal cilia about as long as body, for instance, 35 µm in a Venezuelan specimen, and thus conspicuous, distal third thread-like narrowed; very fragile and frequently shed when cells are immobilised by cover glass pressure. Ciliary rows extend meridionally and equidistantly, commence at oral opening with a pair of basal bodies, slightly shortened posteriorly leaving blank small pole area, the centre of which invariably bears the two caudal cilia described above (Fig. 124a, f, g, i, j, l; 374b, d, e).

Oral opening in centre of anterior pole, rather conspicuous, although being only 2–3 µm across, due to protruding oral flaps; dorsal half surrounded by five dikinetids (undulating membrane) associated with about 3 µm long, paired flaps occasionally moving up and down (Fig. 124a–c, f, g). Invariably three adoral organelles (brosse) side by side in minute grooves at ventral half of oral opening; individual organelles minute, each consisting likely of three dikinetids having 1–2 µm long cilia. Pharynx minute (about 2 × 2 µm), pit-like, dorsally longer than ventrally (Fig. 124a, b, i, j).

Occurrence and ecology: To date found at type location (red, slightly saline soil with much litter from fields in the surroundings of Cotonou; sample kindly provided by Prof. Dr. Jean DRAGESCO, France, in June 1993), in the Republic of South Africa (Cape Peninsula, Sirkelsvlei; soil sandy and with many grass roots, flooded during high water of small lake nearby, pH 5.4; collected on 18.02.1995), in China (soil and mud from a by-pass stream near

the Wei Ming hotel in a suburb of Beijing; soil loamy, darkbrown, pH 6.7; collected on 24.06.1995), at Tenerife (south-east coast of Candelaria Island; lightgrey, non-saline soil with some litter, pH 8.2; collected by Dr. Brigitte KRASSNIGG in 1988), in Saudi Arabia, in Venezuela, and at four sites of Namibia (Table 4). These data indicate that *P. pentadactyla* is cosmopolitan having a wide ecological range occurring in both true terrestrial and semi-terrestrial habitats.

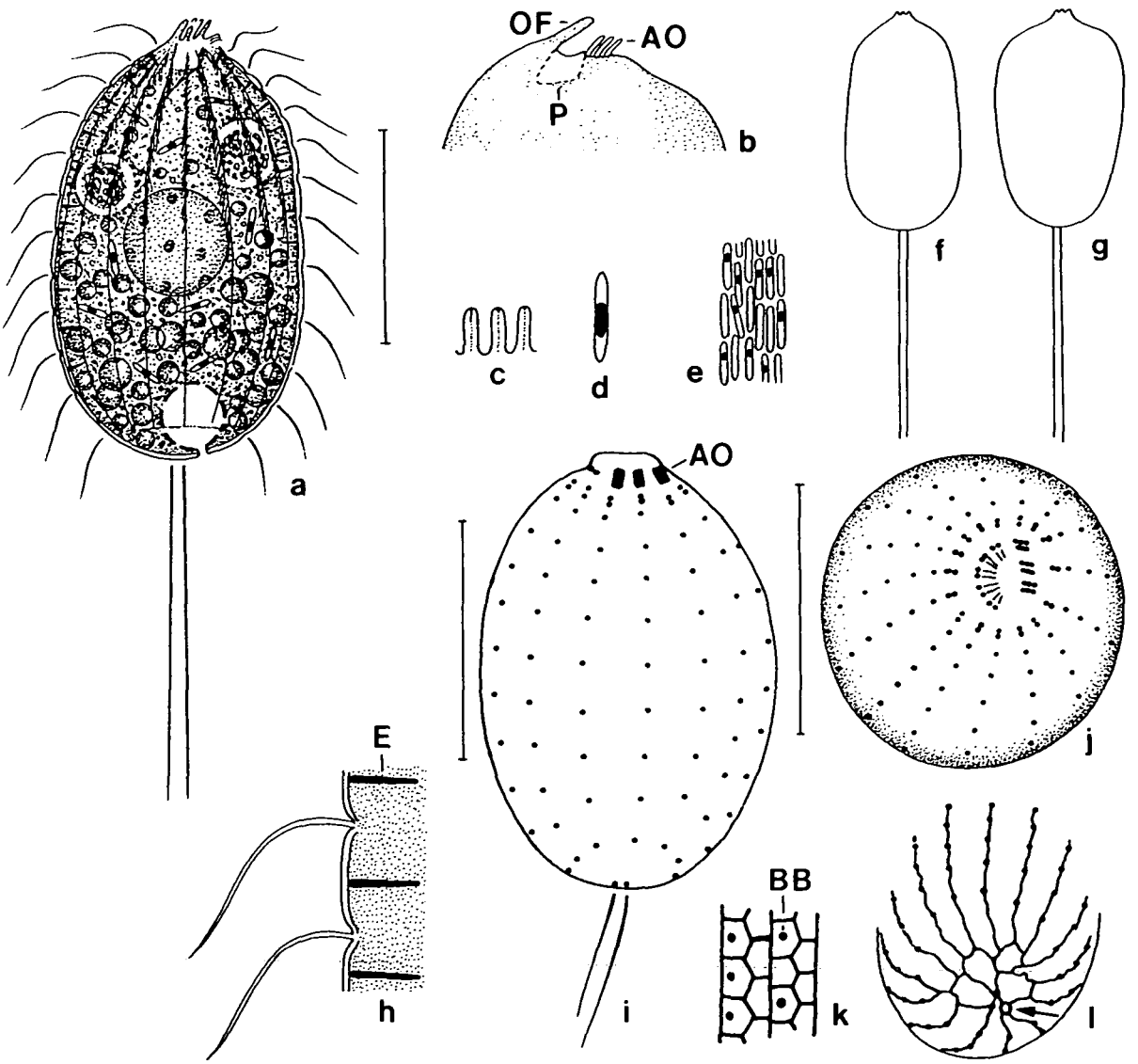


Fig. 124a–l. *Plagiocampa pentadactyla* from life (a–h), after CHATTON-LWOFF silver nitrate impregnation (i, j, l), and after protargol impregnation (k). **a:** Right side view of a representative specimen from type population. **b:** Lateral view of oral structures. **c:** Oral flaps, each composed of two closely spaced, rod-shaped cilia. **d:** Specimens from the type population contained many 4 µm long bacteria with bright, ellipsoidal spores. **e:** Epipellicular, 3 µm long bacteria from Chinese population. **f:** Representative specimen from Chinese population, 30 × 15 µm. **g:** Representative specimen from South African population, 35 × 25 µm. **h:** Optical section of cortex having attached 2 µm long, slightly cuneate extrusomes. **i:** Infraciliature of ventral side of a specimen from type population. **j:** Anterior polar view of infraciliature of a specimen from type population. **k:** Cortex structure of a Chinese specimen. **l:** Oblique posterior polar view of a specimen from type population. Arrow marks excretory pore of contractile vacuole close to the left of the caudal cilia. AO – adoral organelles, BB – basal body, E – extrusome, OF – oral flaps, P – pharyngeal pit. Scale bars 15 µm.

Comparison with related species: There are three other terrestrial *Plagiocampa* species with two caudal cilia, namely, *P. atra* GRANDORI & GRANDORI, 1934, *P. bitricha* FOISSNER, 1999b, and → *P. namibiensis*. *Plagiocampa atra* is considerably larger than *P. pentadactyla* (51 µm vs. 25–40 µm), much more slender (3.1:1 vs. 0.7:1), and has bright, pearl-like mucocysts. → *Plagiocampa bitricha* has a large oral opening surrounded by 14 oral flaps (paroral dikinetids), which are 8 µm long and thus very conspicuous. → *Plagiocampa namibiensis* has three ciliary circlets and a large, unciliated posterior pole area. Further, the somewhat hexagonal body outline and the epipellicular bacteria are highly characteristic for *P. pentadactyla* because both were present in over 20 populations studied so far.

Table 106. Morphometric data on *Plagiocampa pentadactyla* from Benin (B; type location) and China (C).

Characteristics [a]	Population	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	B	29.4	30.0	2.9	0.6	10.0	23.0	33.0	23
	C	22.6	23.0	3.8	1.3	16.2	16.0	30.0	9
Body, width	B	17.8	18.0	2.3	0.5	13.3	12.0	23.0	23
	C	15.0	15.0	3.2	1.1	21.1	9.0	20.0	9
Macronucleus, length	B	not measured because obscured by cytoplasmic inclusions							
	C	6.2	6.0	0.8	0.3	13.4	5.0	8.0	9
Macronucleus, width	B	not measured because obscured by cytoplasmic inclusions							
	C	5.4	5.0	0.7	0.2	13.4	5.0	7.0	9
Somatic ciliary rows, number	B	14.6	15.0	0.6	0.1	4.4	13.0	16.0	23
	C	16.0	17.0	1.4	0.5	8.8	13.0	17.0	9
Cilia in a kinety, number	B	12.8	13.0	1.0	0.2	8.0	10.0	15.0	23
	C	12.0	12.0	1.1	0.4	9.3	11.0	14.0	9
Caudal cilia, number	B	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	C	2.0	2.0	0.0	0.0	0.0	2.0	2.0	9
Oral flaps, number	B	4.8	5.0	–	–	–	4.0	5.0	10
	C	not clearly recognizable							
Brosse rows, number	B	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10

[a] Data based on mounted, CHATTON-LWOFF silver nitrate-impregnated (Benin population) or protargol-impregnated (China population, FOISSNER's method), randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Plagiocampa namibiensis nov. spec. (Fig. 125a–i; 374f–l; Table 107)

Diagnosis: Size about 20 × 15 µm in vivo; ovate. Body extrusomes rod-shaped, about 1 µm long. On average 13–14 somatic kineties with cilia arranged in three distinct circlets. 2 caudal cilia and 4 paroral dikinetids (oral flaps).

Type location: Soil from margin of a pool communicating with the river in the Aubschlucht near the village of Büllsport, Namibia, 24°S 16°20'E (site 30 in figure 2 and chapter 2.1.2).

Etymology: Named after the country discovered.

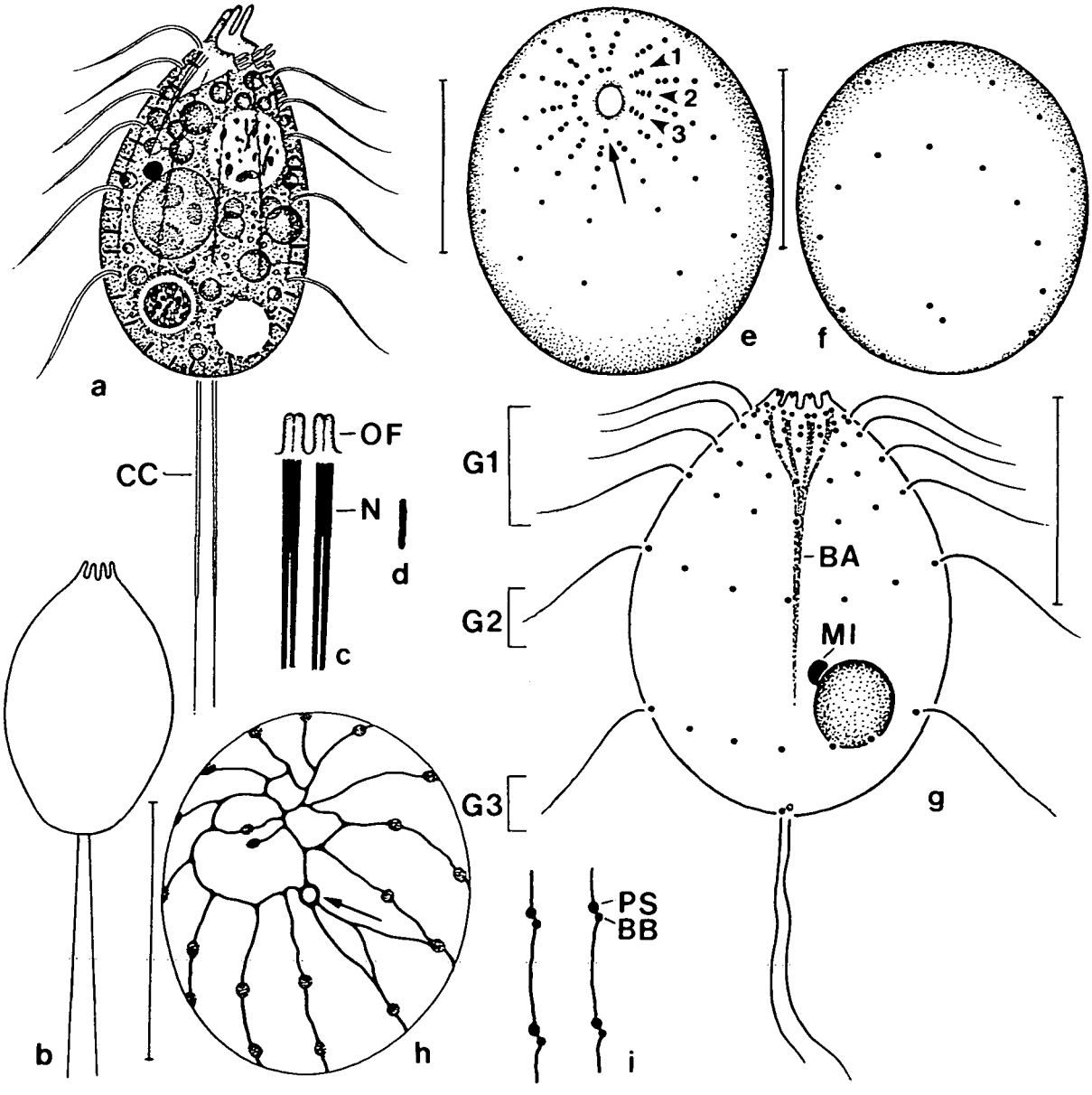


Fig. 125a–i. *Plagiocampa namibiensis* from life (a–d), after protargol impregnation (e–g), and after CHATTON-LWOFF silver nitrate impregnation (h, i). **a:** Ventrolateral view of a representative specimen. **b:** Broadly fusiform shape variant. **c:** Oral structures. **d:** Somatic extrusome, about 1 µm long. **e, f:** Oblique anterior and posterior polar view showing somatic and oral infraciliature. Arrow marks single granule left of paroral membrane, which consists of four dikinetids at dorsal half of oral opening. Arrowheads mark minute adoral organelles. **g:** Infraciliature of dorsal side. The cilia are arranged in three circlets. **h, i:** Infraciliature and silverline pattern in posterior pole area of Benin population. Arrow marks excretory pore of contractile vacuole. BA – oral basket, BB – basal body, CC – caudal cilia, G1-G3 – ciliary circlets, MI – micronucleus, N – nematodesmata (oral basket rods), OF – oral flaps, PS – parasomal sac. Scale bars 10 µm.

Description: We studied two populations of this species (see "occurrence and ecology"). They are very similar, as evident from the morphometric data (Table 107). Thus, the diagnosis and description comprise both populations.

Size 17–27 × 12–18 µm in vivo, that is, very small and thus the two long caudal cilia become especially prominent. Shape ovate to broadly fusiform, slightly asymmetrical because dorsal side more distinctly convex than ventral; posterior end broadly rounded, anterior plug-like narrowed due to projecting oral flaps (Fig. 125a, b). Macronucleus usually in posterior body half, about 5 µm across in vivo, in protargol preparations frequently wrinkled, that is, poorly preserved (Fig. 374i, j). Micronucleus attached or close to macronucleus, about 1 µm across. Contractile vacuole subterminal with single, ventrolateral excretory pore mid-way posterior cilia circlet and caudal cilia (Fig. 125h; 374 l). Somatic extrusomes attached to thin and inconspicuous cortex, rod-shaped and minute, that is, only about 1 µm long and thus difficult to recognize. Cytoplasm colourless, usually contains many lipid droplets 1–3 µm across, mainly in mid-body. Food vacuoles with compact or loose content, possibly from protozoan prey. Swims rather rapidly by rotation about main body axis changing direction frequently by small jumps.

Ordinary somatic cilia about 7 µm long; caudal cilia in centre of posterior pole and distinctly apart from each other and ciliary rows, 20–25 µm long, that is, at least as long as body and thus very prominent, distal third thread-like narrowed (Fig. 125a, b; 374f, g, h, j, l). Ciliary rows extend meridionally and equidistantly, commence at oral opening with a pair of basal bodies each (anterior basal body unciliated and thus often faintly impregnated), posteriorly shortened by about 35% (Table 107), leaving blank large pole area. Five to seven, usually six cilia per row, form three distinct circlets: upper circlet composed of the three to five rather closely spaced anterior cilia of each row, middle and posterior circlet formed by penultimate and last cilium of each row (Fig. 125a, f, g; 374f–h, k, l). Basal bodies with single parasomal sac at right, connected by meridionally extending, slightly wrinkled silverlines forming wide-meshed lattice in posterior pole area and connecting ciliary rows with caudal cilia and excretory pore of contractile vacuole (Fig. 125h, i; 374 l).

Oral opening in centre of anterior pole, rather conspicuous, although being only 2–3 µm across, due to the protruding oral flaps; dorsal half surrounded by four dikinetids (undulating membrane; at right end frequently a single granule, likely an incomplete dikinetid) associated with about 2 µm long, paired flaps occasionally moving up and down (Fig. 125a, c, e; 374g, i). Invariably three adoral organelles (brosse) side by side at ventral half of oral opening; individual organelles minute, each consisting of three (di?) kinetids having 1–2 µm long cilia; proximal kinetid of organelles 1 and 2 very likely bare because frequently smaller and more faintly impregnated than distal kinetids (Fig. 125e; 374i). Pharynx inconspicuous, obconical, extends obliquely to dorsal side of cell, dorsal wall supported by nematodesmata originating from paroral dikinetids and uniting subapically to extend as a single bundle into posterior half of cell (Fig. 125a, g).

Occurrence and ecology: To date found at type location (site 30) and in Benin (red, slightly saline field soil with much litter from the surroundings of Cotonou; sample kindly provided by Prof. Dr. Jean DRAGESCO, France, in June 1993), where it occurred together with → *Plagiocampa pentadactyla*. The occurrence in both undisturbed, humous soil from the flooded margin of a pond and in red, slightly saline field soil indicates that *P. namibiensis* has a wide ecological range.

Comparison with related species: *Plagiocampa namibiensis* is well-defined by the minute size, the two conspicuous caudal cilia, and the three ciliary circlets. The large, unciliated posterior pole area is highly reminiscent of the genus *Urotricha*.

Table 107. Morphometric data on *Plagiocampa namibiensis* from Namibia (N; type location) and Benin (B).

Characteristics [a]	Population	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	N	17.6	17.0	1.8	0.4	10.2	15.0	21.0	19
	B	20.5	21.0	2.0	0.5	9.7	17.0	24.0	19
Body, width	N	13.0	14.0	1.6	0.4	12.3	11.0	15.0	19
	B	13.1	13.0	1.6	0.4	14.1	11.0	16.0	19
Anterior body end to end of ciliary rows	N	13.3	12.0	2.0	0.5	14.6	11.0	19.0	19
Macronucleus, length	N	5.3	5.0	–	–	–	5.0	6.0	19
Macronucleus, width	N	4.0	4.0	1.1	0.3	27.6	2.0	6.0	19
Somatic ciliary rows, number	N	13.7	14.0	0.6	0.1	4.3	13.0	15.0	19
	B	12.7	13.0	–	–	–	12.0	13.0	19
Kinetids in a dorsal kinety, number [b]	N	6.0	6.0	0.0	0.0	0.0	6.0	6.0	19
	B	6.1	6.0	–	–	–	5.0	7.0	19
Caudal cilia, number	N	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
	B	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
Oral flaps, number [c]	N	3.9	4.0	–	–	–	3.0	4.0	19
Brosse rows, number	N	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
Ciliary circlets, number	N	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
	B	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19

[a] Data based on mounted, protargol-impregnated (Namibia population, FOISSNER's method) and CHATTON-LWOFF silver nitrate-impregnated (Benin population), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Dikinetid at anterior end counted as 1 kinetid.

[c] Without the single kinetid present in some specimens.

Plagiocampa ovata GELEI, 1954 (Fig. 126a–c; Table 108)

This species was thoroughly redescribed and neotypified by FOISSNER (2000a), who also discussed in detail the taxonomic problems. Thus, we provide only a brief account, emphasizing deviating features. Generally, the Namibian specimens are slightly larger than those from Madeira and thus fit better to the Hungarian specimens of GELEI (1954). However, basically the Namibian specimens match very well the Madeiran neotype population (Table 108), except in having not two but only one dikinetid at the anterior end of the ciliary rows. This is a rather prominent difference which, however, must not be over-interpreted because the second dikinetid is more variable than the first, that is, may have both basal bodies ciliated

or only the posterior one (FOISSNER 2000a, Fig. 53, 71). The lack of the second dikinetid makes the Namibian specimens rather similar to *P. bitricha* FOISSNER, 1999b, except for the number of caudal cilia: one in *P. ovata*, two in *P. bitricha* (Table 108).

Table 108. Morphometric data on *Plagiocampa ovata* from Madeiran neotype population (first line; from FOISSNER 2000a) and Namibian site 51 (second line). The third line is *P. bitricha* from FOISSNER (1999b).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	24.3	25.0	2.7	0.8	11.1	20.0	28.0	11
	28.6	28.0	2.2	0.5	7.7	25.0	33.0	19
	33.1	33.0	2.1	0.6	6.3	30.0	36.0	11
Body, width	14.7	14.0	2.2	0.7	14.9	11.0	18.0	11
	18.0	18.0	2.0	0.5	11.0	15.0	21.0	19
	24.7	25.0	2.4	0.7	9.6	21.0	29.0	11
Oral opening, diameter	6.0	6.0	0.6	0.2	10.5	5.0	7.0	11
	6.0	6.0	0.9	0.2	14.7	5.0	7.0	19
Macronucleus, length	5.9	6.0	–	–	–	6.0	7.0	11
	9.6	10.0	1.0	0.2	10.0	8.0	12.0	19
	10.1	10.0	0.8	0.2	8.2	9.0	11.0	11
Macronucleus, width	5.8	6.0	–	–	–	5.0	7.0	11
	7.7	8.0	0.8	0.2	9.8	7.0	9.0	19
	8.6	9.0	0.9	0.2	10.7	7.0	10.0	11
Macronuclei, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
Ciliary rows, number	15.9	16.0	0.8	0.3	5.2	15.0	17.0	11
	17.0	17.0	0.8	0.2	4.8	16.0	19.0	19
	18.1	18.0	0.5	0.1	3.0	17.0	19.0	11
Kinetids in a dorsal kinety, number [b]	8.1	8.0	1.1	0.3	14.0	7.0	10.0	11
	11.7	12.0	1.8	0.4	15.3	8.0	15.0	19
	16.4	17.0	2.1	0.6	12.9	13.0	19.0	11
Caudal cilia, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
Oral flaps, number	13.1	13.0	0.8	0.3	6.3	12.0	14.0	11
	12.9	13.0	0.7	0.2	5.7	12.0	14.0	19
	14.4	14.0	–	–	–	14.0	15.0	12

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Dikinetids counted as 1 kinetid.

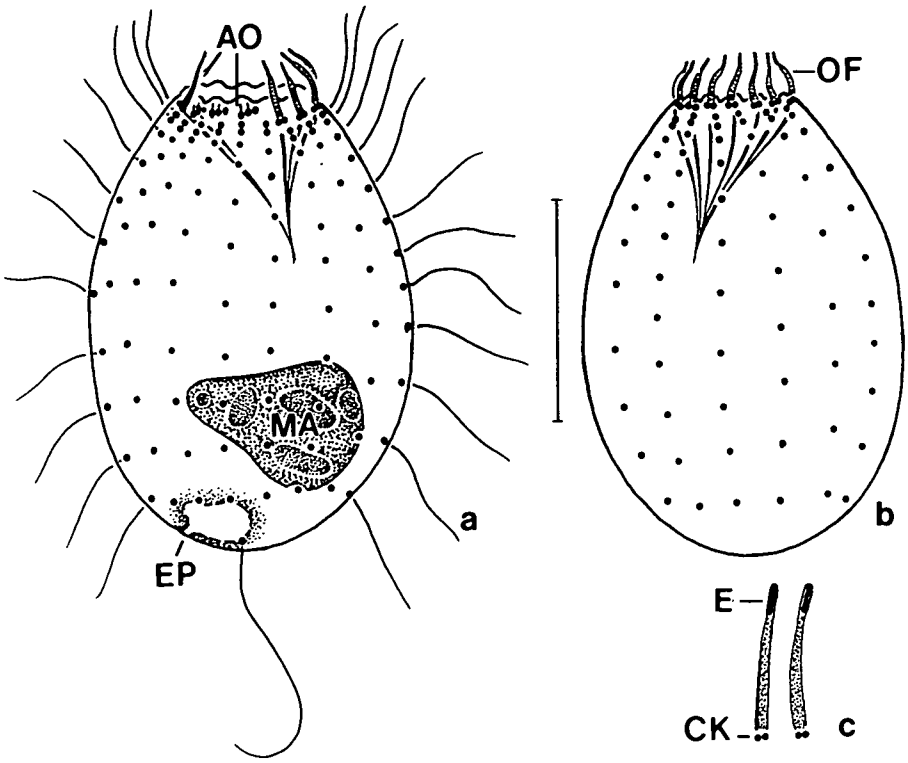


Fig. 126a–c. *Plagiocampa ovata* from Namibian site (51), ciliary pattern of ventral and dorsal side after protargol impregnation. Figure (c) shows a detail of the oral flaps, which originate from the paroral dikinetids and contain a minute extrusome distally. AO – three minute adoral organelles, each very likely composed of three dikinetids, CK – circumoral kinety (paroral membrane), E – extrusome in distal end of oral flap, EP – excretory pore of contractile vacuole, MA – macronucleus, OF – oral flaps originating from circumoral dikinetids. Scale bar 15 µm.

Plagiocampides nov. gen.

Diagnosis: Plagiocampidae (?) with minute, polygonal cortical alveoli and wide-meshed silverline pattern. Brosse (adoral organelles) minute, interrupts circumoral kinety (paroral membrane) composed of dikinetids and oral flaps each containing an extrusome.

Type species: *Plagiocampides halophilus* nov. spec.

Etymology: Composite of the generic name *Plagiocampa* and the Greek suffix *ides* (similar), meaning a ciliate genus similar to *Plagiocampa*. Masculine gender.

Classification and comparison with related genera: This species is difficult to classify. Originally, we identified it as *Chilophrya utahensis* (PACK, 1919) KAHL, 1930a because it matches that species in body size and shape, somatic ciliature, location of the contractile vacuole, the extremely saline habitat, and feeding behaviour. However, the oral structures do not match PACK's description: "The cilia are distributed between ridges that run parallel to the long axis of the body. These ridges project slightly beyond the opening of the mouth (anterior end) and form finger-like projections. One of which is long and well developed, being used to crowd food into the mouth. The oesophagus is short and fitted with short rods that may be extended in the shape of a star" (Fig. 127a, b). If the "finger-like projections" are interpreted as oral flaps and the "extending rods" as exploding extrusomes in the flaps, the oral morphology would be similar to that of → *Plagiocampa*. On the other hand,

VUXANOVICI (1961a) confirmed an important feature of PACK's description, viz., the single specialized oral process. Our populations definitely lack such a finger-like oral process and all oral flaps are inconspicuous and thus identified as such only after thorough investigation of live and silver-impregnated specimens; accordingly, a relationship to → *Plagiocampa* is not obvious. The inconspicuousness of the flaps is at least partially caused by the lack of the beating movements so typical for the flaps of → *Plagiocampa* and *Chilophrya terricola* (FOISSNER 1984, FOISSNER et al. 1994, KAHL 1930a); furthermore, the flaps do not insert at the outer margin of the oral opening but at the entrance to the oral funnel and disappear in strongly squeezed specimens (Fig. 127 l).

The second feature which distinguishes our specimens from *C. utahensis* is the lack of symbiotic algae. However, the evidences provided by PACK (1919) for symbiotic algae in *C. utahensis* are not convincing.

Unfortunately, details of the somatic and oral ciliary pattern of *Chilophrya* are unknown, although FOISSNER (1984) studied carefully a *C. terricola*. However, the generic classification of this species is doubtful because it lacks, like *Plagiocampides halophilus*, the main generic feature, viz., a lip-like cortical structure covering one side of the oral opening (KAHL 1930a).

Plagiocampides halophilus is undoubtedly someway related to the → Plagiocampidae because (i) the oral ciliature consists of paroral dikinetids forming a ring interrupted by the adoral organelles; (ii) the ciliary rows leave blank only a small posterior pole area; and (iii) the cirrus-like oral projections each contain an extrusome (Fig. 127m; 375d; FOISSNER et al. 1994, 1999). However, the cortex and silverline pattern are different from those of *Plagiocampa* (→ *P. pentadactyla*) and *Urotricha* (FOISSNER et al. 1999), but resemble *Holophrya ovum*, which, however, has a different oral ciliature (for a brief review, see FOISSNER et al. 1994). Accordingly, *Plagiocampides* might even be the representative of a new family.

***Plagiocampides halophilus* nov. spec.** (Fig. 127a–q; 375a–n; Table 109)

Diagnosis: Size about 40 × 17 µm in vivo; ovoidal. Macro- and micronucleus globular. On average 13 slightly dextrally twisted ciliary rows, 10 paroral dikinetids, and 3 quadrangular adoral organelles.

Type location: Cyanobacterial crusts from margin of Etosha Pan, Namibia, 19°10'S 15°55'E (site 58 in figures 2, 3 and chapter 2.1.2).

Etymology: Composite of the Greek words *halo* (salt) and *philus* (loving), meaning a salt-loving *Plagiocampides*.

Description: Size 35–45 x 15–20 µm, usually about 40 x 17 µm in vivo. Length:width ratio 2–3:1 in vivo and 1.7–2.6:1 in protargol preparations, while 1.5–1.9:1 in CHATTON-LWOFF silver nitrate slides, where cells are distinctly broader (Table 109). Shape rather constant in vivo, that is, ovoidal to elongate ovoidal and slightly asymmetrical because dorsal side more distinctly convex than ventral; anterior end narrowly, posterior broadly rounded; usually ellipsoidal and with depressed pole area in CHATTON-LWOFF silver nitrate and protargol preparations (Fig. 127a, h, i, m; 375a, b). Macronucleus usually in middle third of cell, broadly ellipsoidal, surrounded by distinct membrane, contains some lobate nucleoli; in

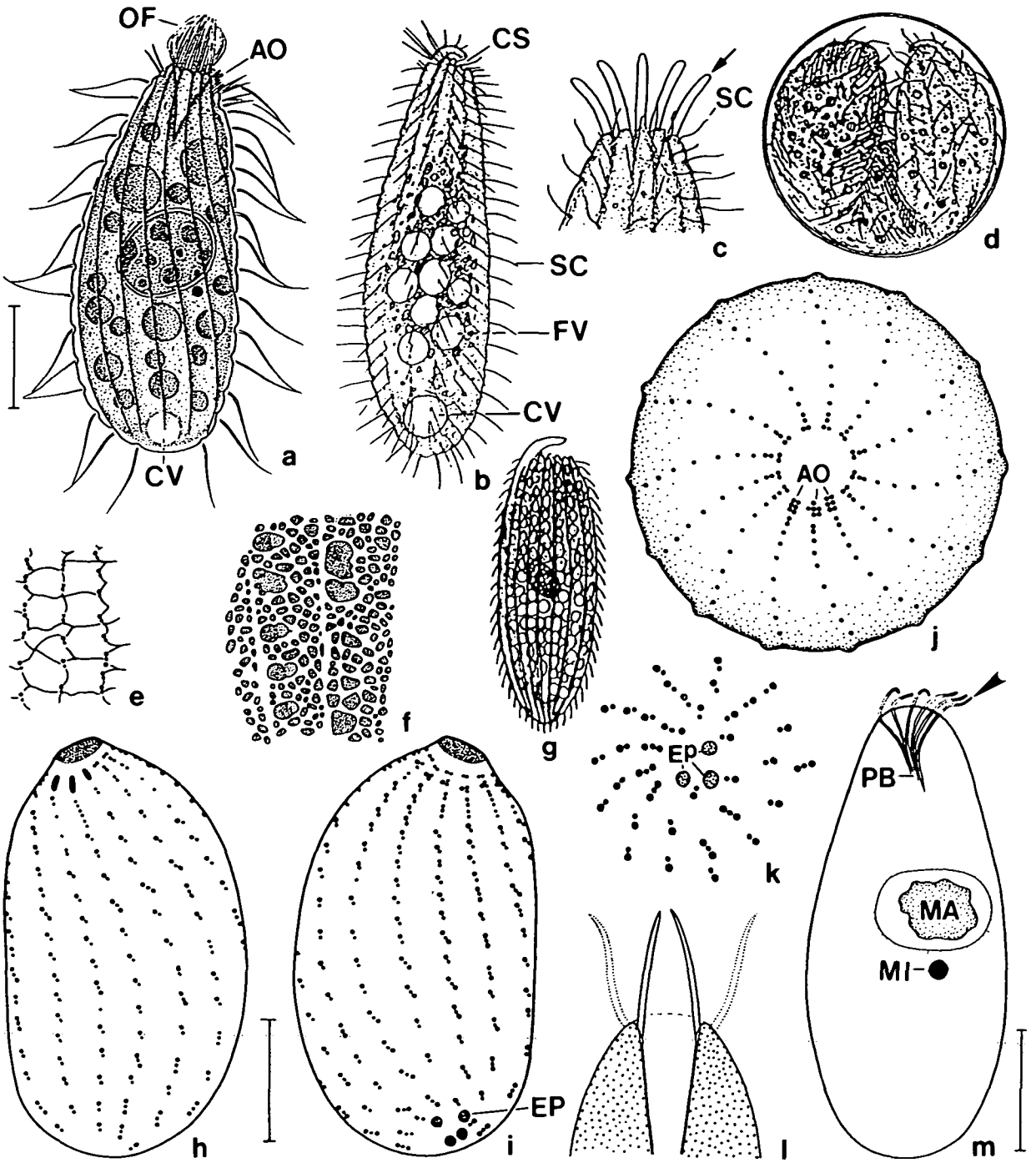


Fig. 127a–m. *Plagiocampides halophilus* (a, e, f, h–m) and *Chilophrya utahensis* (b–d, g) from life (a–d, g), after CHATTON-LWOFF silver nitrate (e, h–k), silver carbonate (f), and protargol (m) impregnation. **a:** Right lateral view of a representative specimen. **b–d:** Lateral view (length 50 µm), anterior body portion with "extended rods" (arrow), and resting cyst 23 µm across (from PACK 1919). **e:** Silverline pattern. **f:** Negatively stained cortical pattern. **g:** Lateral view after VUXANOVICI (1961a). **h, i:** Ventrolateral and dorsolateral view of ciliary pattern. **j:** Slightly schematized anterior polar view. The ring of ten paroral dikinetids is interrupted by three adoral organelles. **k:** Posterior polar view. **l:** Optical section of oral region showing location of oral flaps compared to those of → *Plagiocampa* (dotted). **m:** Extrusomes (arrowhead) in the oral flaps. AO – adoral organelles, CS – cytostome, CV – contractile vacuole, EP – excretory pores, FV – food vacuoles, MA – macronucleus, MI – micronucleus, OF – oral flaps, PB – pharyngeal basket, SC – somatic cilia. Scale bars 10 µm.

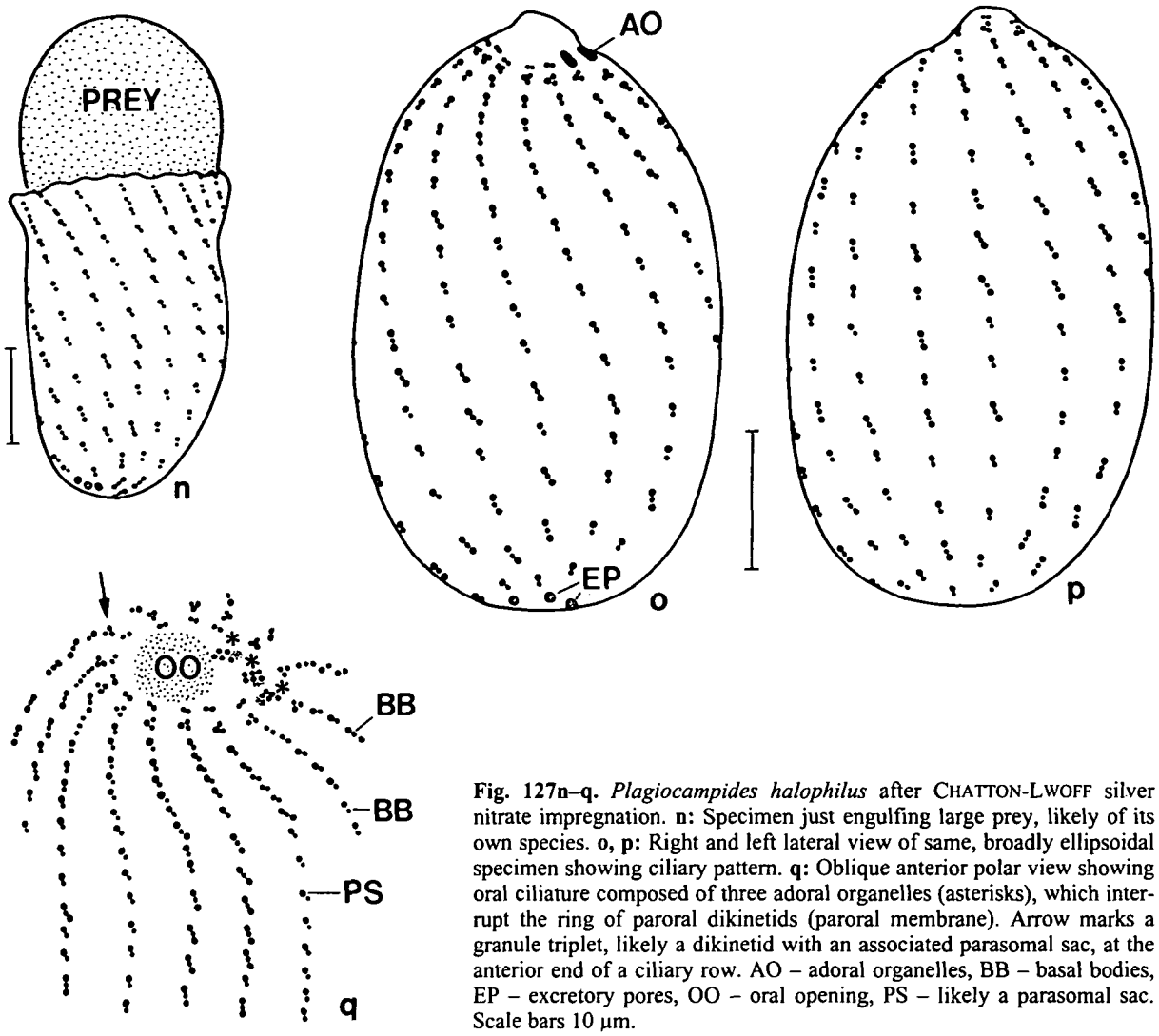


Fig. 127n–q. *Plagiocampides halophilus* after CHATTON-LWOFF silver nitrate impregnation. **n**: Specimen just engulfing large prey, likely of its own species. **o, p**: Right and left lateral view of same, broadly ellipsoidal specimen showing ciliary pattern. **q**: Oblique anterior polar view showing oral ciliature composed of three adoral organelles (asterisks), which interrupt the ring of paroral dikinetids (paroral membrane). Arrow marks a granule triplet, likely a dikinetid with an associated parasomal sac, at the anterior end of a ciliary row. AO – adoral organelles, BB – basal bodies, EP – excretory pores, OO – oral opening, PS – likely a parasomal sac. Scale bars 10 µm.

two out of 75 specimens investigated two globular macronuclear nodules, in one cell four, and in one even sixteen beads. Micronucleus adjacent to macronucleus, globular, often not recognizable due to similarly sized cytoplasmic inclusions. Contractile vacuole terminal, two to four, usually three excretory pores in pole centre. Cytopyge extends longitudinally in posterior quarter of right side, faintly impregnated. Cortex about 0.7 µm thick, distinctly notched likely by ciliary pits, lacks extrusomes; forms distinct rib right of ciliary rows and contains narrow, irregular meshes recognizable both in vivo and after silver carbonate and protargol impregnation, where they are occasionally negatively stained (Fig. 127f; 375j–n). Silverline pattern widely and rather regularly meshed in CHATTON-LWOFF silver nitrate preparations (Fig. 127e). No extrusomes recognizable in vivo, but minute black rods became evident after silver impregnation in the cytoplasm and distal half of the oral flaps (Fig. 127 l, 375d), just as in → *Plagiocampa* and *Balanion*, in which the rods were proved to be toxicysts

(BARDELE 1999, FAURÉ-FREMIET & ANDRÉ 1965, FOISSNER 1984). Cytoplasm colourless, contains many fat globules 2–4 µm across and some optically almost empty food vacuoles about 5 µm across. Feeds mainly on ciliates, even cannibalistic, rarely on filamentous cyanobacteria; when engulfing the prey, the oral opening widens up to body diameter (Fig. 127n). Swims moderately rapidly by rotation about main body axis.

Ordinary somatic cilia about 8 µm long in vivo, originate from distinct pits; distances between individual cilia increase slightly from anterior to posterior; no caudal cilia. On average 13 equidistant ciliary rows, which commence directly underneath paroral dikinetids and adoral organelles and extend slightly dextrally twisted to near body end, where they leave blank a small pole area containing the excretory pores of the contractile vacuole; monokinetidal, except for one (perioral) dikinetid with two about 3 µm long cilia at anterior end of kineties. Kinetids usually composed of a small, ciliated granule having attached a large, bare granule (probably a parasomal sac) at right anterior margin in CHATTON-LWOFF silver nitrate preparations; occasionally another large, bare granule occurs at left posterior margin of basal body; in silver carbonate preparations, kinetids are associated with a short (kinetodesmal?) fibre extending almost parallel to kinety axis anteriad at right side of basal body (Fig. 127h–k, o, p; 375c; Table 109).

Oral opening occupies central anterior pole area, almost entirely surrounded by 9–11 paroral dikinetids each associated with a 6 µm long, cirrus-like projection (oral flap) containing an extrusome, as described above; flaps almost immobile and thus dissimilar to those of the Plagiocampidae, disappear in strongly squeezed specimens. Paroral dikinetids (paroral membrane) orientated perpendicularly to main kinety axis, lighter impregnated than ordinary and adoral kinetids, difficult to recognize because at entrance of oral funnel (Fig. 127a, j, l, m, q; 375a, b, d–i). Invariably three slightly staggering adoral organelles (brosse) in shallow groove at top of three ventral ciliary rows, orientated parallel or slightly obliquely to main body axis, interrupt paroral membrane; individual organelles minute, that is, likely composed of two short kineties each with up to four basal bodies bearing 1 µm long cilia. Pharyngeal basket composed of fine fibres originating from paroral dikinetids and hardly recognizable in vivo, but distinct in protargol preparations; basket short and slightly oblique-conical because ventrally almost closed and slightly longer than dorsally, appears empty in vivo.

Occurrence and ecology: *Plagiocampides halophilus* likely is an extreme halophile because it occurred in the highly (15‰) to extremely (40‰) saline and alkaline (pH 8.7–9.7) samples from Namibian sites (57), (58), (61) and (69) as well as in an extremely saline (> 40‰) soil sample from a dry salt lagoon in the Santa Rosa National Park, Pacific west coast of Costa Rica.

Comparison with related species: *Plagiocampides halophilus* is small and lacks conspicuous features. Thus, it is difficult to distinguish from other small, inconspicuous ciliates. Specifically, it is easily confused with small *Enchelys* species (oral apparatus less conspicuous due to lack of flaps; with longitudinal dorsal brush), *Chilophrya* spp. (single, lip-like oral process) and, especially, *Plagiocampa* spp. Fortunately, most *Plagiocampa* species have one or more caudal cilia and/or are distinctly larger (60–100 µm). Further, the contractile vacuole is located slightly subterminally and ventrally, while that of *P. halophilus* is in the posterior pole centre (Fig. 127a, k). Thus, it is unlikely that our organism is identical with one of the *Plagiocampa* species described and reviewed by KAHL (1930a).

Table 109. Morphometric data on *Plagiocampides halophilus*.

Characteristics [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	CHL	35.9	36.0	3.5	0.9	9.8	30.0	41.0	15
	PA	36.6	37.0	2.5	0.7	6.9	32.0	40.0	15
Body, width	CHL	22.0	21.0	2.7	0.7	12.1	18.0	26.0	15
	PA	17.9	18.0	2.7	0.7	15.2	14.0	23.0	15
Body length:width, ratio	CHL	1.6	1.6	0.1	0.0	7.2	1.5	1.9	15
	PA	2.1	2.0	0.3	0.1	15.5	1.7	2.6	15
Anterior body end to macronucleus, distance [b]	PA	13.9	15.0	2.5	0.6	17.9	9.0	18.0	15
Macronucleus, length [b]	PA	9.4	9.0	1.1	0.3	11.9	7.0	11.0	15
Macronucleus, width [b]	PA	7.5	8.0	1.1	0.3	14.9	5.0	9.0	15
Micronucleus, diameter	PA	1.0	1.0	–	–	–	1.0	1.0	9
Pharyngeal basket, length	PA	7.5	8.0	1.9	0.5	25.5	5.0	13.0	15
Pharyngeal basket, apical diameter	PA	4.3	4.0	–	–	–	4.0	5.0	15
Macronuclear nodules, number [c]	PA	1.0	1.0	–	–	–	1.0	1.0	75
Micronucleus, number	PA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	9
Excretory pores, number	CHL	3.3	3.0	0.6	0.2	18.2	2.0	4.0	15
Somatic ciliary rows, number	SC	13.3	13.0	0.6	0.2	4.5	12.0	14.0	16
Basal bodies in a dorsal ciliary row, number	CHL	16.5	17.0	1.1	0.3	6.4	14.0	18.0	15
Adoral organelles, number	CHL, SC	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11

[a] Data based on mounted, silver-impregnated, and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, PA – protargol impregnation (FOISSNER's method), SC – silver carbonate impregnation, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Specimens with one macronuclear nodule.

[c] Of 75 specimens investigated, two have 2 macronuclear nodules, one has 4, and one even 16.

PERITRICHIA

Echinovorticella nov. subgen.

Diagnosis: Stalked Vorticellidae EHRENBERG, 1838 with scattered cortical spines. Silverline system transversely striated.

Type species: *Vorticella echini* KING, 1931.

Etymology: Composite of *echinos* (Greek, hedgehog, referring to the spines) and the generic name *Vorticella* (Latin; small vortex). Feminine gender.

Discussion: Our subgeneric separation might be questioned because the spines are a highly variable, phenotypic feature. However, they are maintained in the resting cysts, indicating a rather strong genetic fixation. Exactly the same situation exists in *Hastatella* and *Astylozoon*, two planktonic vorticellids. *Hastatella* may reduce the conspicuous spines almost completely and then looks like an *Astylozoon* (DINGFELDER 1962, FOISSNER et al. 1999). Thus, if *V. echini* and related species are **not** recognized as representatives of a distinct taxon, *Hastatella* and *Astylozoon* could be also questioned. *Hastatella* even lacks spines in the cystic stage (FOISSNER et al. 1999). On the other hand, *Hastatella* and *Astylozoon* are stalkless which justifies generic separation from *Vorticella*. *Vorticella echini* and *V. voeltzkowi* have a stalk plus spines, suggesting subgeneric level.

JANKOWSKI (1976) transferred, without any new evidence, *V. voeltzkowi*, a proposed senior synonym of *V. echini* (WARREN 1986), to *Pseudovorticella*. Our investigations show that this is very likely wrong because the silverline pattern is of the vorticellid type.

Vorticella (*Echinovorticella*) *echini* KING, 1931 **nov. stat.** (Fig. 128a–g, i–p, s; 376a–z, 377a, c–o; Table 110)

Description of Namibian population: All observations are from cultivated material as described below. Size 35–45 × 20–30 µm, usually 40 × 25 µm in vivo (Table 110); in American specimens 25–50 × 20–35 µm (KING 1931). Shape highly variable, that is, elongate ellipsoidal or roughly fusiform, very broadly ellipsoidal (ratio < 1.6:1), slightly urnulate and, in one out of 100 specimens photographed, even almost globular; peristomial area, however, invariably narrower than broadest body region in or slightly underneath mid-body; length:width ratio 1.4–1.9:1, on average 1.6:1, that is, broadly ellipsoidal (Table 110). Contracted cells globular with portion between aboral ciliary wreath and scopula distinctly invaginated (Fig. 128b, c, g, j; 376j, m–p). Body processes (spines) confined to transverse cortical ridges in area between peristomial disk and anlage of aboral ciliary wreath, up to 4 µm long and slightly to distinctly flattened, rarely truly conical (Fig. 376g–o; Table 110). Spines obviously part of the cell proper because containing mitochondria (Fig. 128e; 376f), covered by the ordinary cortex, including the crest containing the silverline. Number and size

of spines highly variable between and within individuals. "Spiny" specimens possess about 68 large and many small spines, both irregularly alternating on the same cortical ridges (Fig. 376k–n). Rarely specimens have no spines (Fig. 376o), few large and many small spines (Fig. 376g–k, l–n), or numerous minute, almost globular processes (Fig. 376p, q). Actually, all transitions between "very spiny" and "smooth" cells can be observed in a single culture and at any time. However, some of this variability might be caused by precystic specimens, which very likely resorb the spines (see below).

Macronucleus transverse or oblique to main body axis in or above mid-body, horseshoe-shaped to circular with ends sometimes slightly overlapping, 4–6 µm wide in vivo; nucleoli moderately numerous and up to 1 µm across (Fig. 128a, g; 376f). Micronucleus recognizable neither in vivo nor in protargol preparations probably because attached to macronucleus as recognizable in FEULGEN-prepared cysts (Fig. 128o). Contractile vacuole at mid-ventral wall of vestibulum, that is, distinctly underneath peristomial collar. Cytopyge between contractile vacuole and cytostome. Food vacuoles 4–7 µm across, contain bacterial remnants and spores. Stalk without peculiarities and distinct granules, unbranched and helically contracting, 75–140 × 3 µm in Namibian (Table 109) and 70–100 µm long in American specimens (KING 1931), anterior end with cuff-like, longitudinally striated bulge (scopula ?; Fig. 128a; 376k, n). Scopula composed of a ring of ellipsoidal granules and some globular granules within ring (Fig. 128d). Cells attached to a wide variety of substrates, such as bacterial flocks, bark particles, and resting cysts of *Colpoda cavicola amicronucleata*. Often several specimens attach very close together, forming colony-like aggregates, especially in flourishing cultures (Fig. 376a, c, d).

Cortex of concave type, that is, with distinct, occasionally anastomosing transverse ridges extending across spines (Fig. 128e; 376i, m, r, s). Silverline pattern as in *Vorticella* (FOISSNER 1979a), widely striated (ratio body length to number of silverlines 1.15) according to the classification by FOISSNER & SCHIFFMANN (1974); individual silverlines extend across spines[21], almost equidistant, except for three more widely spaced apical lines and the rather closely spaced lines below the aboral ciliary wreath. Pellicular pores rather numerous, that is, 49–71, on average 57 per 100 µm^2, invariably anterior to silverlines between oral opening and aboral ciliary wreath, while posterior between aboral ciliary wreath and scopula (Fig. 128c; 377a, c–f). Anlage of aboral ciliary wreath composed of closely spaced, clockwise inclined dikinetids in protargol preparations, while of two closely spaced, possibly poreless silverlines framed by slightly narrowed somatic ones in KLEIN-FOISSNER silver nitrate preparations (Fig. 128c; 377c, e; Table 110).

Myoneme system very similar to that of other small vorticellids, for instance, *V. infusionum* and *V. aquadulcis* (FOISSNER et al. 1992, 1999). Briefly, it consists of a compact ring in the peristomial collar and about ten rather thick, more or less distinctly anastomosing, longitudinal strands originating from the stalk myoneme; anteriorly, the strands attach to the adoral ciliary spiral and dispatch fine branches into the peristomial disc (Fig. 128b; 376z).

Oral apparatus of usual structure, peristomial collar 2–3 µm thick and never projecting above widest body region. Peristomial disk flat and obliquely raised in feeding specimens, not

[21] In most specimens, some of the spines are seemingly without a silverline (Fig. 128e; 377a, c–f). We suppose, however, a preparation artifact, that is, during dehydration of the unfixed cells some spines are deformed in such a way that the silverlines cannot impregnate because they become located between body and spine surface.

umbilicate. Vestibulum (ciliated part of mouth funnel) and pharynx (where the food vacuoles are formed) rather conspicuous because extending to dorsal side and mid-body. Oral ciliature quite similar to that of small congeners because the proximal portion of the peniculi is gradually shortened[22] (Fig. 128a, f, j, s; 376t–y). Cilia about 10 μm long; haplokinety (undulating membrane) and polykinety (adoral ciliary spiral) describe about 1¼ turns (about 450°) on peristomial disc before plunging into the vestibulum, accomplishing a further ½ turn. Haplokinety commences, like in *V. astyliformis* and *V. convallaria*, a few basal bodies behind polykinety, composed of dikinetids orientated obliquely to kinety axis. Polykinety composed of many oblique rows of three basal bodies each, proximal portion forms peniculus 1. Peniculi 1 and 2 close together, long compared to peniculus 3, each composed of three rows of basal bodies; peniculus 3 short, attached to proximal half of peniculi 1 and 2 and likely composed of two rows only. Two epistomial membranes difficult to recognize because each comprising only a few basal bodies (Fig. 128j, s; 376v, w): first membrane near distal end of polykinety, second at vestibular opening, that is, about 90° distant from distal end of polykinety.

Swarmers about 50 × 20 μm in vivo, opaque due to many granules and some food vacuoles; cylindroidal to inconspicuous obconical with slightly narrowed mid,. bluntly pointed posteriorly, transversely truncate anteriorly; highly contractile becoming spheroidal (Fig. 128p; 377g–j). Spines as conspicuous as in stalked specimens, directed orally, that is, opposite to swimming direction. Cilia of aboral wreath about 13 μm long and very closely spaced; thus, swarmers can swim very rapidly, changing direction abruptly. Epistomial membrane composed of about four 10 μm long cilia; we did not look for the second epistomial membrane.

Resting cyst as spiny as trophont, develops on stalk whose myoneme disorganizes; two weeks old cysts spherical, 22–28 μm ($\bar{x}$ = 24.3 μm; Table 110) across in Namibian and 10–20 μm in American specimens (KING 1931); colourless and opaque containing many minute (~ 0.5 μm) granules (Fig. 128k–o; 377k–o). Wall 1.5–2.5 μm thick and with yellowish shimmer, slightly wrinkled in vivo, while distinctly so in preparations where spines are on conspicuous, reticular crests; spines scattered and truly conical, that is, not flattened as in trophonts. Macronucleus almost circular with single micronucleus attached, reorganizes by splitting into several globules of different size (Fig. 128m, n); micronuclear divisions were not observed. We recognized too late that encystment is possibly much more complicated than described above, that is, have evidence that the spines are resorbed and rebuilt during the process: (i) the seven cysts studied in the scanning electron microscope all have spines of very similar length (1.4–2.1 μm), that is, the high variability of the spine length recognizable in the trophic cells (≤ 0.5–3.3 μm in the SEM) disappears; (ii) some light micrographs of young cysts, still being attached to the stalk, strongly suggest that the spines are partially or fully resorbed and rebuilt (Fig. 377 l, k) while the organism is still attached to the stalk; (iii) the spine pattern changes, that is, the transverse arrangement becomes scattered (Fig. 377n, o). Furthermore, a change in spine length becomes obvious when the proportions of the largest spines (3.3 μm and 2.1 μm) are calculated (all from SEM micrographs): mean trophic cell width (without spines)/maximum trophic spine length 5.2:1; mean cyst diameter (without spines)/maximum cyst spine length 9.4:1. Thus, spines are disproportionally shorter in cysts than in trophonts.

[22] In the campanulate species, peniculus 2 is distinctly shorter than peniculi 1 and 3. This produces an arrow-like pattern in the proximal part of the ciliary spiral (FOISSNER et al. 1992).

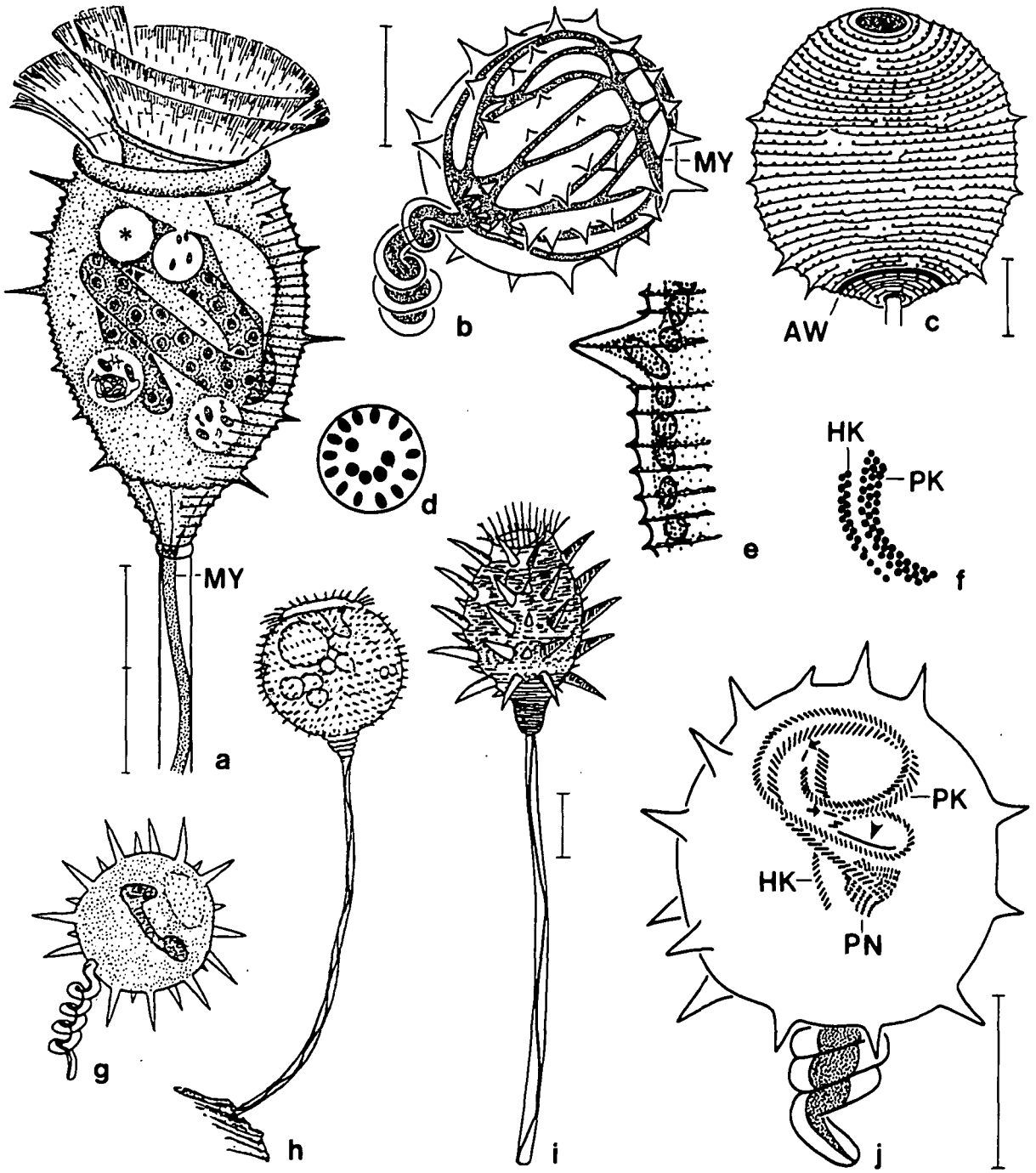


Fig. 128a–j. *Vorticella (Echinovorticella) echini* from Namibian (a–f, j) and American (g, i) population, and *V. voeltzkowi* (h) from life (a, e, g–i) and after protargol (b, d, f, j) and dry silver nitrate (c) impregnation. **a:** Representative specimen from Namibia just releasing wastes through the cytopyge proximal to the contractile vacuole (asterisk). **b:** Myoneme system. **c:** Silverline pattern. Pellicular pores are invariably anterior to silverlines above ciliary wreath. Spines without silverlines are preparation artifacts. **d:** Scopula. **e:** Numerous up to 2 µm long mitochondria are underneath the cortex. **f, j:** Distal end of haplokinety and polykinety and oblique top view of oral ciliature. Arrows mark the two epistomial membranes, arrowhead denotes the germinal kinety. **g, i:** Contracted and extended specimen from American type population (from KING 1931). **h:** *Vorticella voeltzkowi* is 30–40 µm across and has many short spines in about 14 rows (from SONDHEIM 1929). AW – aboral ciliary wreath, HK – haplokinety, MY – myonemes, PK – polykinety, PN – peniculi. Scale bar divisions 10 µm.

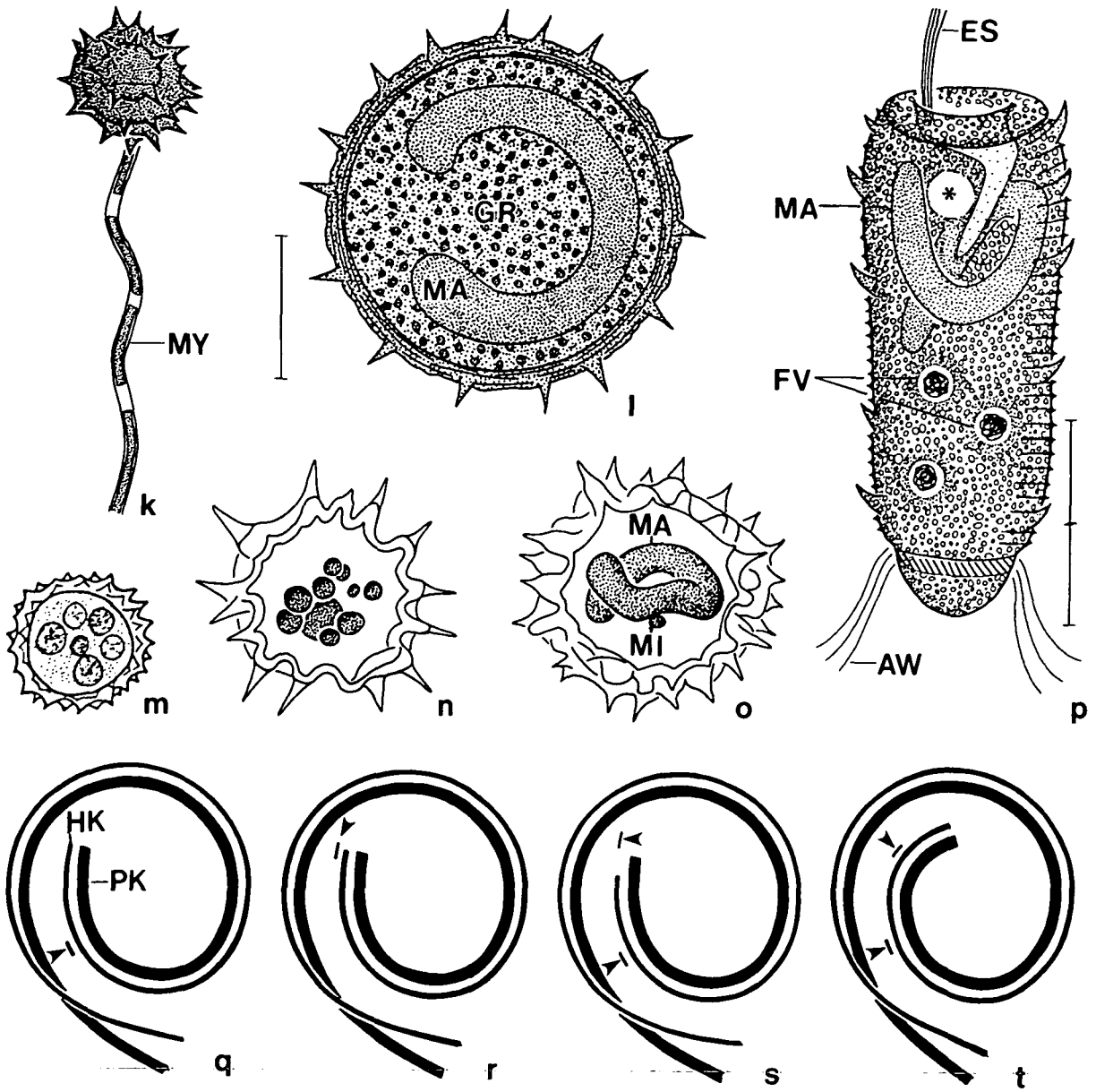


Fig. 128k–t. *Vorticella (Echinovorticella) echini* from Namibian (k, l, n–p, s) and American (m) population, and other peritrichs (q, r, t) from life (k–m, p), after FEULGEN staining (n, o), and protargol impregnation (q–t). **k–o:** Resting cysts are formed on stalk (k). The cyst wall is slightly wrinkled in vivo (k, l), while distinctly so in preparations (n–o). The spines are scattered and of rather similar size and shape. The nuclear apparatus reorganizes (m, n), that is, splits into several globules in the American type population (m, from KING 1931) and the Namibian specimens (n, o). **p:** Swarmers have a cylindroidal shape and conspicuous, orally directed spines. Asterisk marks contractile vacuole. **q–t:** Schematic anterior polar views of the peritrich oral ciliature showing variation in number and location of the epistomial membranes (arrowheads): one membrane at vestibular entrance in *V. vernalis* (q; from FOISSNER et al. 1999); one membrane at distal end of adoral spiral in *Opisthonecta henneguyi* (r; from FOISSNER et al. 1999); two epistomial membranes, namely, one at distal end of adoral spiral and another at vestibular opening in *V. echini* (s); two epistomial membranes, namely, one at distal quarter of adoral spiral and another at vestibular opening in *V. infusionum* (t; from FOISSNER et al. 1992). AW – aboral ciliary wreath, ES – epistomial membrane, FV – food vacuole, HK – haplokinety, GR – granules, MA – macronucleus, MI – micronucleus, MY – stalk myoneme, PK – polykinety. Scale bar divisions 10 µm.

Whether the cyst spines are a product of the cell or the ectocyst needs transmission electron microscope investigations. If the spines are a product of the ectocyst, the species should be separated at genus level because all other peritrich cysts, including those of *V. voeltzkowi*, lack any spines, and this feature is as distinct as any other used in peritrich genus taxonomy. In principle, it is not impossible that the spines belong entirely to the cyst wall because, for instance, many hypotrich resting cysts have conspicuous spines although trophonts have none (BERGER 1999).

Table 110. Morphometric data on *Vorticella (Echinovorticella) echini*.

Characteristics [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Zooid, length	IV	39.4	40.0	2.5	0.6	6.3	36.0	45.0	19
	PA	20.1	20.0	1.6	0.4	7.9	18.0	23.0	15
Zooid, width (without spines)	IV	24.7	25.0	1.9	0.4	7.5	20.0	28.0	19
	PA	18.2	18.0	1.1	0.3	6.3	16.0	20.0	15
	SEM	17.2	17.0	2.2	0.7	12.9	15.0	21.0	9
Zooid, length:width ratio (without spines)	IV	1.6	1.6	0.1	0.0	6.8	1.4	1.9	19
	PA	1.1	1.1	0.1	0.0	7.4	1.0	1.2	15
Stalk, length	IV	103.9	100.0	18.1	4.4	17.4	75.0	137.0	17
Stalk, width	IV	3.0	3.0	0.0	0.0	0.0	3.0	3.0	17
Spine, length	IV	2.4	2.0	1.1	0.3	45.6	0.5	4.0	17
	SEM	1.9	2.1	0.8	0.2	43.8	0.3	3.3	15
Spines, number	SEM [b]	68.0	64.0	21.6	7.2	31.8	34.0	100.0	9
Macronucleus, width	PA	4.7	5.0	–	–	–	4.0	5.0	15
Silverlines between anterior end and aboral ciliary wreath, number	KF	30.4	30.0	0.7	0.2	2.4	29.0	32.0	15
Silverlines between aboral ciliary wreath and scopula, number	KF	4.4	5.0	0.7	0.2	16.7	3.0	5.0	15
Distance between silverlines in mid-body	KF	1.3	1.3	0.1	0.0	6.1	1.0	1.3	15
Pellicular pores, number in 100 μm^2	KF	57.4	56.0	6.6	1.7	11.5	49.0	71.0	15
Cyst, diameter (without spines)	IV	24.3	24.0	1.4	0.4	5.8	22.0	28.0	16
	SEM	19.7	20.0	2.2	0.8	11.2	17.0	23.0	7
Cysts (ripe), spine length	IV [c]	2.4	2.3	0.3	0.1	11.8	2.2	2.8	4
	SEM	1.9	1.9	0.3	0.1	13.2	1.4	2.1	7

[a] Data based on specimens from a wheat grain culture. Measurements in µm. CV – coefficient of variation in %, IV – in vivo, KF – KLEIN-FOISSNER silver nitrate impregnation, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, PA – protargol impregnation (FOISSNER's method), SD – standard deviation, SE – standard error of arithmetic mean, SEM – from scanning electron micrographs, $\bar{x}$ – arithmetic mean.

[b] Values doubled because only one side can be seen in the micrographs.

[c] Estimated from micrographs.

Occurrence and ecology: KING (1931) discovered *V. echini* in a culture of greenhouse soil and pond water from Iowa, USA. The Namibian population was found in a

moderately saline sample containing thin, paper-like bark from live and dead Moringa trees. It grew well in cultures set up in Eau de Volvic containing some crashed wheat grains and part of the indigenous bacterial flora and protist community.

Comparison with related species: WARREN (1986) suggested synonymy of *V. voeltzkowi* and *V. echini*. We disagree, mainly because *V. voeltzkowi* SONDHEIM, 1929 has smooth resting cysts (like *Hastatella*!) distinctly different from the spiniferous cysts of *V. echini* (Fig. 128m) and the Namibian specimens (Fig. 128k, l, n, o; 377k–o). Further differences occur, namely, in body shape and number of spine rows. SONDHEIM (1929) definitely states (translated from German): "Size 30–40 µm **in diameter**" and, later, "the body is usually **entirely globular**" (Fig. 128h). SONDHEIM illustrates 14 transverse spine rows (Fig. 128h), while the spines of *V. echini* and our population are much more scattered, showing only about five spines along body margin in optical section (Fig. 128a, i). The Namibian specimens agree well with those observed by KING (1931), with a significant difference, however: the spines of KING's cells are 10 µm long, while those of the Namibian specimens measure only up to 4 µm both in raw (non-flooded Petri dish) and pure cultures. This produces a rather different appearance (Fig. 128a, i). Further, the resting cysts of the American population are distinctly smaller (10–20 µm) than those of the Namibian specimens (22–28 µm; Table 109). Thus, our identification may be questioned, and the material cannot serve as neotype. On the other hand, our observations show that the length of the spines is highly variable. Possibly, optimal conditions were lacking in our cultures.

In vivo, the conspicuous spines are a unique feature of the *V. echini* zooids, swarmers, and cysts. The length of the spines, however, varies like in *Hastatella radians* ERLANGER, 1890, whose spines become fewer and distinctly smaller when reproducing for some weeks in patch culture (FOISSNER 1977, FOISSNER et al. 1999). Zooids of *V. echini* detached from the stalk may be confused with such poorly developed specimens of *Hastatella radians*; if in doubt, check arrangement of spines (scattered on body vs. arranged in an anterior and equatorial girdle; FOISSNER 1977, FOISSNER et al. 1999). Only spineless individuals of *V. echini* can be confused with other small congeners, namely, *V. astyliformis* [49–71 vs. 70–120 pellicular pores per 100 µm^2, pores invariably attached anteriorly vs. usually posteriorly to silverlines above ciliary wreath, 29–32 ($\bar{x}$ = 30) vs. 17–30 ($\bar{x}$ = 21, 25 in two populations) silverlines above aboral ciliary wreath; Fig. 378a–g; FOISSNER 1981a]; *V. infusionum* (common body size 40 × 25 µm vs. 45–60 × 30–40 µm, 3–5 vs. 6–13 silverlines below aboral ciliary wreath, pellicular pores invariably attached anteriorly vs. occasionally posteriorly to silverlines above aboral ciliary wreath, epistomial membrane 1 at vs. about 90° distant from distal end of adoral ciliary spiral; Fig. 128t; 377b; FOISSNER et al. 1992); and *V. octava* (body shape never vs. slightly campanulate, 3–5 vs. 9–16 silverlines below aboral ciliary wreath; FOISSNER et al. 1992). Both, *V. infusionum* and *V. octava*, occur very rarely in terrestrial biotopes.

Of high interest is the occurrence of two epistomial membranes in *V. echini*, a feature as yet documented only in *V. infusionum* (FOISSNER et al. 1992). Unfortunately, the second epistomial membrane is difficult to recognize and thus could have been overlooked in other species. On the other hand, there can hardly be any doubt that peritrichs, such as *V. convallaria* and *Opisthonecta* spp., possess only a single epistomial membrane. Certainly, the single or double epistomial membrane is a strong feature that can be used for a meaningful further split (first split: *Pseudovorticella* FOISSNER & SCHIFFMANN 1974) of the large genus *Vorticella* (Fig. 128q–t). However, more data are required, as explained above.

Epistylis alpestris FOISSNER, 1978 (Fig. 379a–r)

1977 *Epistylis alpestris* (FOISSNER, 1977) — FOISSNER, Protistologica, 13: 372 (protargol impregnation of oral structures and myoneme system).

1978 *Epistylis alpestris* FOISSNER, Annln naturh. Mus. Wien, 81: 558 (original description).

Epistylis alpestris was discovered in astatic pools of the Austrian Central Alps. Since then, we have found it in similar habitats all over the world. In Namibia, *E. alpestris* occurred at sites (49, 70, 73), viz., in a small, astatic saline pan and in mud of rock pools of a stream, showing that it is euryhaline.

The various populations are highly similar in size, shape of body and macronucleus, number of cortical striae (silverlines), and the facetted resting cysts. For details, see figure explanations.

HYPOTRICHIA

About one third of 128 new species discovered in the 73 soil samples are hypotrichs. This matches the high dominance of soil hypotrichs in general (FOISSNER 1998a) and might be associated with the flexible, elongated body pre-adapting hypotrichs for life in microporous (soil) environments. Both saline and desert habitats are rich in new species, showing the evolutionary pressure of extreme habitats.

Many of the new species look inconspicuous, that is, are small and of ordinary shape. However, more detailed investigations show that they are not only undescribed, but also representatives of new genera. Indeed, some of the new "ontogenetic" genera established in this book are so surprising and unexplainable that hypotrich classification appears hopelessly complicated. Thus, we renounced to classify them in new families. And there is no indication that further new taxa to be discovered will clear the matter!

We still have about 200 undescribed soil hypotrichs in our notebooks, showing that the present study just touched the peak of an iceberg. It is even possible that there are more terrestrial than (described) limnetic hypotrichs. This bewildering diversity shows that there must be thousands of hypotrich species, most still undescribed.

Bakuella granulifera nov. spec. (Fig. 129a–k; 380a–c, f–h; Table 111)

Diagnosis: Size about 320 × 100 µm in vivo; oblong. About 350 macronuclear nodules. Cortical granules citrine, in series between cirral and bristle rows. On average 54 adoral membranelles, 8 buccal cirri, 4 frontoterminal cirri, 18 pairs of midventral cirri, 4 short and long midventral rows, and 12 transverse cirri.

Type location: Sieved litter from the bank of the Bukaos River, about 80 km north of the town of Keetmanshoop, Namibia, 25°40'S 18°10'E (site 4 in figure 2 and chapter 2.1.2).

Etymology: The Latin *granulifera* (bearing granules) refers to the conspicuous cortical granules.

Description: Size 270–400 × 70–120 µm in vivo, usually about 320 × 100 µm, length:width ratio 3.0–4.1:1, on average 3.2:1 in vivo and protargol preparations; only 200–300 × 70–120 µm in Namibian site (60) specimens. Outline elongate elliptical, anterior portion curved leftwards during foraging, providing cells with a reniform appearance; body flattened about 2:1 dorsoventrally, very flexible and contractile by about 10% under mild cover glass pressure (Fig. 129a–e; Table 111). Macronuclear nodules scattered throughout cell, small but numerous and thus difficult to count; type specimen with about 356 nodules, indicating that the range is somewhere between 250 and 400; individual nodules about 7–10 × 3–4 µm in vivo, usually ellipsoidal to elongate ellipsoidal, but also globular, reniform, or dumb-bell-shaped, each with some small nucleoli (Fig. 129j, k). Micronuclei difficult to recognize in vivo and protargol preparations, likely several scattered throughout cell, 3–4 µm across after protargol impregnation. Contractile vacuole with two conspicuous collecting

canals at left body margin distinctly above mid-body at level of buccal vertex. Cells yellow at low (×100) magnification due to conspicuous cortical granules in short series mainly between cirral and bristle rows; individual granules 1.3–1.5 × 0.8–1.0 µm in size, that is, ellipsoidal and brilliant citrine, do not impregnate with the protargol method used (Fig. 129f, g; 380a–f). Cytoplasm colourless, contains fat globules 1–3 µm across, 10–20 µm-sized food vacuoles with compact content, and irregular egestion vacuoles up to 50 µm across. Voracious predator, ingesting fungal spores, diatoms, testate amoebae (*Euglypha* sp., *Trinema lineare*), ciliates (*Colpoda* sp., *Uroleptus notabilis*, *Urosoma karinae*), and even rotifers up to 80 µm long. Moves quickly on microscope slide and soil particles showing great flexibility.

Cirral pattern and number of cirri of usual variability (Fig. 129a, h; 380g, h; Table 111). Marginal, frontoterminal, and midventral cirri 15–17 µm long in vivo. Right marginal row extends onto dorsolateral surface anteriorly, ends more subterminally than left, which is J-shaped, curving along rear body margin. Frontal cirri conspicuously enlarged and about 22 µm long in vivo, right one, as is usual, at distal end of adoral zone of membranelles; frequently two cirri behind right frontal cirrus. Buccal cirral row right of anterior half of paroral, cirri become slightly smaller from anterior to posterior. Frontoterminal cirral row short, right of anteriormost pair of midventral cirri. Midventral row composed of an anterior portion of about 18 cirral pairs terminating near mid-body, and a posterior portion of slightly oblique, short and long rows (terminology according to EIGNER 1994); rightmost long midventral row terminates at right transverse cirrus, as in some congeners. Transverse cirri about 18 µm long in vivo, small and closely spaced in oblique row, do not, or only slightly, project beyond body end.

Dorsal bristles about 4 µm long in vivo, arranged in, likely invariably, three bipolar rows leaving blank broad, fusiform stripe in midline; rows 1 and 2 extend near left body margin, row 3 runs near right (Fig. 129i). Caudal cirri lacking.

Adoral zone conspicuous because occupying 30–42%, on average 35% of body length, of usual shape and structure; composed of an average of 54 membranelles, bases of largest membranelles about 20 µm wide in vivo (Fig. 129a, h; 380g, h; Table 111). Buccal cavity deep and large, at right partially covered by slightly curved, hyaline lip bearing paroral membrane in inconspicuous furrow and covering proximal end of adoral zone of membranelles. Paroral membrane distinctly curved anteriorly, likely composed of zigzagging basal bodies having about 15 µm long cilia, optically intersects with bow-shaped endoral membrane ahead or near mid of buccal cavity; cilia of endoral anteriorly about 20 µm, posteriorly about 40 µm (!) long, extending deeply into the pharynx. Pharyngeal fibres conspicuous in vivo and protargol preparations, of ordinary length and structure, extend almost longitudinally to posterior half of cell.

Occurrence and ecology: To date found at type location, where it was moderately abundant, and at Namibian site (60), a saline soil from the *Sporobolus* zone around the Etosha Pan. Thus, it is euryhaline.

Comparison with related species: *Bakuella granulifera* is very likely closely related to *B. edaphoni* SONG, WILBERT & BERGER, 1992, which is also very large (190–300 × 50–85 µm in vivo) and has an almost identical cirral pattern. The main difference is the conspicuous cortical granules (Fig. 380a–f), which are lacking in *B. edaphoni* (pers. comm. of W. SONG, who investigated *B. edaphoni*, to H. BERGER). However, *Bakuella granulifera* and *B. edaphoni* also differ significantly in several morphometrics, namely, size (319 × 101 µm

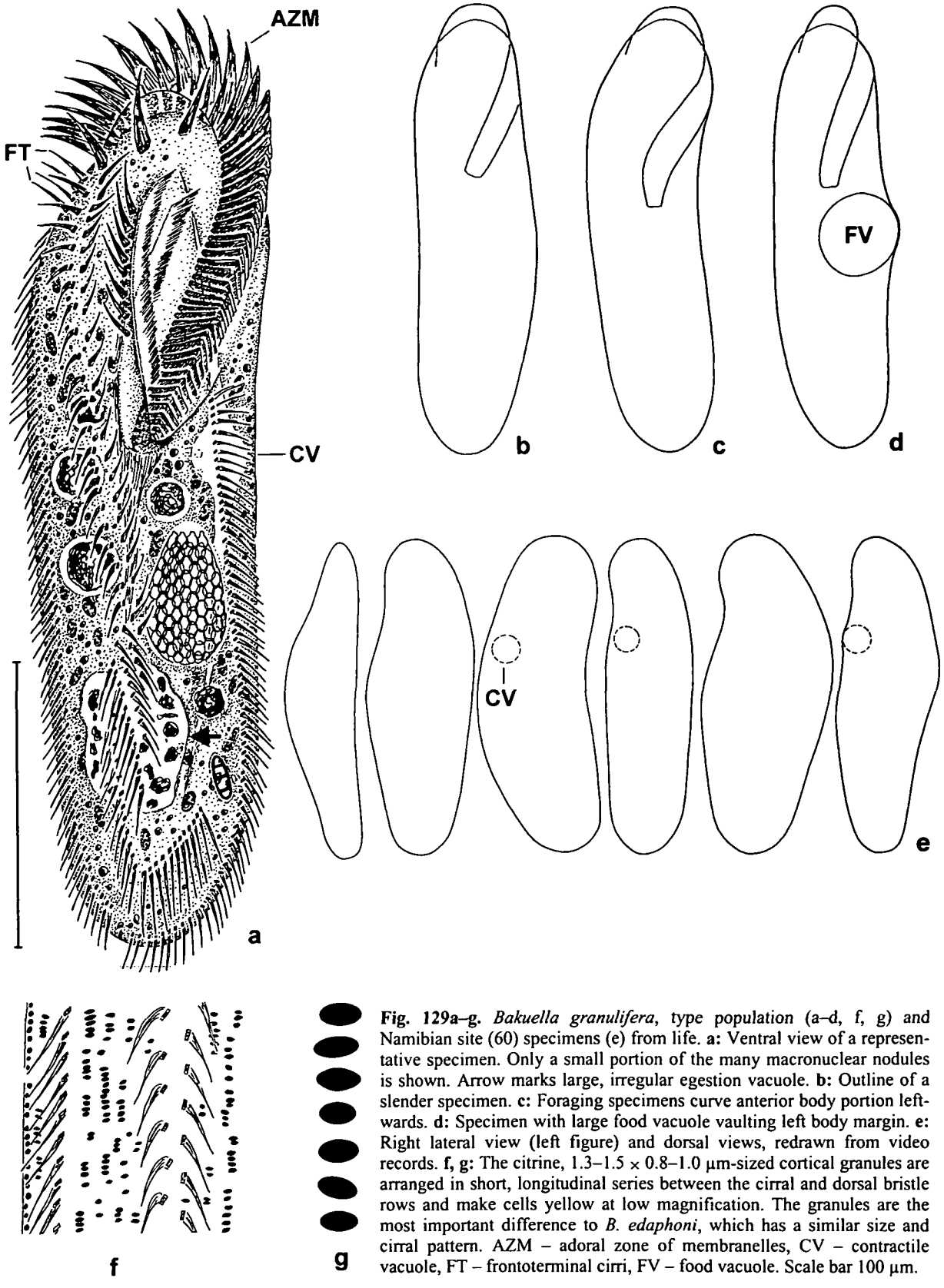


Fig. 129a–g. *Bakuella granulifera*, type population (a–d, f, g) and Namibian site (60) specimens (e) from life. **a:** Ventral view of a representative specimen. Only a small portion of the many macronuclear nodules is shown. Arrow marks large, irregular egestion vacuole. **b:** Outline of a slender specimen. **c:** Foraging specimens curve anterior body portion leftwards. **d:** Specimen with large food vacuole vaulting left body margin. **e:** Right lateral view (left figure) and dorsal views, redrawn from video records. **f, g:** The citrine, 1.3–1.5 × 0.8–1.0 µm-sized cortical granules are arranged in short, longitudinal series between the cirral and dorsal bristle rows and make cells yellow at low magnification. The granules are the most important difference to *B. edaphoni*, which has a similar size and cirral pattern. AZM – adoral zone of membranelles, CV – contractile vacuole, FT – frontoterminal cirri, FV – food vacuole. Scale bar 100 µm.

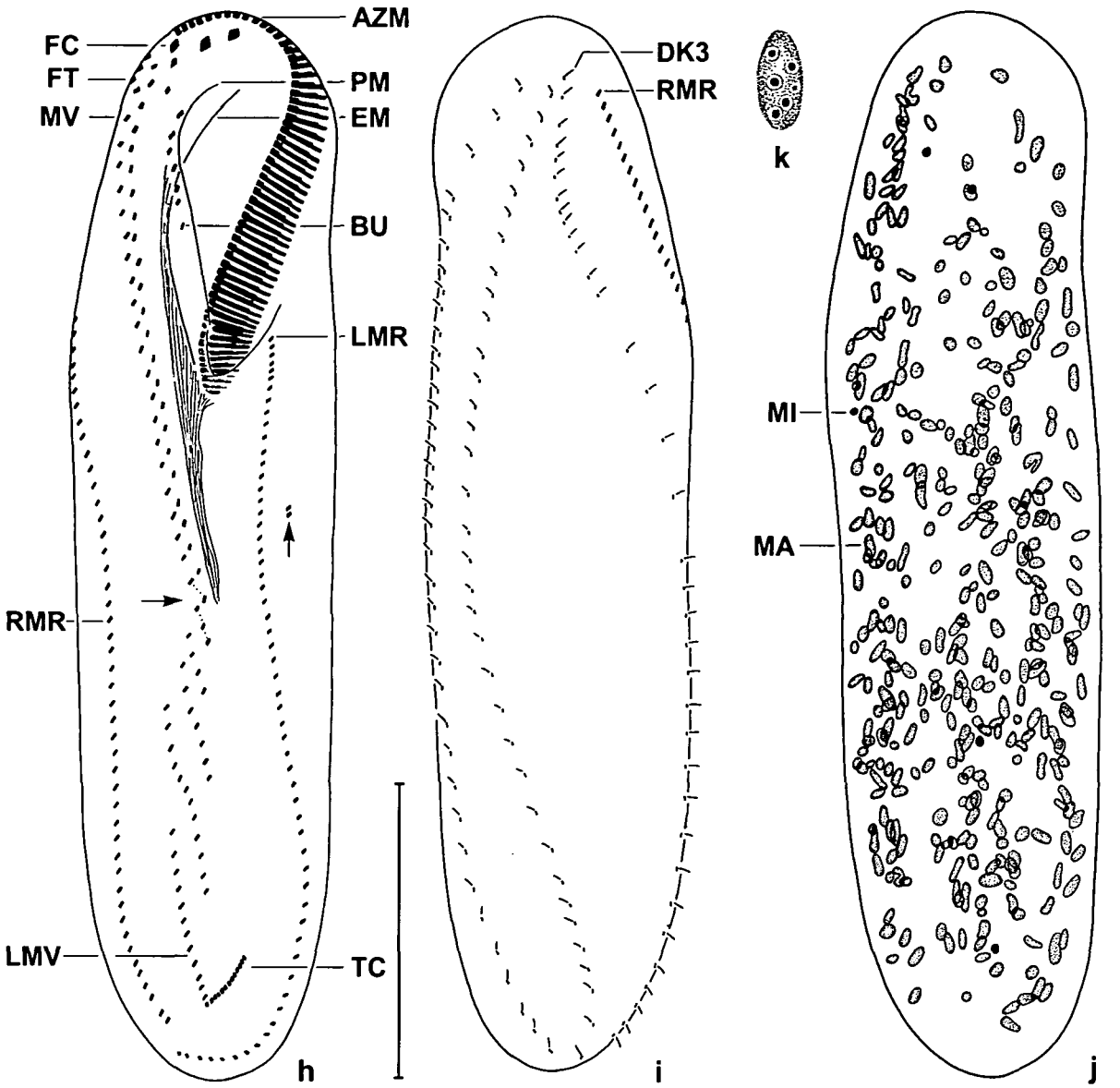


Fig. 129h–k. *Bakuella granulifera* after protargol impregnation. Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Vertical arrow in (h) marks two supernumerary left marginal cirri, transverse arrow denotes the last cirral pair of the midventral row. Figure (k) shows a macronuclear nodule at higher magnification. AZM – adoral zone of membranelles, BU – posteriormost buccal cirrus, DK3 – dorsal kinety 3, EM – endoral membrane, FC – right frontal cirrus, FT – frontoterminal cirri, LMR – left marginal row, LMV – rightmost long midventral row, MA – macronuclear nodules, MI – micronucleus, MV – midventral row, PM – paroral membrane, RMR – right marginal row, TC – transverse cirri. Scale bar 100 μm.

vs. 219 × 70 μm after protargol impregnation), length of adoral zone (113 μm vs. 63 μm), number of adoral membranelles (54 vs. 39), number of cirral pairs in the midventral row (18 vs. 10), number of short and long midventral rows (4 vs. 7), number of transverse cirri (12 vs. 8), and number of macronuclear nodules (more than 300 vs. likely less than 200).

Bakuella pampinaria EIGNER & FOISSNER, 1992, which has, like *B. granulifera*, yellow cortical granules, is distinctly smaller (90–180 × 25–60 μm in vivo), has a lower number of

Table 111. Morphometric data on *Bakuella granulifera*.

Characteristics[a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	319.0	320.0	33.1	7.6	10.4	274.0	396.0	19
Body, width	101.2	100.0	14.1	3.2	13.9	77.0	144.0	19
Body length:width, ratio	3.2	3.2	0.5	0.1	15.3	2.3	4.0	19
Anterior body end to proximal end of adoral zone, distance	113.5	113.0	13.0	3.0	11.5	88.0	140.0	19
Body length:length of adoral zone, ratio	2.8	2.8	0.2	0.1	8.3	2.3	3.3	19
Anterior body end to paroral membrane, distance	19.9	20.0	3.1	0.9	15.5	14.0	25.0	13
Paroral membrane, length	76.4	76.0	10.2	2.8	13.4	60.0	93.0	13
Anterior body end to endoral membrane, distance	20.7	21.5	3.5	1.0	17.1	16.0	27.0	12
Endoral membrane, length	86.2	85.0	7.5	2.2	8.7	76.0	102.0	12
Anterior body end to first buccal cirrus, distance	30.6	32.0	4.9	1.5	16.1	20.0	37.0	11
Anterior body end to last buccal cirrus, distance	75.6	78.0	7.8	2.3	10.3	64.0	86.0	11
Anterior body end to first frontoterminal cirrus, distance	16.7	17.0	4.1	1.4	24.6	10.0	24.0	9
Anterior body end to last frontoterminal cirrus, distance	29.3	28.0	6.7	2.2	22.9	22.0	44.0	9
Posterior end to posteriormost transverse cirrus, distance	28.6	28.0	8.0	1.8	27.9	14.0	48.0	19
Posterior body end to right marginal row, distance	15.8	12.5	9.6	2.3	60.9	4.0	35.0	18
Anteriormost macronuclear nodule, length	7.4	7.0	1.6	0.6	21.7	6.0	10.0	8
Anteriormost macronuclear nodule, width	4.0	4.0	0.5	0.2	13.4	3.0	5.0	8
Macronuclear nodules, number	about 300–400							
Anteriormost micronucleus, length	3.3	3.0	–	–	–	3.0	4.0	7
Anteriormost micronucleus, width	3.0	3.0	0.0	0.0	0.0	3.0	3.0	7
Adoral membranelles, number	54.6	54.0	4.5	1.0	8.2	44.0	62.0	19
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
Cirri behind right frontal cirrus, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	7
Buccal cirri, number	8.2	8.0	1.1	0.3	13.2	7.0	10.0	11
Frontoterminal cirri, number	3.6	3.5	0.7	0.2	19.4	3.0	5.0	10
Transverse cirri, number	11.9	12.0	1.6	0.4	13.6	9.0	15.0	18
Cirral pairs in midventral row, number	18.3	19.0	4.0	1.3	21.8	12.0	23.0	9
Short and long midventral rows, number[b]	4.3	4.0	0.7	0.3	16.6	3.0	5.0	8
Cirri in rightmost long midventral row, number[c]	11.4	11.0	1.2	0.4	10.6	9.0	14.0	11
Right marginal cirri, number	63.2	63.0	5.3	1.5	8.4	54.0	76.0	13
Left marginal cirri, number	63.4	64.0	7.0	1.8	11.0	54.0	77.0	15
Dorsal kineties, number	likely invariably 3							

[a] Data based on protargol-impregnated (WILBERT's protocol), mounted, and randomly selected specimens from a pure culture. As the species is very fragile, some drops of osmium tetroxide (2%) were added to STIEVE's fluid for fixation. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Terminology according to EIGNER (1994). All rows having more than two cirri (Fig. 129h; horizontal arrow).

[c] LMV in figure 129h.

adoral membranelles (31), buccal cirri (5), cirral pairs in the midventral row (9), transverse cirri (4), and macronuclear nodules (about 100), and a slightly higher number of frontoterminal cirri (6 vs. 3–4 in *B. granulifera*). There is no basic morphological difference

between these two species, and thus subspecies rank would probably be more appropriate. On the other hand, the quantitative differences are conspicuous and not caused by a simple size increase of the cell (which may depend on culture conditions; → *Hemiurosoma goertzi*), but concern the entire organism, as evident from, e.g., the doubled number of adoral membranelles, midventral cirral pairs, and macronuclear nodules.

In vivo, *Bakuella granulifera* is easily confused with *Holosticha muscorum* KAHL, 1932, which has a similar size (220–330 × 70–90 µm in vivo), cortical granulation, and cirral pattern (for detailed redescription, see FOISSNER 1982). However, *Holosticha* species lack the short and long cirral rows at the posterior end of the midventral row.

Uroleptus paranotabilis nov. spec. (Fig. 130a–i; 381e, h, i; Table 112)

Diagnosis: Size about 130 × 20 µm in vivo; very slenderly lanceolate. Usually 16 macronuclear nodules forming ± distinct strand left of midline. Cortical granules yellowish to citrine, ≤ 0.5 µm across, scattered throughout cortex and in clusters around cirri and dorsal bristles. Midventral row terminates above mid-body, composed of about 14 cirri. On average 22–24 adoral membranelles, about 30 cirri each in right and left marginal row, 1 buccal cirrus, 1 cirrus behind right frontal cirrus, 2 frontoterminal cirri, 2 transverse cirri very near to posterior body end, 4 dorsal kineties, and 3 caudal cirri.

Type location: Dung balls formed by a large *Scarabaeus* at the Bambatsi Guest Farm in Namibia, 20°10'S 15°25'E (site 52 in figure 2 and chapter 2.1.2).

Etymology: Composite of the Greek word *para* (beside) and the Latin adverb *notabilis* (curious), meaning a ciliate similar to *Uroleptus notabilis*.

Description: Two Namibian populations were studied, namely from site (52; type population) and site (4). They agree so well in all features that conspecificity is beyond reasonable doubt. In spite of this, morphometric data are kept separate, but the diagnosis contains both, while the Antarctic population is excluded because it might be a distinct subspecies.

Size 110–170 × 15–30 µm in vivo, length:width ratio 5–8:1 in vivo, 4.7–9.1:1, on average 6.6:1 in protargol preparations; dorsoventrally flattened up to 2:1. Outline slenderly lanceolate and often slightly sigmoidal with posterior portion narrowed and curved rightwards; anterior region usually with distinct furrow along dorsal kinety 4 (Fig. 130a–c; Table 112); body very flexible but acontractile, frequently slightly to distinctly twisted about main axis. Macronuclear nodules mainly left of midline in a ventral and dorsal strand one upon the other in about 50% of specimens, while slightly scattered in 15% and distinctly so in 35% of cells; anteriormost nodules usually dislocated rightwards; individual nodules ellipsoidal to elongate ellipsoidal, rarely globular or reniform, contain small to medium-sized nucleoli and sometimes a cubic protein crystal (Fig. 130a, i, h; 381i). On average two to three micronuclei within macronuclear strand; individual micronuclei globular to ellipsoidal, up to 5 × 2.5 µm in vivo. Contractile vacuole with inconspicuous collecting canals slightly above mid-body at left cell margin. Cortical granules clustered around cirri and dorsal bristles and scattered throughout cortex, although only ≤ 0.5 µm in size well recognizable because brilliant citrine

in type population and yellowish in Namibian site (4) specimens (Fig. 130d); impregnate slightly to heavily with the protargol method used. Cytoplasm colourless, contains some fat globules 1–5 µm across and many, almost empty food vacuoles 4–6 µm in diameter. Movement without peculiarities, that is, swims and glides rather rapidly on microscope slide and debris showing great flexibility.

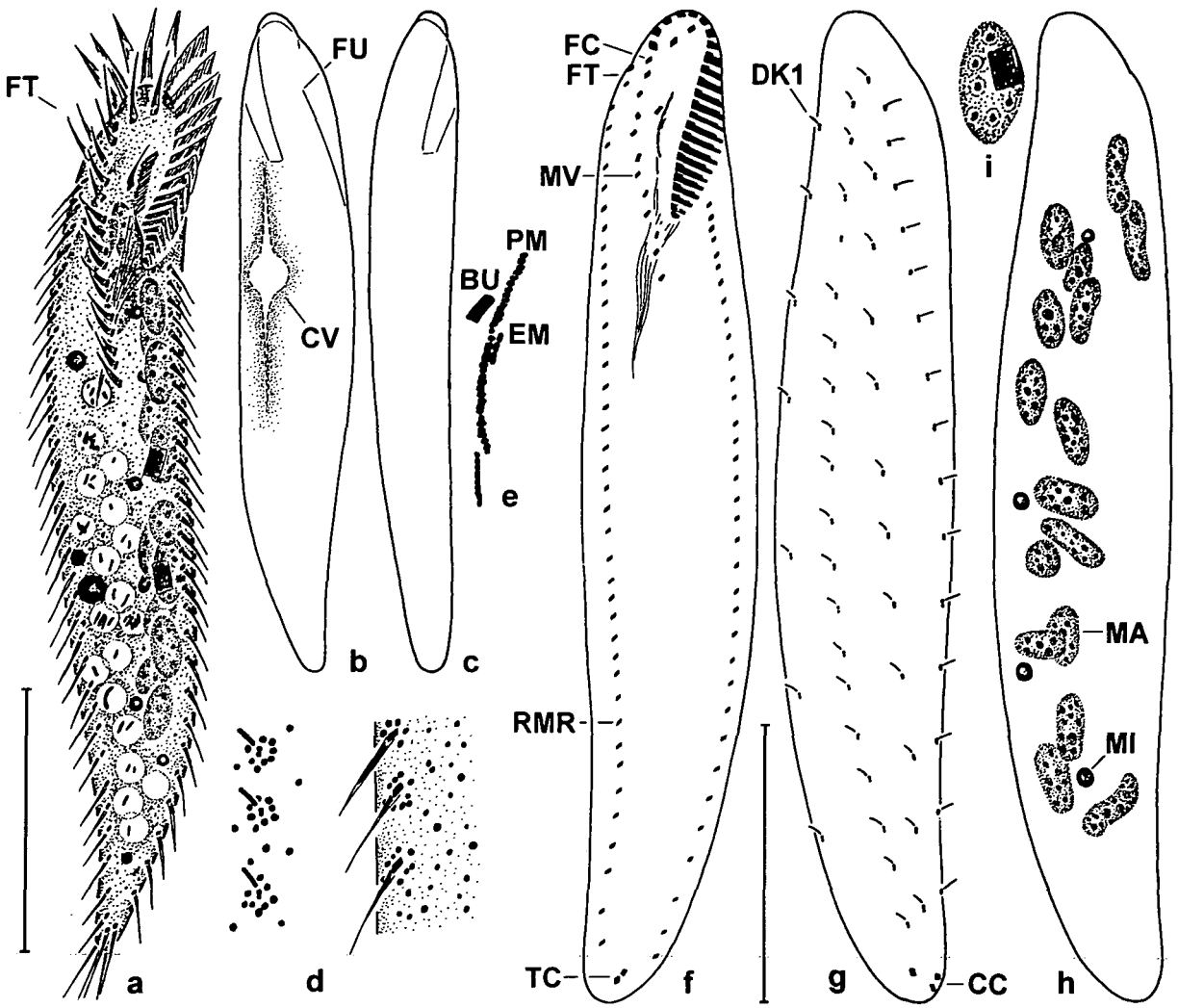


Fig. 130a–i. *Uroleptus paranotabilis*, type population (a, b, d–i) and Namibian site (4) specimen (c) from life (a–d, i) and after protargol impregnation (e–h). **a:** Ventral view of a representative specimen with macronuclear nodules arranged in two distinct strands one upon the other. **b:** Dorsal view showing contractile vacuole with inconspicuous collecting canals and dorsal furrow. **c:** Ventral view of slender shape variant. **d:** Minute (0.3–0.5 µm), yellow to brilliant citrine cortical granules are scattered throughout the cortex and clustered around dorsal bristles and cirri. **e:** Undulating membranes and buccal cirrus. **f–h:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. **i:** Macronuclear nodule with a cubic, about 3 µm large protein crystal. BU – buccal cirrus, CC – caudal cirri, CV – contractile vacuole, DK1 – dorsal kinety 1, EM – endoral membrane, FC – right frontal cirrus, FT – frontoterminal cirri, FU – dorsal furrow, MA – macronuclear nodules, MI – micronucleus, MV – midventral row, PM – paroral membrane, RMR – right marginal row, TC – transverse cirri. Scale bars 40 µm.

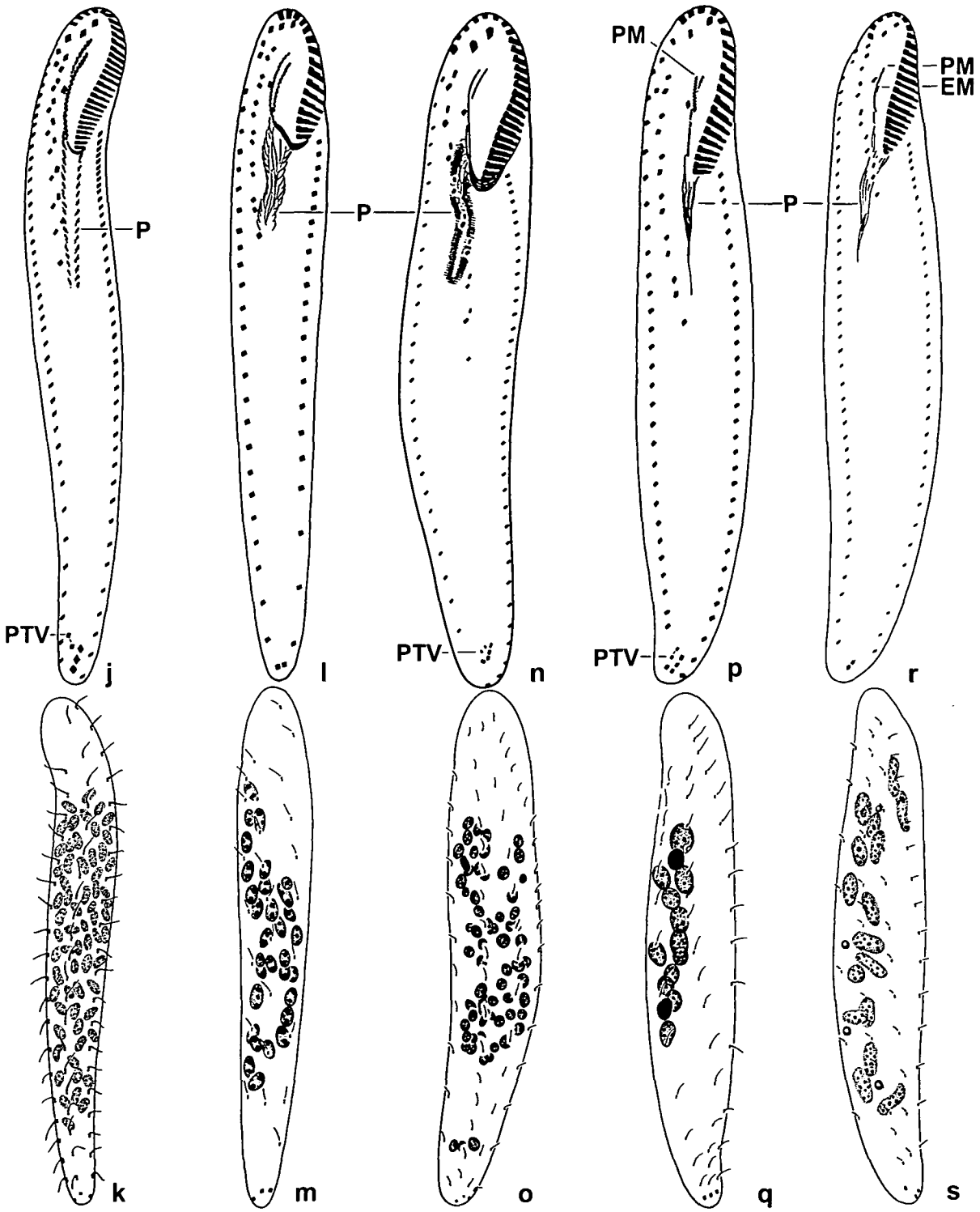


Fig. 130j–s. *Uroleptus notabilis* (j–o) and *U. paranotabilis* (p–s), infraciliature of ventral and dorsal side after protargol impregnation. **j, k:** Austrian specimen, 150 µm (from FOISSNER 1982). **l, m:** German specimen, 110 µm (from BERGER & FOISSNER 1987). **n, o:** Australian specimen, 137 µm (from BLATTERER & FOISSNER 1988). **p, q:** Antarctic specimen, 100 µm (from FOISSNER 1996a). **r, s:** Namibian specimen, 140 µm. EM – endoral membrane, P – pharynx (surrounded by rod-shaped structures only in *U. notabilis*), PM – paroral membrane, PTV – ventral cirri ahead transverse cirri.

Cirral pattern and number of cirri of usual variability, except for the rather strongly varying number of midventral cirri (Fig. 130a, f; Table 112). Most cirri 8–10 µm long in vivo and of similar size. Marginal rows end subterminally, right row commences near level of buccal cirrus. Frontal cirri slightly enlarged, form oblique row with right cirrus, as is usual, behind distal adoral membranelle; invariably one cirrus behind right frontal cirrus. Buccal cirrus slightly behind anterior end of paroral membrane and near level of anterior end of endoral. Two frontoterminal cirri slightly ahead anterior end of right marginal row. Frontoventral cirri only indistinctly zigzagging, midventral pattern thus difficult to recognize in live and prepared specimens; midventral row terminates between 26% and 46%, on average at 33% of body length. Transverse cirri terminal and thus distinctly projecting, although only inconspicuously longer than marginal cirri.

Dorsal bristles about 3 µm long in vivo, arranged in four rows usually easily recognizable both in vivo and protargol preparations due to the cortical granules clustered around the bristles (Fig. 130d, g). Row 1 composed of only few (about 5–7), widely spaced bristles and likely without caudal cirrus, indicating that it is a vestige from the previous generation. Rows 2 to 4 almost bipolar and associated with one caudal cirrus each. Caudal cirri not longer than marginal and transverse cirri.

Adoral zone occupies 17–26%, on average 21% of body length, of usual shape and structure; composed of an average of 23 membranelles, bases of largest membranelles up to 7 µm wide in vivo (Fig. 130a, e, f; 381e, h, i; Table 112). Buccal cavity flat and narrow, right margin forms inconspicuous lip partially covering proximal portion of adoral zone and bearing paroral membrane composed of an about 9 µm long, slightly curved, zigzagging series of 5 µm long cilia; endoral membrane about as long and curved as paroral, but shifted slightly backwards. Pharynx without peculiarities in vivo and protargol preparations, that is, lacks the rod-shaped structures described in all *Uroleptus notabilis* populations.

Occurrence and ecology: To date found at type location, where it was abundant, and at Namibian site (4), where it was rare. Furthermore, *Uroleptus paranotabilis* occurred in soil from the South Shetland Islands, Antarctica, where it was misidentified as *Uroleptus notabilis* (see below). *Uroleptus paranotabilis* is well adapted to soil life with its slender body shape.

Generic assignment and comparison with related species: Generic assignment is according to FOISSNER et al. (1991, p. 248 and 252). Briefly, *Holosticha*, *Paruroleptus*, and *Uroleptus* pose nomenclatural and taxonomic problems not yet solved. Thus, we assign our populations to the oldest genus *Uroleptus*. However, the very different oral apparatus of *U. paranotabilis* and *U. notabilis* indicate that the former might belong to another genus altogether, viz., *Holosticha*, *Hemisincirra*, or *Holostichides*. Possibly, ontogenesis will provide deeper insights.

The overall appearance of *Uroleptus paranotabilis* is very similar to *U. notabilis* (FOISSNER, 1982) FOISSNER, 1998a, of which four populations have been described, namely from Austria (Fig. 130j, k), Germany (Fig. 130 l, m), Australia (Fig. 130n, o), and Antarctica (Fig. 130p, q). However, the oral apparatus[23] is different, not only in the Namibian but also the Antarctic population, which thus belongs to *Uroleptus paranotabilis*: the buccal field is large and deep

[23] We re-examined the protargol slides of all *U. notabilis* populations mentioned and found that the undulating membranes and pharyngeal structures were correctly illustrated, that is, as shown in figures 130j, l, n, p.

vs. narrow and flat; the undulating membranes are long and distinctly curved vs. short and almost straight; the distance between the anterior end of the undulating membranes and the buccal cirrus is considerable larger in *U. notabilis* than *U. paranotabilis*; and the pharynx is surrounded by conspicuous, rod-shaped organelles only in *U. notabilis* (Fig. 130j, l, n, p, r). Furthermore, the cortical granules are usually larger (about 2 × 1 µm) in *U. notabilis* than *U. paranotabilis* (< 1 µm across), and the macronuclear nodules are more numerous (25–70 vs. up to 30) and scattered (vs. in ± distinct series left of midline) in the former than the latter (Fig. 130k, m, o, q, s).

Table 112. Morphometric data on *Uroleptus paranotabilis* from Namibian site 52 (type location, upper line) and Namibian site 4 (lower line).

Characteristics[a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	118.1	113.0	15.6	3.2	13.2	99.0	164.0	23
	128.0	128.0	10.8	3.8	8.5	113.0	146.0	8
Body, width	18.0	18.0	2.6	0.5	14.5	14.0	25.0	23
	19.0	18.5	1.6	0.6	8.4	17.0	22.0	8
Body length:width, ratio	6.6	6.7	1.0	0.2	15.4	4.7	9.1	23
	6.8	6.8	0.8	0.3	11.6	5.6	8.1	8
Anterior body end to proximal end of adoral zone, distance	25.7	26.0	1.9	0.4	7.4	20.0	29.0	23
	30.0	30.5	2.2	0.8	7.3	26.0	32.0	8
Body length:length of adoral zone, ratio	4.6	4.5	0.5	0.1	11.1	3.8	5.9	23
	4.3	4.2	0.5	0.2	11.6	3.5	5.0	8
Anterior body end to last midventral cirrus, distance	39.6	38.0	5.6	1.2	14.0	33.0	50.0	22
	48.0	47.0	4.2	1.5	8.8	43.0	56.0	8
Body length:length of midventral row, ratio	3.0	3.1	0.5	0.1	16.6	2.2	3.9	22
	2.7	2.7	0.4	0.1	13.4	2.0	3.2	8
Anterior body end to buccal cirrus, distance	12.7	13.0	1.5	0.3	11.5	10.0	16.0	23
	13.8	14.0	1.8	0.6	12.7	10.0	16.0	8
Anterior body end to paroral membrane, distance	9.9	10.0	1.0	0.2	10.3	8.0	13.0	23
	11.6	12.0	1.6	0.6	13.7	8.0	13.0	8
Anterior body end to endoral membrane, distance	13.2	13.0	1.4	0.3	10.5	11.0	16.0	20
	14.6	15.0	1.7	0.6	11.8	11.0	16.0	7
Paroral membrane, length	8.7	8.0	–	–	–	8.0	10.0	18
	9.6	10.0	–	–	–	9.0	10.0	5
Endoral membrane, length	8.8	8.5	1.0	0.2	11.8	7.0	10.0	18
	9.0	10.0	1.7	1.0	19.2	7.0	10.0	3
Anterior body end to first frontoterminal cirrus, distance	7.0	7.0	1.0	0.2	14.9	6.0	9.0	23
	8.3	9.0	1.4	0.5	16.8	6.0	10.0	8
Anterior body end to second frontoterminal cirrus, distance	10.7	10.5	1.1	0.2	10.0	9.0	13.0	22
	12.5	12.5	1.2	0.4	9.6	11.0	14.0	8
Anterior body end to right marginal row, distance	12.2	13.0	2.5	0.6	20.8	6.0	17.0	21
	14.1	14.0	1.6	0.6	11.6	11.0	16.0	8
Posterior body end to posteriormost transverse cirrus, distance	1.2	1.0	–	–	–	0.0	3.0	18
	1.1	1.0	–	–	–	1.0	2.0	8
Anterior body end to first macronuclear nodule, distance	20.4	21.0	3.6	0.7	17.6	12.0	28.0	23
	27.5	28.5	3.1	1.1	11.2	23.0	31.0	8
Nuclear figure, length	74.8	73.0	11.7	2.4	15.7	56.0	99.0	23

(continued)

Characteristics[a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	74.6	73.5	8.0	2.8	10.7	64.0	86.0	8
Anteriormost macronuclear nodule, length	7.7	8.0	1.8	0.4	23.0	4.0	11.0	23
	7.3	7.5	1.2	0.4	16.1	6.0	9.0	8
Anteriormost macronuclear nodule, width	3.4	3.0	0.6	0.1	18.8	2.5	5.0	23
	4.4	4.8	0.7	0.3	16.4	3.0	5.0	8
Posteriormost macronuclear nodule, length	7.9	8.0	2.0	0.4	25.2	5.0	12.0	22
	8.4	8.5	1.3	0.5	15.6	7.0	10.0	8
Posteriormost macronuclear nodule, width	3.8	4.0	0.8	0.2	20.2	2.5	5.0	22
	4.1	4.0	0.6	0.2	15.5	3.0	5.0	8
Macronuclear nodules, number	15.4	16.0	1.0	0.2	6.7	13.0	18.0	23
	15.8	16.0	–	–	–	15.0	16.0	8
Anterior micronucleus, length	2.6	2.5	–	–	–	1.5	3.0	23
	2.5	2.5	–	–	–	2.0	3.0	8
Anterior micronucleus, width	2.2	2.0	–	–	–	1.5	3.0	23
	2.4	2.5	–	–	–	2.0	3.0	8
Micronuclei, number	3.0	3.0	0.9	0.2	28.4	2.0	5.0	23
	2.1	2.0	1.2	0.4	58.7	1.0	4.0	8
Adoral membranelles, number	21.9	22.0	1.5	0.3	6.9	19.0	25.0	23
	23.9	24.5	2.2	0.8	9.1	19.0	26.0	8
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	8
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	23
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	8
Frontoterminal cirri, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	23
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	8
Cirri behind right frontal cirrus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	22
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	8
Midventral row, number of cirral pairs	6.6	6.0	1.4	0.3	20.5	5.0	9.0	21
	7.3	7.0	0.8	0.3	10.4	6.0	8.0	7
Midventral cirri, number[b]	13.4	12.0	3.0	0.7	22.3	10.0	19.0	21
	15.4	16.0	0.8	0.3	5.1	14.0	16.0	7
Transverse cirri, number	2.2	2.0	–	–	–	2.0	3.0	20
	1.9	2.0	–	–	–	0.0	3.0	8
Right marginal cirri, number	33.6	34.0	4.2	0.9	12.6	26.0	42.0	23
	33.4	33.5	1.8	0.7	5.5	31.0	37.0	8
Left marginal cirri, number	31.4	32.5	3.9	0.8	12.4	25.0	38.0	22
	28.0	27.0	3.7	1.4	13.0	23.0	34.0	7
Caudal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	14
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	7
Dorsal kineties, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	18
	4.0	4.0	0.0	0.0	0.0	4.0	4.0	5

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Cirrus behind right frontal cirrus not included.

The Antarctic population of *Uroleptus paranotabilis* differs rather distinctly from the Namibian specimens, indicating that it is a distinct subspecies: three dorsal kineties vs. four (Fig. 130q, s); cortical granules colourless vs. yellowish; buccal cirrus at posterior vs. anterior half of paroral membrane (Fig. 130p, r); six vs. two transverse and pretransverse cirri (Fig. 130p, r). However, similar differences occur in the *Uroleptus notabilis* populations (Fig. 130j–o). The German specimens differ from the type population and the Australian population in body size and correlated features, the size of the cortical granules (0.5 µm across vs. 2 × 1 µm), the number of macronuclear nodules (25–35 vs. 47–70), and the number of transverse cirri (2 vs. 2–6, usually 4). The Australian specimens differ from the European populations in having four instead of three dorsal kineties.

In vivo, *Uroleptus paranotabilis* is not only easily confused with *U. notabilis* (look at the buccal field!), but also with quite a lot of other soil hypotrichs, such as multinucleate → *Hemiurosoma*, → *Hemisincirra* and → *Periholosticha* species, as well as certain amphisiellids. Thus, both in vivo observation (cortical granules!) and protargol impregnation are necessary for a reliable identification. However, if a specimen has the following features in vivo, then it is likely *Uroleptus paranotabilis*: size about 130 × 20 µm, that is, slenderly lanceolate; buccal field moderately narrow and flat; about 20 macronuclear nodules in indistinct series left of midline; frontoventral row slightly to distinctly longer than adoral zone and composed of rather indistinct cirral pairs; cortical granules colourless to yellowish, minute (< 1 µm) and mainly around cirri and dorsal bristles, do not form distinct rows; 3–4 dorsal kineties; 1 buccal cirrus and 1–6 transverse and pretransverse ventral cirri.

Eschaneustyla lugeri nov. spec. (Fig. 131a–n; 382a–c; Table 113)

Diagnosis: Size about 220 × 55 µm in vivo, slightly contractile. Outline elongate elliptical to slightly sigmoidal. On average 60 macronuclear nodules and 56 adoral membranelles. Cortical granules colourless, around cirri and dorsal bristles and scattered throughout cortex. On average 4 buccal cirri, a long ventral row consisting of about 28 cirri, and a conspicuously long row of frontoterminal cirri ending in rear third of body. Frontal area densely ciliated by an average of 32 cirri forming distinct, curved rows.

Type location: Forest soil from Taveuni island, Fiji Islands, 16°52'S 180°W.

Dedication: Dedicated to Mr. Gerhard LUGER (Salzburg), an excellent orthopaedist, who collected the sample.

Description: Size 180–260 × 45–65 µm in vivo, usually near 220 × 55 µm, length:width ratio 3.5–5:1 in vivo, on average 4:1 in vivo and protargol preparations (Table 113). Outline elongate elliptical and often slightly sigmoidal, frequently somewhat irregular, that is, with small convexities and concavities, possibly due to slight contractions, as indicated by specimens under mild cover glass pressure which contract by up to 30%. Anterior body portion frequently slightly set off from body proper, that is, cephalized. Flattened about 2:1 dorsoventrally with anterior and posterior portion rather thin (Fig. 131a–d; 382a). Macronuclear nodules moderately variable in number and shape (Table 113), usually arranged as shown in figure 131k; individual nodules about 10 × 5 µm in vivo, ellipsoidal to elongate ellipsoidal, globular, or dumb-bell-shaped, each with some small nucleoli. Micronuclei

scattered, sometimes clumped, about 4 µm across, compact and thus easy to recognize in vivo and protargol preparations. Contractile vacuole with two conspicuous collecting canals at left body margin slightly above mid-body. Cortex very flexible, contains two size types of colourless granules and rather conspicuous crystals (Fig. 131f–h): type I granules about 1 × 0.5 µm, around cirri and dorsal bristles; type II granules < 0.5 µm, scattered, highly refractive and thus rather conspicuous despite their minuteness; both granule types do not impregnate with protargol, but stain pink and swell to 2–3 µm long rods forming a thin cover after addition of methyl green-pyronin. Cortical or subcortical crystals rod-shaped, 2–4 µm long and often orientated in main body axis, do not occur in deeper cytoplasmic areas. Cytoplasm colourless, without conspicuous inclusions. Food vacuoles with bacteria only about 5 µm across, those with heterotrophic flagellates and organic debris up to 20 µm across; also feeds on up to 100 µm long fungal hyphae, 20–30 × 5–10 µm-sized fungal conidia, and small *Euglypha* species (Fig. 131a; 382a). Movement inconspicuous, glides rather rapidly on microscope slide and soil particles showing great flexibility.

Cirral pattern and number of cirri of usual variability (Fig. 131a, i, n; Table 113). Most cirri only 10 µm long in vivo. Right marginal row distinctly shortened anteriorly, ends subterminal; left row distinctly curved rightwards anteriorly, terminates on average 18 µm ahead of rear body end. Frontal area very conspicuous because densely covered by an average of 32 slightly enlarged cirri forming rather distinct rows[24]; prominent frontal cirri and midventral pairs absent. Usually four buccal cirri right of mid-portion of paroral membrane, last cirrus often slightly smaller. Invariably two long, slightly oblique ventral cirral rows, left begins at 13% of body length and terminates at 49% on average; according to EIGNER's (1994) ontogenetic investigations, it is a long midventral row. Right ventral row, which is a row of frontoterminal cirri according to EIGNER (1994), commences at 11% of body length and terminates at 69%. Transverse cirri lacking.

Dorsal cilia about 3 µm long in vivo, arranged in four meridional rows; rows 3 and 4 usually slightly shortened anteriorly. Each row with two or three small and thus inconspicuous caudal cirri (Fig. 131j, m).

Adoral zone occupies 25–38%, on average 30% of body length, composed of an average of 56 membranelles, bases of largest membranelles about 13 µm wide in vivo; distal portion extends far on right body side causing the slight cephalization mentioned above; proximal portion slightly sigmoidal, a conspicuous (compared to many other hypotrichs) feature not described in the congeners studied by FOISSNER (1982) and EIGNER (1994), but recognizable in their figures; such peculiarities are usually lost in protargol preparations, as also evident from the following observations (Fig. 131a, e, i, n; 382a, c). Buccal apparatus in vivo as in congeners, that is, extremely narrow and flat compared to size of cell and many other hypotrichs (Fig. 131a, e; 382b, c); much more prominent and thus of ordinary appearance in protargol preparations, possibly due to slight inflation of cavity and/or some contraction of the oral region. Likewise, paroral and endoral pattern very different in vivo and after protargol impregnation: paroral in vivo at base of buccal lip, almost straight and slightly curved rightwards, while distinctly curved leftwards and optically intersecting with endoral in silver preparations. Both membranes likely composed of dikinetids, paroral slightly thickened (broadened) in anterior 5 µm, cilia up to 6 µm long (Fig. 131a, e, i, n). Pharyngeal fibres

[24] We did not find dividers and thus cannot define the pattern; a proposal is given in figure 131n.

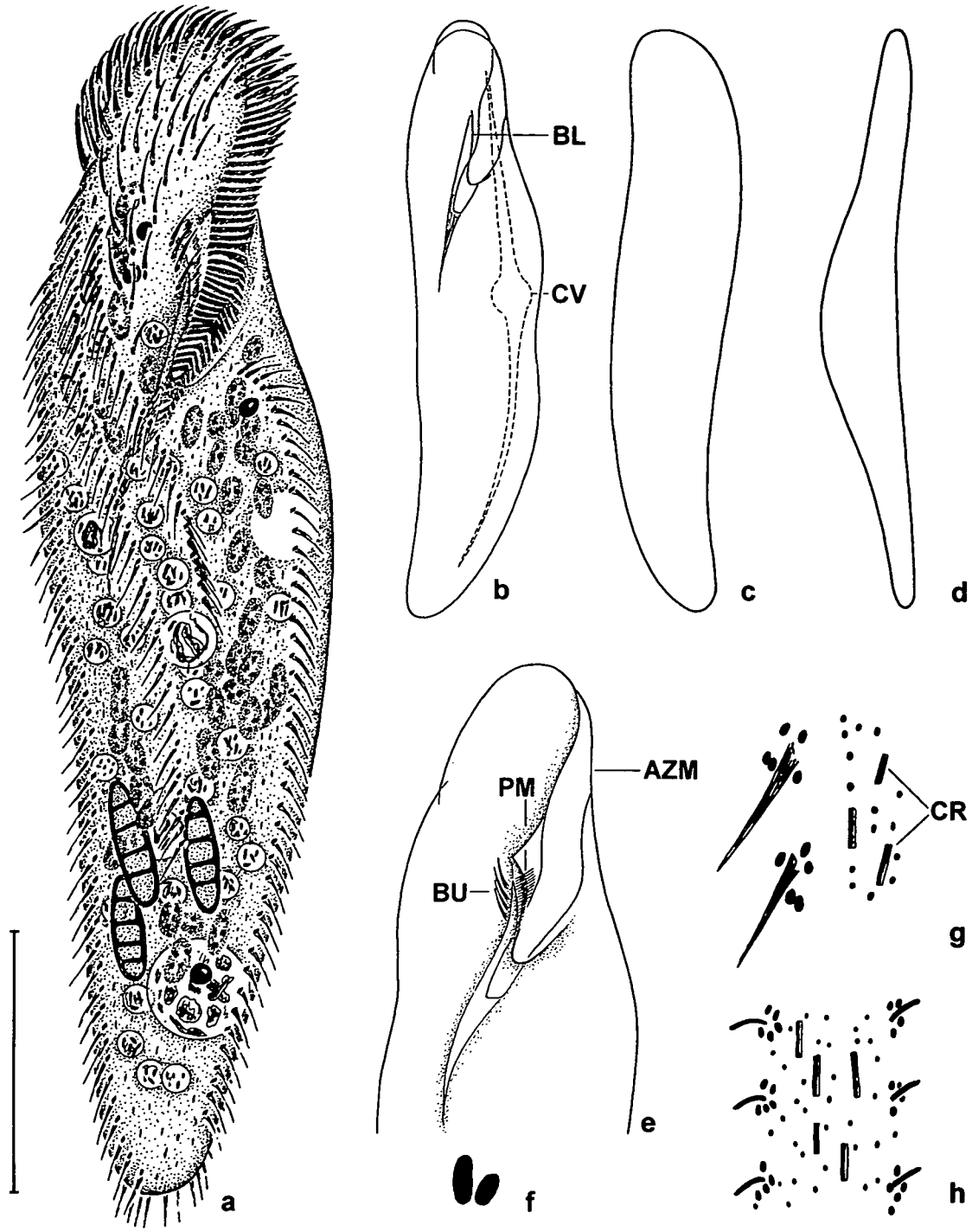


Fig. 131a–h. *Eschaneustyla lugeri* from life. **a:** Ventral view of a representative specimen. **b, c:** Shape variants in ventral and dorsal view. **d:** Right lateral view showing dorsoventral flattening. **e:** Oral apparatus showing sigmoidal proximal portion of adoral zone and the minute buccal cavity, which becomes heavily inflated in protargol preparations (Fig. 131n). **f:** Colourless cortical granules, about 1 × 0.5 µm in size, occur around cirri and dorsal bristles. **g, h:** Arrangement of large (about 1 × 0.5 µm) and small (about 0.2 µm across) cortical granules and subcortical crystals in ventral and dorsal cortex. AZM – adoral zone of membranelles, BL – buccal lip, BU – buccal cirri, CR – subcortical crystals 2–4 µm long, CV – contractile vacuole with collecting canals, PM – paroral membrane. Scale bar 50 µm.

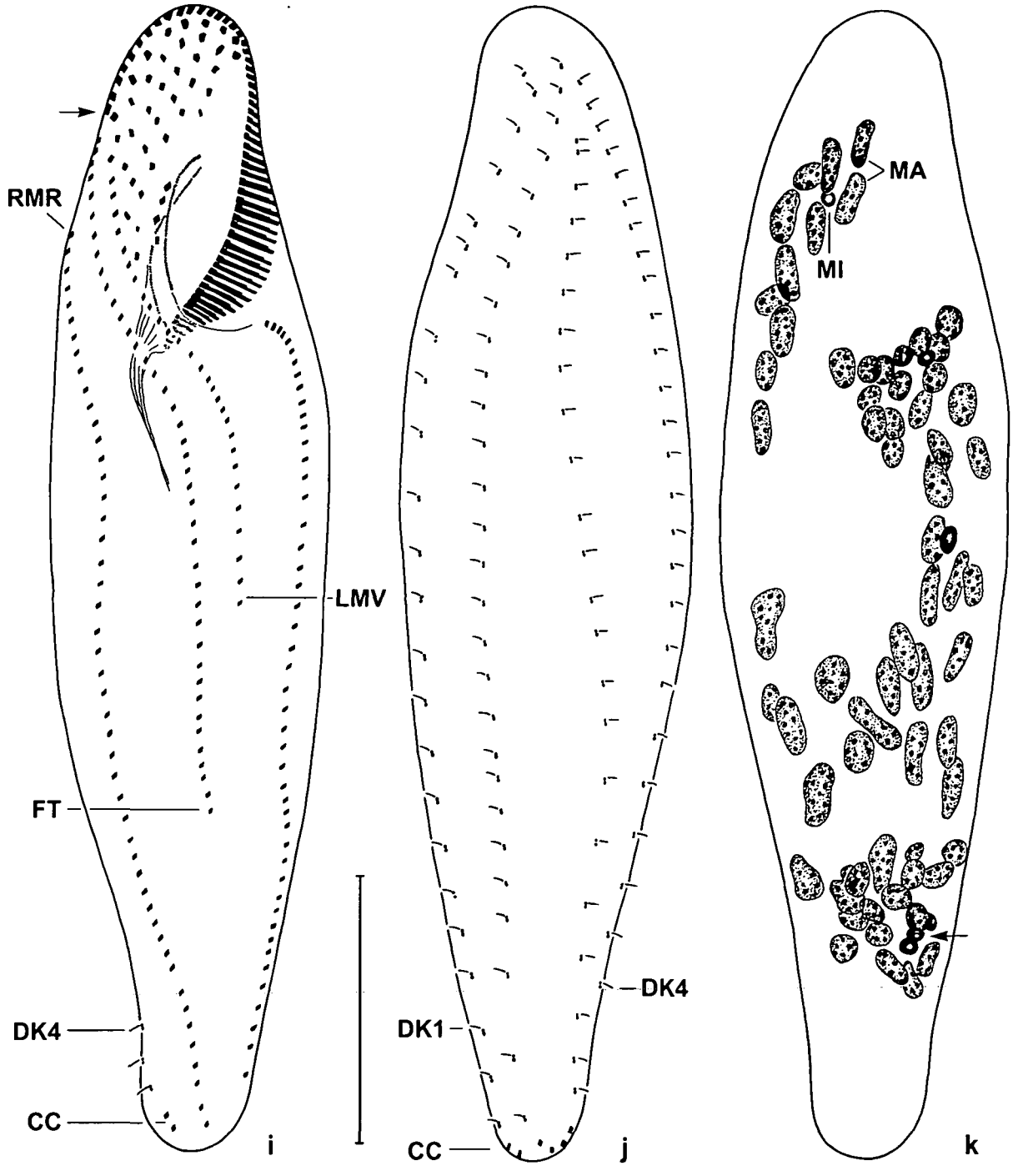


Fig. 131i–k. *Eschaneustyla lugeri*, infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen after protargol impregnation. Arrow in (i) denotes distal end of adoral zone, which is far subapical, producing a slight cephalization of the organism. Arrow in (k) denotes clumped micronuclei. Note that the buccal cavity is much more conspicuous than in vivo, indicating inflation due to the preparation procedures. CC – caudal cirri, DK1, 4 – dorsal kineties, FT – row of frontoterminal cirri, LMV – long ventral row, which is a midventral row according to EIGNER (1994), MA – macronuclear nodules, MI – micronuclei, RMR – first cirrus of right marginal row. Scale bar 50 μm.

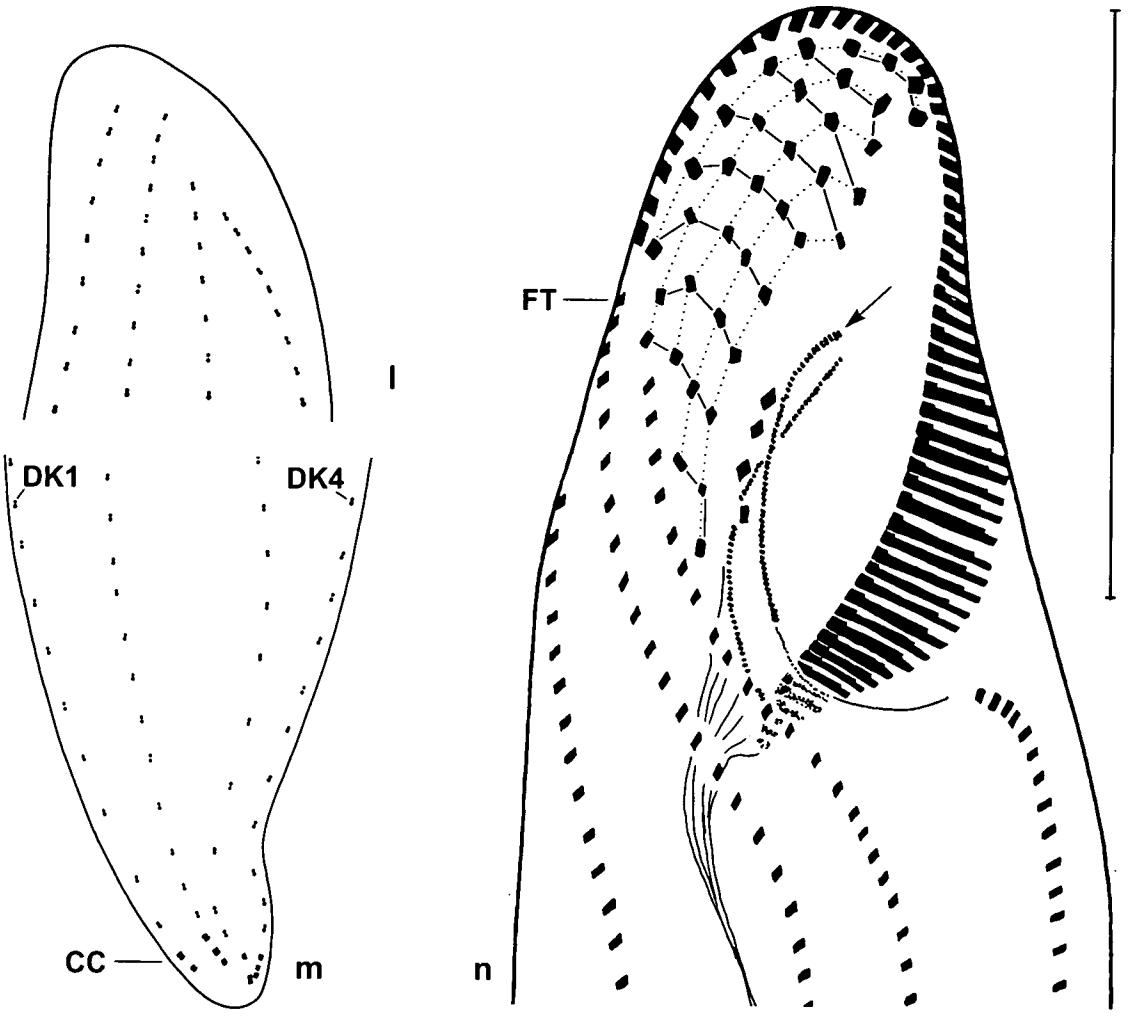


Fig. 131 l–n. *Eschaneustyla lugeri*, somatic and oral infraciliature after protargol impregnation. **l, m:** Anterior and posterior portion of dorsal side of an excellently impregnated specimen. **n:** Enlarged part of figure 131i. The conspicuous cirri in the frontal area of *E. lugeri* can be interpreted as belonging to about nine oblique cirral rows (solid lines) or about five coronal cirral rows (dotted lines). Arrow marks broadened (thickened) anterior portion of paroral membrane. CC – caudal cirri, DK1, 4 – dorsal kineties, FT – first cirrus of frontoterminal row. Scale bar 50 μm.

clearly recognizable in vivo and after protargol impregnation, of ordinary length and structure, extend obliquely backwards.

Occurrence and ecology: To date found only at type location, where it was very rare.

Generic classification and comparison with related species: At first glance, this species looks like the representative of a new genus because of the numerous frontal cirri forming distinct coronas (Fig. 131a, i). However, the following features assign it rather unequivocally to *Eschaneustyla* STOKES, 1886a, which belongs to the Urostylidae, according to the ontogenetic data of EIGNER (1994): (i) ventral cirral pattern in short and long rows (midventral rows according to EIGNER 1994); (ii) buccal cavity very flat and narrow compared to size of cell; (iii) slightly sigmoidal adoral zone extending far on right side of cell;

Table 113. Morphometric data on *Eschaneustyla lugeri*.

Characteristics[a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	202.7	213.0	28.7	8.6	14.1	162.0	246.0	11
Body, width	50.8	50.0	4.6	1.4	9.0	45.0	58.0	11
Body length:width, ratio	4.0	3.9	0.6	0.2	14.2	3.2	5.4	11
Anterior body end to proximal end of adoral zone, distance	61.4	61.0	4.8	1.4	7.8	52.0	68.0	11
Anterior body end to distal end of adoral zone, distance	18.9	18.0	2.3	0.7	12.4	16.0	22.0	11
Body length:length of adoral zone, ratio	3.3	3.3	0.5	0.1	13.6	2.7	4.1	11
Anterior body end to paroral membrane, distance	27.8	28.0	3.0	1.0	10.9	24.0	32.0	9
Paroral membrane, length	26.0	24.0	3.5	1.3	13.6	22.0	32.0	8
Anterior body end to first buccal cirrus, distance	33.1	33.0	3.1	0.9	9.5	27.0	38.0	11
Anterior body end to last buccal cirrus, distance	43.6	44.0	3.7	1.1	8.5	37.0	50.0	11
Anterior body end to long ventral row, distance	27.5	26.0	2.7	0.8	10.0	24.0	32.0	11
Anterior body end to end of long ventral row, distance	99.3	104.0	11.1	3.3	11.2	78.0	111.0	11
Anterior body end to frontoterminal row, distance	23.1	24.0	2.5	0.8	10.9	20.0	28.0	11
Anterior body end to end of frontoterminal row, distance	140.2	149.0	16.2	4.9	11.5	114.0	156.0	11
Anterior body end to right marginal row, distance	37.5	40.0	5.3	1.6	14.2	28.0	46.0	11
Posterior body end to right marginal row, distance	6.0	6.0	0.7	0.2	11.1	5.0	7.0	10
Posterior body end to left marginal row, distance	18.0	18.0	7.7	2.4	43.0	9.0	33.0	10
Anterior body end to first macronuclear nodule, distance	18.5	20.0	4.0	1.2	21.6	10.0	24.0	11
Anteriormost macronuclear nodule, length	9.0	10.0	2.1	0.6	23.3	6.0	12.0	11
Anteriormost macronuclear nodule, width	4.5	5.0	1.3	0.4	29.0	3.0	6.0	11
Posterior body end to rearmost macronuclear nodule, distance	31.2	35.0	10.3	3.1	32.9	10.0	46.0	11
Posteriormost macronuclear nodule, length	7.6	6.0	2.8	0.8	36.2	5.0	13.0	11
Posteriormost macronuclear nodule, width	4.7	5.0	1.1	0.3	23.3	3.0	6.0	11
Macronuclear nodules, number	60.3	60.0	9.0	2.7	14.9	49.0	76.0	11
Anteriormost micronucleus, length	3.8	4.0	–	–	–	3.0	5.0	11
Anteriormost micronucleus, width	3.2	3.0	–	–	–	2.5	4.0	11
Micronuclei, number	8.7	8.0	3.2	1.0	36.6	5.0	14.0	11
Adoral membranelles, number	56.1	57.0	5.1	1.5	9.1	48.0	64.0	11
Frontal cirri, number	32.4	31.0	3.8	1.3	11.7	27.0	39.0	9
Buccal cirri, number	4.0	4.0	–	–	–	3.0	5.0	11
Left ventral row, number of cirri	27.9	28.0	2.5	0.8	9.0	23.0	31.0	11
Right ventral (frontoterminal) row, number of cirri	38.7	38.0	2.3	0.7	5.9	35.0	42.0	11
Right marginal cirri, number	47.6	45.0	3.0	0.9	6.6	42.0	52.0	11
Left marginal cirri, number	45.3	45.0	3.0	0.9	6.6	42.0	52.0	11
Caudal cirri, total number	9.9	11.0	1.4	0.5	13.8	8.0	11.0	9
Dorsal kineties, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	11

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

(iv) broadened anterior end of paroral; (v) four dorsal kineties each associated with more than one caudal cirrus; (vi) lack of transverse cirri. Furthermore, both terrestrial species now assigned to *Eschaneustyla* (see below) have cortical granules, many small macronuclear

nodules, and an anteriorly shortened right marginal row. A broadened anterior end of the paroral, first described by EIGNER (1994) in *E. brachytona*, evolved convergently in the oxytrichid *Notohymena* BLATTERER & FOISSNER, 1988. However, the vitiphilan species could belong to another, or even a new genus if ontogenetic data show that the frontal cirri are not arranged in oblique rows but in curved coronas (Fig. 131n). This is emphasized by some further differences mentioned in the next paragraph.

Eschaneustyla lugeri differs from *E. brachytona* STOKES, 1886a and → *E. terricola* FOISSNER, 1982 by the numerous and thus conspicuous frontal cirri evenly distributed on the frontal area; no single (left) frontal cirrus, so conspicuous in *E. brachytona* and → *E. terricola*, is recognizable. Furthermore, the leftmost ventral cirral row of *E. lugeri* borders the cirri on the frontal field, while it commences farther subapically in *E. brachytona* and → *E. terricola*, where the oblique frontal rows thus abut on the frontoterminal cirral row. There are also several distinct quantitative differences: 4 buccal cirri vs. 1 cirrus, 2 vs. 4 long ventral rows, 56 vs. 39–46 adoral membranelles. In vivo, *Eschaneustyla lugeri* can be easily recognized by the following combination of features: length 180–260 µm; many macronuclear nodules; many cirri on frontal field forming several coronas; four buccal cirri; two ventral cirral rows.

Generally, in vivo *Eschaneustyla* spp. are difficult to separate from *Bakuella* spp. and large *Holosticha* species. Thus, identifications should be checked by protargol impregnation.

Eschaneustyla terricola FOISSNER, 1982 (Fig. 381f, g)

The specimens from Namibian site (30) are rather different from the type; specifically, they are larger (about 200 × 40 µm vs. 160 × 45 µm in vivo) and have a distinct midventral row in the frontal area, lacking in the Austrian type population. However, the specimens studied by EIGNER (1994) are between these extremes, indicating high variability or cryptic speciation. The latter is emphasized by the yellowish cortical granules, which are more distinct and differently arranged in the Namibian specimens, where they are brilliantly yellowish and form conspicuous clusters around the dorsal bristles, while they are loosely arranged in the unciliated body parts (Fig. 381f, g). Furthermore, the clusters consist of two size and shape types of granules: ellipsoidal to ovate and about 1 × 0.5 µm in size and globular 0.4–0.6 µm across.

EIGNER (1994) hastily synonymized the yellowish *E. terricola* FOISSNER, 1982 with the colourless, limnetic *E. brachytona* STOKES, 1886a. As STOKES (1886a) was a careful observer, this indicates that the species lacks, or has colourless granules. Accordingly, EIGNER's synonymization should not be followed until a limnetic *Eschaneustyla* population has been investigated in detail. As shown by the previous species and the Namibian population described above, the genus is richer than hitherto recognized.

Holosticha brachysticha nov. spec. (Fig. 132a–g; Table 114)

Diagnosis: Size about 90 × 17 µm in vivo; elongate ellipsoidal. On average 32 scattered macronuclear nodules. Cortical granules around cirri and dorsal bristles, yellowish, about 1.0–1.5 × 0.5–0.8 µm in size. Midventral row terminates at about 1/3 of body length, composed of about 10 cirri. On average 16 adoral membranelles, 23 cirri each in right and left marginal row, 1 buccal cirrus, 2 frontoterminal cirri, 3 transverse cirri, and 3 dorsal kineties.

Type location: Sandy, saline coastal soil (pH 7.6) near Punta Pirikiki, about 54 km south of Limon, Caribbean coast of Costa Rica, Central America, 09°40'N 82°40'W.

Etymology: Composite of the Greek adjective *brachy* (short) and the Greek noun *sticha* (row), referring to the short midventral row.

Description: Size 70–110 × 15–20 µm, usually around 90 × 17 µm in vivo, length:width ratio on average 5.3:1 both in vivo and protargol preparations (Table 114); dorsoventrally flattened up to 2:1. Body elongate elliptical, very flexible but acontractile (Fig. 132a, b). Macronuclear nodules usually scattered in U-shaped pattern in central portion of cell; individual nodules usually ellipsoidal, rarely globular, elongate ellipsoidal, or dumb-bell-shaped; nucleoli small. On average two ellipsoidal micronuclei within macronuclear figure. Contractile vacuole slightly above mid-body at left cell margin, without distinct collecting canals. Cortical granules only in clusters around cirri and dorsal bristles, yellowish, conspicuously brilliant because compact, about 1.0–1.5 × 0.5–0.8 µm in size, do not impregnate with the protargol method used. Cytoplasm colourless, without peculiarities, that is, contains some ordinary, yellowish crystals about 1–2 µm long and some food vacuoles 5–7 µm across. Feeds on tuberous bacteria. Swims and glides moderately quickly on microscope slide and debris showing great flexibility.

Cirral pattern and number of cirri of usual variability (Fig. 132a, e; Table 114). Marginal and midventral cirri about 10 µm long in vivo and of similar size, that is, usually composed of 2 × 2 cilia. Right marginal row shortened anteriorly, terminates, like left row, near posterior end of cell. Frontal cirri slightly enlarged, in transverse, concave line, as in most congeners. Buccal cirrus usually composed of two cilia only, slightly behind anterior end of paroral membrane and thus near level of anterior end of endoral. Two frontoterminal cirri right of anterior end of midventral row usually composed of four to five cirral pairs only, thus terminating at about 34% of body length. Transverse cirri almost terminal, about 15 µm long in vivo and thus distinctly projecting beyond rear body end; anterior cirrus usually smaller than other cirri and thus likely a pretransverse cirrus.

Dorsal bristles about 3 µm long in vivo, arranged in three rows easily recognizable in vivo due to the granule clusters around the individual bristles. Rows 1 and 2 distinctly shortened anteriorly, row 3 bipolar. Caudal cirri lacking.

Adoral zone occupies 20–27%, on average 23% of body length, composed of an average of 16 membranelles of usual shape and structure (Fig. 132a, e). Buccal cavity of ordinary width but flat, right margin forms inconspicuous lip partially covering proximal portion of adoral zone of membranelles. Paroral and endoral of about same length and almost in parallel, with endoral on average 2 µm rearward. Pharyngeal fibres distinct after protargol impregnation, extend to near mid-body.

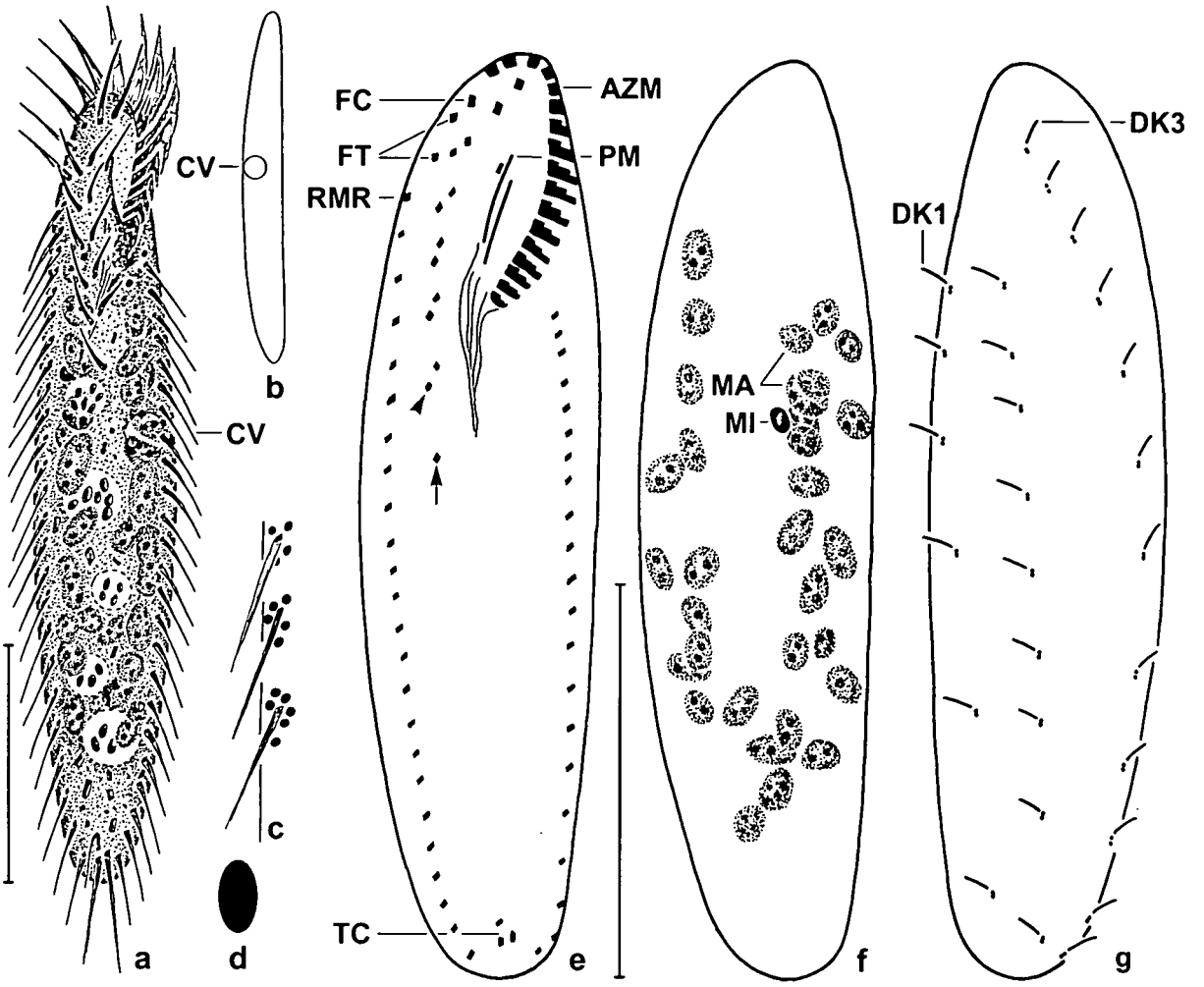


Fig. 132a–g. *Holosticha brachysticha* from life (a–d) and after protargol impregnation (e–g). **a:** Ventral view of a representative specimen. **b:** Right lateral view showing dorsoventral flattening and contractile vacuole. **c, d:** Yellowish, compact and thus brilliant, cortical granules, 1.0–1.5 × 0.5–0.8 µm in size, occur around cirri and dorsal bristles. **e–g:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrow in (e) marks last midventral cirrus, arrowhead denotes last cirral pair. AZM – adoral zone of membranelles, CV – contractile vacuole, DK1, 3 – dorsal kineties, FC – right frontal cirrus, FT – frontoterminal cirri, MA – macronuclear nodules, MI – micronucleus, PM – paroral membrane, RMR – right marginal row, TC – transverse cirri. Scale bars 30 µm.

Occurrence and ecology: To date found at type location and Namibian site (53). Abundances were low at both sites.

Comparison with related species: The overall appearance of *Holosticha brachysticha* is similar to *H. mancoidea* HEMBERGER, 1985; *H. sigmoidea* FOISSNER, 1982; *H. tetracirrata* BUITKAMP & WILBERT, 1974; *H. manca plurinucleata* GELLÉRT, 1956; and → *Uroleptus paranotabilis*. However, *H. mancoidea* has fewer macronuclear nodules (6–12 vs. 28–38), more transverse and pretransverse cirri (5 plus 2 vs. 2 plus 1), and the distal four adoral membranelles are distinctly set off. Furthermore, HEMBERGER (1985) did not describe

Table 114. Morphometric data on *Holosticha brachysticha*.

Characteristics[a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	78.8	82.0	9.5	2.6	12.0	57.0	90.0	13
Body, width	15.2	14.0	2.1	0.6	14.0	12.0	20.0	13
Body length:width, ratio	5.3	5.3	1.0	0.3	18.7	3.8	6.7	13
Anterior body end to rear end of adoral zone, distance	17.6	18.0	1.6	0.4	9.1	14.0	20.0	13
Body length:length of adoral zone, ratio	4.5	4.4	0.4	0.1	9.2	3.7	5.0	13
Anterior body end to last midventral cirrus, distance	26.7	26.0	2.8	0.8	10.5	22.0	32.0	13
Body length:length of midventral row, ratio	3.0	3.1	0.4	0.1	14.4	2.2	3.5	13
Anterior body end to buccal cirrus, distance	8.6	9.0	1.3	0.3	14.6	6.0	10.0	13
Anterior body end to paroral membrane, distance	6.2	6.0	1.0	0.3	16.3	5.0	8.0	13
Anterior body end to endoral membrane, distance	7.9	8.0	1.3	0.4	16.1	6.0	10.0	9
Paroral membrane, length	7.8	8.0	1.3	0.6	16.7	6.0	9.0	5
Endoral membrane, length	8.0	8.0	0.0	0.0	0.0	8.0	8.0	3
Anterior body end to first frontoterminal cirrus, distance	5.0	5.0	0.9	0.3	17.9	3.0	6.0	11
Anterior body end to second frontoterminal cirrus, distance	8.5	8.0	1.4	0.4	16.2	6.0	11.0	11
Anterior body end to right marginal row, distance	13.4	13.5	2.3	0.7	17.2	11.0	18.0	12
Posterior body end to rear transverse cirrus, distance	2.5	2.3	1.3	0.4	54.0	1.0	5.0	10
Anterior body end to first macronuclear nodule, distance	13.5	14.0	3.2	0.9	23.7	6.0	19.0	13
Nuclear figure, length	55.0	58.0	7.5	2.1	13.6	41.0	65.0	13
Anteriormost macronuclear nodule, length	4.7	5.0	0.9	0.3	20.2	3.0	6.0	13
Anteriormost macronuclear nodule, width	2.3	2.5	–	–	–	1.5	3.0	13
Macronuclear nodules, number	31.7	31.0	2.9	0.8	9.1	28.0	38.0	13
Anterior micronucleus, length	1.8	1.5	–	–	–	1.5	3.0	7
Anterior micronucleus, width	1.6	1.5	–	–	–	1.0	2.4	7
Micronuclei, number	2.0	2.0	1.1	0.3	52.7	1.0	4.0	10
Adoral membranelles, number	15.8	16.0	1.2	0.3	7.5	13.0	17.0	12
Frontal cirri, number	2.9	3.0	–	–	–	2.0	3.0	13
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13
Frontoterminal cirri, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	10
Midventral row, number of cirral pairs	4.7	4.5	–	–	–	4.0	6.0	12
Midventral cirri, total number	10.3	10.5	1.4	0.4	13.3	9.0	13.0	12
Transverse cirri, number	2.1	2.0	–	–	–	2.0	3.0	10
Pretransverse cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10
Transverse and pretransverse cirri, number	3.1	3.0	–	–	–	3.0	4.0	10
Right marginal cirri, number	22.6	22.5	2.5	0.7	11.1	19.0	26.0	12
Left marginal cirri, number	23.1	23.0	2.1	0.6	9.3	19.0	27.0	13
Dorsal kineties, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

cortical granules; however, such granules might have been overlooked because he did not study live specimens in detail. *Holosticha sigmoidea* has, inter alia, a series of 6–9 macronuclear nodules (vs. 28–38 scattered nodules), more dorsal kineties (4 vs. 3), transverse cirri (5–8 vs. usually 3), and adoral membranelles (16–24, on average 20 vs. 13–17, on average

16), and the colourless cortical granules are arranged in many longitudinal rows (vs. clustered around cirri and bristles). *Holosticha tetracirrata*, which has almost the same average number and pattern of macronuclear nodules, has four dorsal kineties (vs. three), more adoral membranelles (24 vs. 16), a longer midventral row (67% of body length vs. 34%), and lacks cortical granules. *Holosticha manca plurinucleata* has only 22 macronuclear nodules (vs. 32) and 11 adoral membranelles (vs. 16), but possesses more transverse (5 vs. 3) and midventral cirri (21 vs. 9–13). → *Uroleptus paranotabilis* and *U. notabilis* (FOISSNER, 1982) FOISSNER, 1998a have caudal cirri; furthermore, most populations are longer (> 110 µm) and have more adoral membranelles (> 22 vs. 13–17) and marginal cirri (> 34 vs. 23).

In vivo, *Holosticha brachysticha* is recognizable by the rather small size (around 100 × 20 µm), the ellipsoidal, yellowish cortical granules around the cirri and dorsal bristles, the short midventral row, the low number of transverse cirri, and the scattered macronuclear nodules.

Periholosticha lanceolata HEMBERGER, 1985 (Fig. 133a–l, q–y; Table 115)

Improved diagnosis (based on original description and our data): Size about 110 × 12 µm in vivo; slenderly lanceolate with posterior region narrowed, more or less distinctly tail-like. On average 16 macronuclear nodules in two strands one upon the other along left postoral body margin. Cortical granules between cirri and around dorsal bristles, colourless, compact and thus refractive, 0.5–1 × 0.4–0.8 µm. Cirri composed of 2–4 cilia. On average 16 adoral membranelles, 3 frontal separated by minute gap; 13 frontoventral cirri forming indistinct midventral pattern in anterior half of row extending to second body third; 30 right and 26 left marginal cirri; 3 dorsal kineties and caudal cirri each.

Description of Maldivean population (Fig. 133a–j; Table 115): Size 70–150 × 10–15 µm in vivo, usually about 110 × 12 µm, length:width ratio highly variable, viz., 6.3–11.8:1, on average 8.7:1 in protargol preparations; usually only slightly, rarely up to 2:1 flattened dorsoventrally. Slenderly lanceolate, posterior region narrows rather abruptly, tail-like, most specimens slightly to distinctly twisted about main body axis (Fig. 133a, b, j; Table 115); acontractile but very flexible. Macronuclear nodules in two more or less distinct strands on upon the other along postoral left body margin; individual nodules globular to elongate ellipsoidal, on average 4 × 3 µm in protargol preparations; nucleoli of ordinary size. Usually one slightly ellipsoidal micronucleus in anterior and in posterior portion of nuclear figure. Contractile vacuole distinctly above mid-body at left cell margin, collecting canals long but thin and thus inconspicuous. Cortical granules between cirri and around dorsal bristles, stain red with methyl green-pyronin and, occasionally, black with the protargol method used; individual granules colourless, but compact and thus highly refractive, about 1 × 0.8 µm (Fig. 133a, c–e). Cytoplasm densely granulated, contains some crystals and lipid droplets 1–3 µm across, tail usually black under low (×100) bright field magnification because packed with refractive fat globules and crystals up to 3 µm long (Fig. 133f). Food vacuoles about 5 µm across, likely contain bacterial remnants. Glides, swims or winds slowly on microscope slide and between soil particles showing great flexibility.

Cirral pattern and number of cirri of usual variability, except for frontoventral row with a variability coefficient of 15% (Fig. 133a, g–j; Table 115). All cirri conspicuously short and

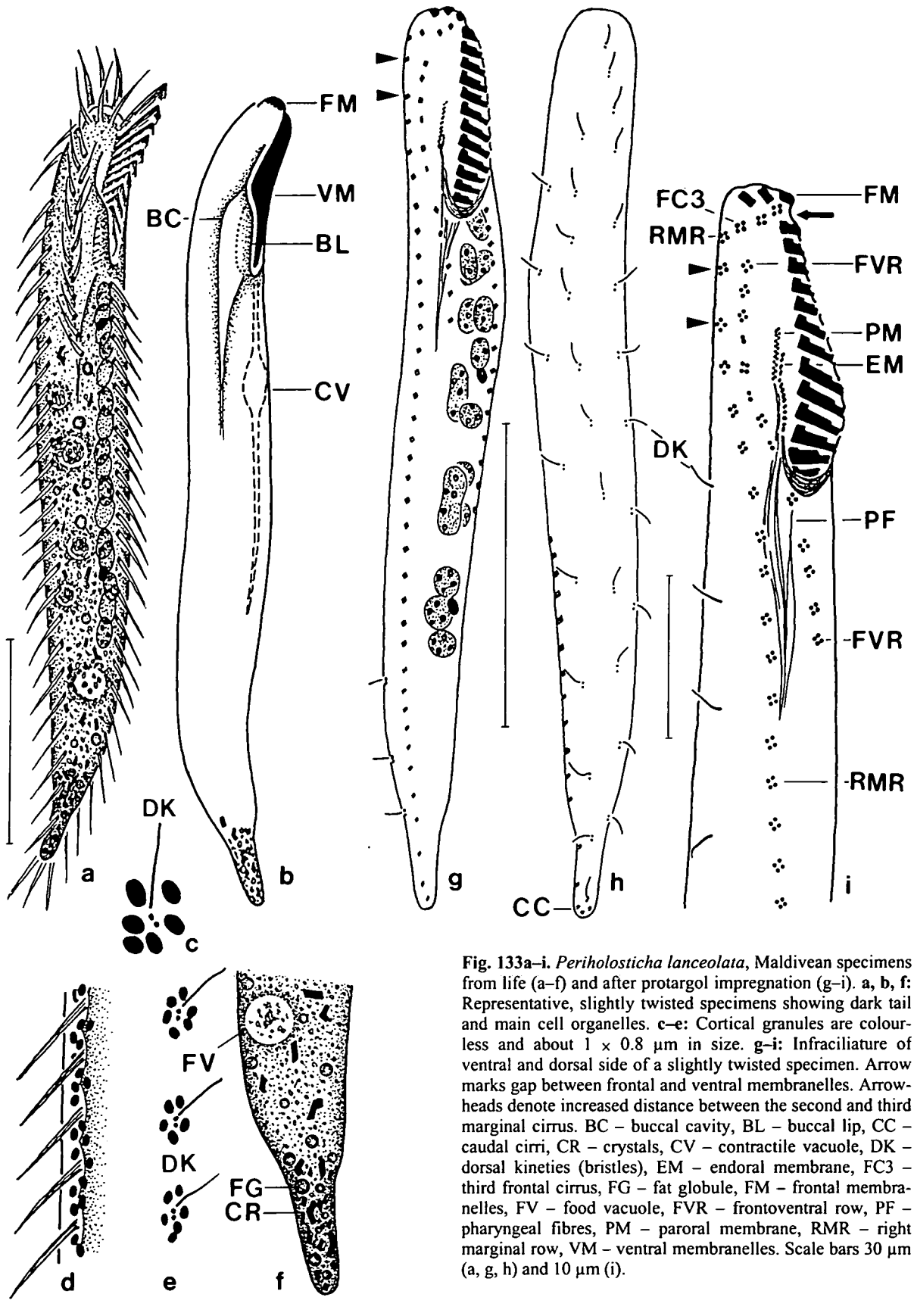


Fig. 133a–i. *Periholosticha lanceolata*, Maldivean specimens from life (a–f) and after protargol impregnation (g–i). **a, b, f:** Representative, slightly twisted specimens showing dark tail and main cell organelles. **c–e:** Cortical granules are colourless and about 1 × 0.8 µm in size. **g–i:** Infraciliature of ventral and dorsal side of a slightly twisted specimen. Arrow marks gap between frontal and ventral membranelles. Arrowheads denote increased distance between the second and third marginal cirrus. BC – buccal cavity, BL – buccal lip, CC – caudal cirri, CR – crystals, CV – contractile vacuole, DK – dorsal kineties (bristles), EM – endoral membrane, FC3 – third frontal cirrus, FG – fat globule, FM – frontal membranelles, FV – food vacuole, FVR – frontoventral row, PF – pharyngeal fibres, PM – paroral membrane, RMR – right marginal row, VM – ventral membranelles. Scale bars 30 µm (a, g, h) and 10 µm (i).

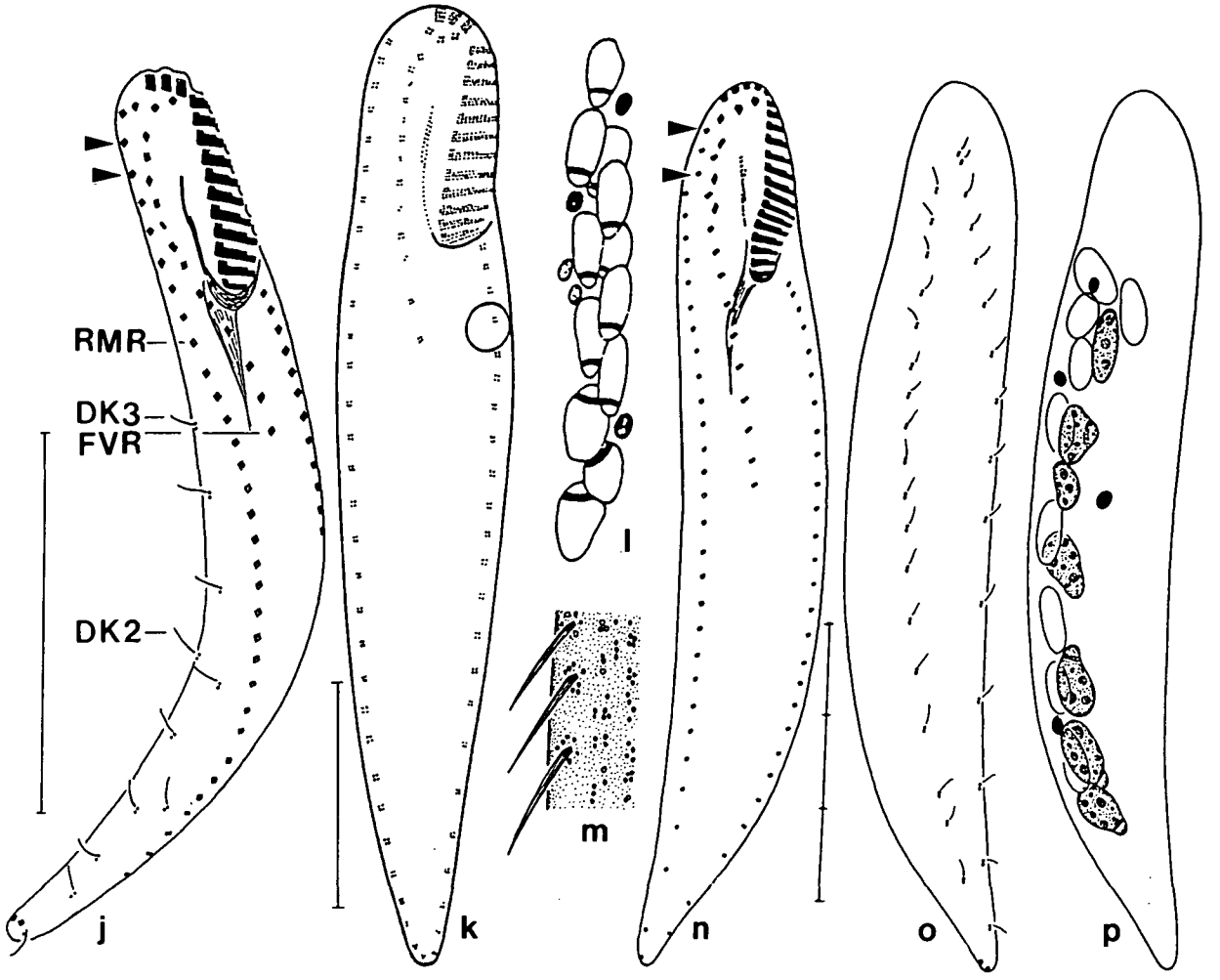


Fig. 133j–p. *Periholosticha lanceolata* (j–l) and *Holostichides terricola* (m–p; from FOISSNER 1988a) from life (m) and after protargol impregnation (j–l, n–p). **j:** Maldivean specimen, which is distinctly twisted about main body axis. Arrowheads mark the second and third marginal cirrus, which are separated by a slightly increased distance in about 60% of specimens (Fig. 133g, i); thus, the occurrence of frontoterminal cirri cannot be entirely excluded. **k, l:** Infraciliature of ventral side and nuclear apparatus of Peruvian holotype specimen (from HEMBERGER 1985). **m–p:** *Holostichides terricola* looks very similar to *P. lanceolata*, but differs by three important features: (i) cortical granules yellow forming loose rows in whole cortex (m) vs. colourless and restricted to cirral and dorsal bristle bases; (ii) with (arrowheads) vs. without frontoterminal cirri; (iii) two vs. three dorsal kineties (Fig. 133h, o). DK2, 3 – dorsal kineties, FVR – last cirrus of frontoventral row, RMR – right marginal row. Scale bars 30 µm.

fine, viz., about 7 µm long in vivo and composed of only two (some frontoventral and posterior marginal cirri) or four cilia. Marginal rows extend to near body end, right row commences near distalmost adoral membranelle with the first two cirri frequently set off by a slightly increased distance; thus, these could be frontoterminal cirri which are, however, lacking according to the ontogenetic data of HEMBERGER (1982). Frontal cirri in slightly concave, transverse or oblique line, first frontal cirrus in gap between frontal and ventral adoral membranelles. Frontoventral cirral row extends slightly obliquely in anterior body third and is thus distinctly longer than adoral zone of membranelles, but variability is considerable; cirri form indistinct midventral pattern (pairs) in anterior half of row. Frontoterminal (likely), buccal and transverse cirri lacking.

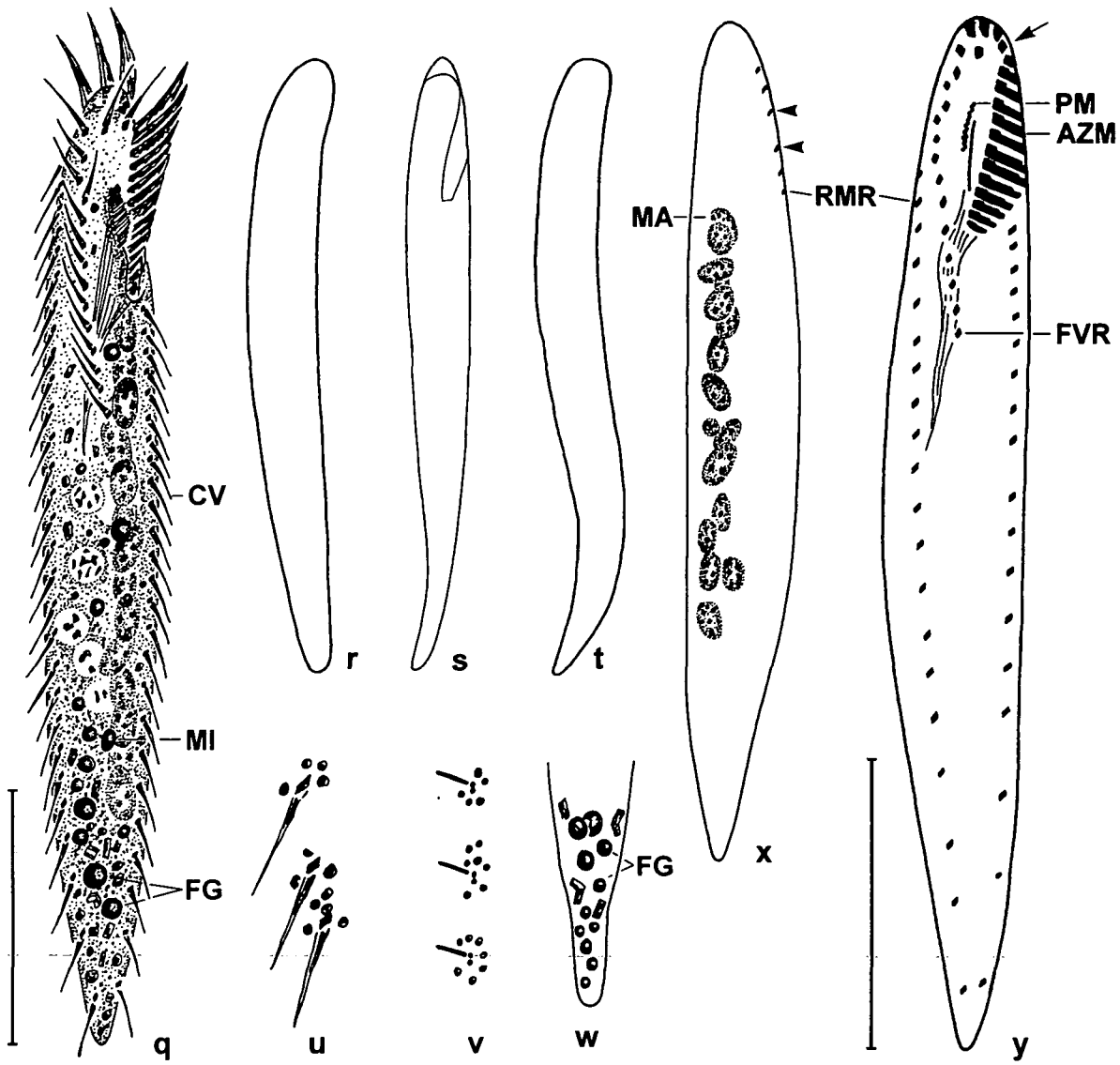


Fig. 133q–y. *Periholosticha lanceolata*, Namibian site (4) specimens from life (q–w) and after protargol impregnation (x, y). **q:** Ventral view of a representative specimen. **r–t:** Shape variants. **u, v:** The cortical granules are about 0.5 µm across, colourless, and found mainly between cirral bases and around dorsal bristles. **w:** The narrowed posterior end is usually packed with fat globules and crystals up to 3 µm in size and thus dark at low (×100) bright field magnification. **x, y:** Nuclear apparatus and infraciliature of ventral side. Arrow marks gap separating the adoral zone in a frontal portion with three and a ventral portion with 11–14 membranelles; the gap is occupied by the first frontal cirrus. Arrowheads mark increased distance between third and fourth cirrus of right marginal row, indicating that frontoterminal cirri might be present. AZM – adoral zone of membranelles, CV – contractile vacuole, FG – fat globules, FVR – last cirrus of frontoventral row, MA – anteriormost macronuclear nodule, MI – micronucleus, PM – paroral membrane, RMR – right marginal row. Scale bars 30 µm.

Dorsal bristles 2–3 μm long in vivo and widely spaced, invariably arranged in three rows, well recognizable even in live specimens due to the cortical granules surrounding the individual bristles; rows 1 and 2 slightly shortened anteriorly. Likely two or three caudal cirri that are difficult to separate from marginal cirri due to the tail-like body end.

Adoral zone occupies about 20% of body length, composed of 16 membranelles on average, bases of largest membranelles about 4 μm wide in vivo, anterior (frontal) three membranelles set off from ventral ones by minute gap; individual membranelles of ordinary fine structure, anterior row composed of only two or three basal bodies. Buccal cavity narrow and flat; buccal lip very hyaline, projects angularly, covering proximal portion of adoral zone. Paroral and endoral membrane form slightly curved row along posterior half of adoral zone of membranelles. Paroral membrane short, straight to slightly curved, composed of zigzagging basal bodies bearing 5 μm long cilia. Endoral membrane almost in line and anteriorly slightly overlapping with paroral. Pharyngeal fibres of ordinary length and structure (Fig. 133a, g, i, j; Table 115).

Description of Namibian site (4) population (Fig. 133q–y; Table 115): The Namibian specimens are highly similar to the Maldivean ones. Thus, only deviating or supplementary features will be mentioned: (i) size 90–130 × 10–20 μm in vivo, length:width ratio 7–11:1, on average 9:1 in vivo, and 5.4–11:1, on average 8.8:1 in protargol preparations; (ii) micronuclei about 3 × 2 μm; (iii) cortical granules smaller (about 0.5 × 0.4 μm) and less compact than in Maldivean specimens; (iv) distances between marginal cirri become distinctly wider posteriorly; (v) similarly to the Maldivean specimens, gap often increased between the third and fourth cirrus of the right marginal row (22% of 14 specimens investigated), the second and third (39%) or the second and third plus the third and fourth cirrus (22%); only 17% of the specimens lack this interruption.

Occurrence and ecology: HEMBERGER (1982, 1985) discovered *P. lanceolata* in meadow soil from Peru. We found it in highly saline and alkaline (pH 8.6) sandy soil and plant litter at the coast of the Maldives (North-Male Atoll, Himmafushi; collected by Dr. Wolfgang PETZ in 1990) and at Namibian site (4), that is, the floodplain of a river. Thus, *P. lanceolata* has a broad ecological range and possibly cosmopolitan distribution, although Laurasian records are not known. However, the species is difficult to identify and thus might have been confused with other taxa.

Table 115. Morphometric data on *Periholosticha lanceolata* from the Maldives (upper line) and Namibian site (4) [a].

Characteristics [b]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	89.4	87.0	17.4	3.8	19.4	63.0	130.0	21
	97.3	98.0	11.3	3.0	11.6	75.0	110.0	14
Body, width	10.4	10.0	1.2	0.3	12.0	9.0	14.0	21
	11.2	11.0	1.6	0.4	14.5	10.0	15.0	14
Body length:width, ratio	8.7	8.7	1.7	0.4	19.3	6.3	11.8	21
	8.8	9.2	1.4	0.4	16.2	5.4	11.0	14
Anterior body end to proximal end of adoral zone, distance	18.8	19.0	1.7	0.4	9.2	16.0	22.0	21
	21.9	22.0	1.9	0.5	8.8	18.0	26.0	14
Body length:length of adoral zone, ratio	4.7	4.6	0.6	0.1	12.2	3.7	5.9	21

(continued)

Characteristics [b]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	4.5	4.4	0.5	0.1	11.9	3.6	5.5	14
Anterior body end to last cirrus of frontoventral	30.1	30.0	3.9	0.9	12.9	22.0	40.0	21
row, distance	33.5	32.5	4.5	1.2	13.3	29.0	42.0	14
Anterior body end to first macronuclear nodule,	18.0	18.0	2.9	0.6	15.8	10.0	23.0	21
distance	21.0	21.0	2.4	0.6	11.4	17.0	17.0	14
Nuclear figure, length	49.4	46.0	10.2	2.2	20.7	35.0	78.0	21
	52.1	53.5	6.6	1.8	12.6	38.0	64.0	14
Macronuclear nodules, length	4.6	4.0	1.6	0.3	33.7	2.0	8.0	21
	5.9	6.0	1.5	0.4	24.9	4.0	10.0	14
Macronuclear nodules, width	2.7	3.0	0.5	0.1	19.7	2.0	4.0	21
	2.7	3.0	0.6	0.2	23.8	1.5	4.0	14
Macronuclear nodules, number	17.0	16.0	4.0	0.9	23.5	10.0	27.0	21
	15.6	16.0	1.7	0.5	10.9	11.0	18.0	13
Micronuclei, length	2.3	2.0	–	–	–	2.0	3.0	21
	2.7	2.5	–	–	–	2.5	3.0	13
Micronuclei, width	1.8	1.8	–	–	–	1.5	2.0	21
	2.1	2.0	–	–	–	1.5	2.5	13
Micronuclei, number	2.5	2.0	0.8	0.2	30.3	1.0	4.0	21
	2.2	2.0	0.8	0.2	37.2	1.0	3.0	14
Adoral membranelles, number	15.8	16.0	1.1	0.2	6.8	13.0	18.0	21
	16.1	16.0	0.8	0.2	5.2	14.0	17.0	14
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	14
Frontoventral row, number of cirri	12.1	12.0	1.7	0.4	14.0	9.0	15.0	21
	13.6	13.0	1.7	0.5	12.8	11.0	17.0	14
Right marginal cirri, number [c]	33.6	33.0	4.3	0.9	12.8	28.0	45.0	21
	28.5	29.0	4.3	1.2	15.0	20.0	35.0	13
Left marginal cirri, number	28.0	28.0	3.1	0.7	10.9	23.0	38.0	21
	25.9	26.0	4.9	1.4	18.9	17.0	35.0	13
Dorsal kineties, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10

[a] HEMBERGER (1982, 1985) provided the following measurements (n?) from the Peruvian type population (likely all from protargol-impregnated cells, WILBERT's method): length 130 µm; width 20 µm; length:width ratio 6–7:1; body length:length of adoral zone, ratio 4:1; right marginal cirri 30; left marginal cirri 25; frontal cirri 3; frontoventral row cirri 13; caudal cirri 3; adoral membranelles 15–17; dorsal kineties 3; macronuclear nodules 15; micronuclei 4–5.

[b] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[c] Including supposed frontoterminal cirri.

Comparison with original description and related species: *Perihologsticha lanceolata* has several specific features (HEMBERGER 1985), all found in the Maldivean and Namibian specimens: body slenderly lanceolate; a row of frontoventral cirri forming an

indistinct midventral pattern in the frontal half; lack of buccal, frontoterminal and transverse cirri; all cirri composed of only 2–4 cilia; three dorsal kineties. Furthermore, the illustrations and those morphometrics which are independent of the preparation method are highly similar in the type population and our specimens (Fig. 133i–l; Table 115). Thus identification is beyond reasonable doubt, although we cannot entirely exclude the occurrence of frontoterminal cirri in our populations. There is only one main feature deviating, viz., the cortical granules. However, HEMBERGER studied live cells only superficially, if at all, and thus it is reasonable to assume that he overlooked these colourless and thus inconspicuous granules.

Periholosticha lanceolata is an inconspicuous species easily confused with many other medium-sized, slender soil hypotrichs, such as *Hemisincirra* spp., *Holostichides* spp. (Fig. 133m–p), and *Paragastrostyla* spp. Thus, protargol impregnation is indispensable for reliable identification. In vivo, the following combination of features indicates *P. lanceolata*: size about 110 × 20 µm, lanceolate; about 15 macronuclear nodules in indistinct series left of midline; ellipsoidal, colourless cortical granules 0.5–1 µm across around cirri and dorsal bristles; no buccal cirrus; frontoventral cirral row extends to mid-body, that is, longer than adoral zone; buccal cavity flat and narrow; about 16 adoral membranelles; three dorsal kineties.

Periholosticha lacks frontoterminal cirri, according to the ontogenetic data of HEMBERGER (1982). Thus, *P. wilberti* SONG, 1990b, which has distinct frontoterminal cirri, belongs to *Holostichides*, as already discussed by EIGNER (1994) and FOISSNER (2000a). Likewise, *Paragastrostyla* HEMBERGER, 1985 has frontoterminal cirri. Furthermore, the *Paragastrostyla* cirral pattern is rather different and the type species has only two dorsal kineties. Thus, it cannot be identical to our populations.

Afrothrix multinucleata nov. spec. (Fig. 134a–l; Table 116)

Diagnosis: Size about 150 × 20 µm in vivo. Slender with posterior portion distinctly narrowed. Cortical granules about 1.2 × 0.8 µm, colourless, around cirral bases and dorsal bristles. Midventral row usually composed of 2 cirral pairs, terminates slightly underneath adoral zone of membranelles. On average 10 macronuclear nodules forming strand left of midline, 5 frontal and 8 ventral adoral membranelles, about 44 cirri each in right and left marginal row, 3 frontal cirri, 2 frontoterminal cirri, 1 buccal cirrus, 4 transverse cirri, and 2 dorsal kineties.

Type location: Litter and *Stipagrostis* roots from a sand dune between the villages of Aus and Helmeringhausen, Namibia, 26°05'S 16°35'E (site 17 in figure 2 and chapter 2.1.2).

Etymology: The Latin adjective *multinucleata* refers to the numerous macronuclear nodules.

Description: Size 100–200 × 15–30 µm in vivo, usually about 150 × 20 µm, length:width ratio 7–8:1 both in vivo and after protargol impregnation (Table 116); dorsoventrally flattened up to 2:1; very flexible but acontractile. Slender and often slightly curved, widest near mid-body, anterior portion less distinctly narrowed than posterior often inflated in protargol preparations (cp. figures 134a, g, j). Anterior end transverse truncate, without distinct process

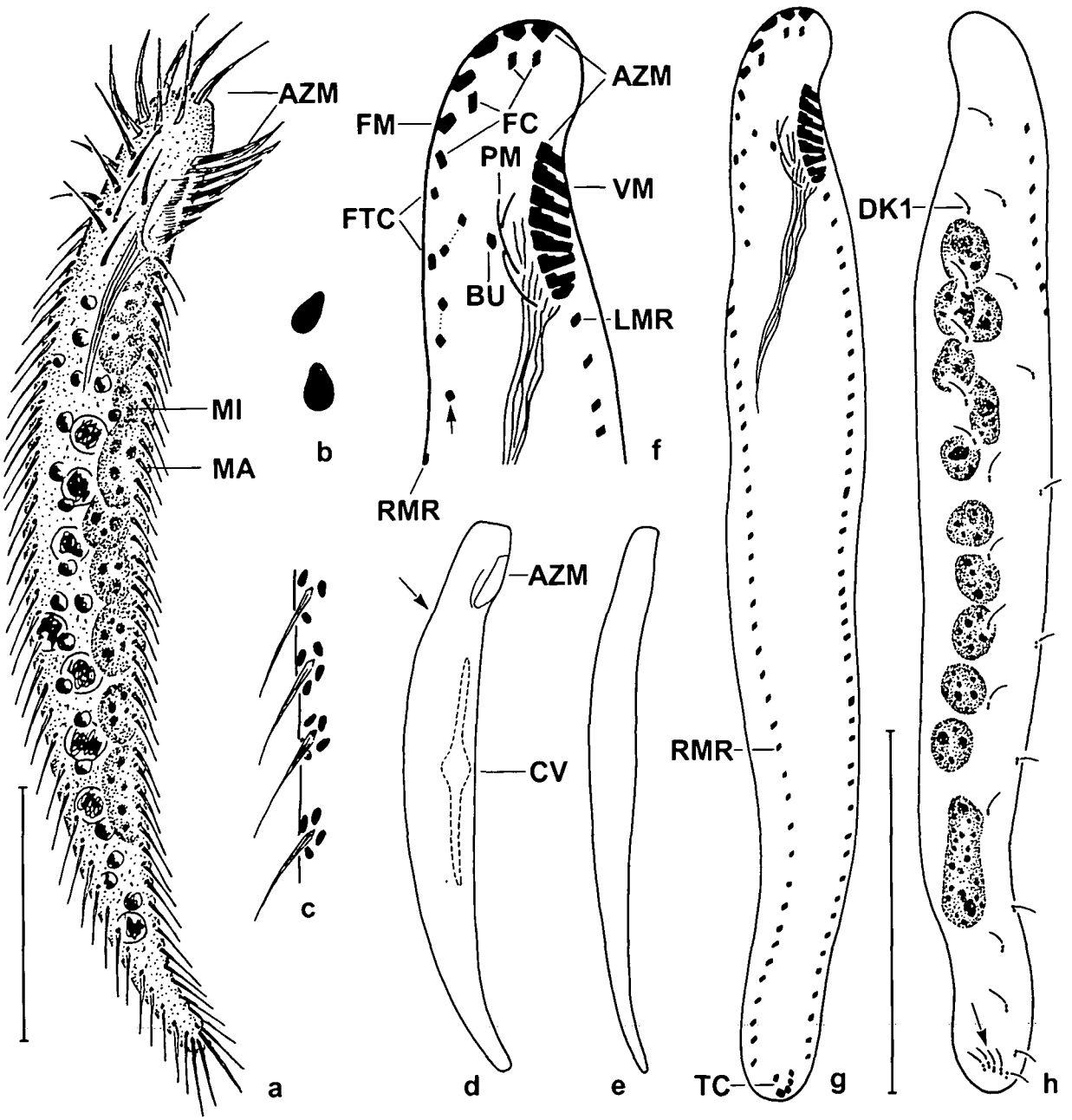


Fig. 134a–h. *Afrothrix multinucleata* from life (a–e) and after protargol impregnation (f–h). **a, d:** Ventral view and outline of a representative specimen. Arrow in (d) denotes a characteristic, slight indentation at level of buccal vertex causing inconspicuous cephalization. **b, c:** Colourless, about 1.2 × 0.8 µm-sized cortical granules occur around bases of cirri and dorsal bristles. **d, e:** Ventral and lateral view showing dorsoventral flattening. **f–h:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrow in (f) marks last frontoventral cirrus. The cirri of the two midventral pairs are connected by dotted lines. The left frontal cirrus is bipartited in this specimen. Arrow in (h) denotes a cluster of dorsal bristles near posterior body end. AZM – bipartited adoral zone of membranelles, BU – buccal cirrus, CV – contractile vacuole with two longitudinal collecting canals, DK1 – dorsal kinety 1, FC – frontal cirri, FM – frontal adoral membranelles, FTC – frontoterminal cirri, LMR – left marginal row, MA – strand of macronuclear nodules, MI – micronucleus, PM – paroral membrane, RMR – right marginal row, TC – transverse cirri, VM – ventral adoral membranelles. Scale bars 40 µm.

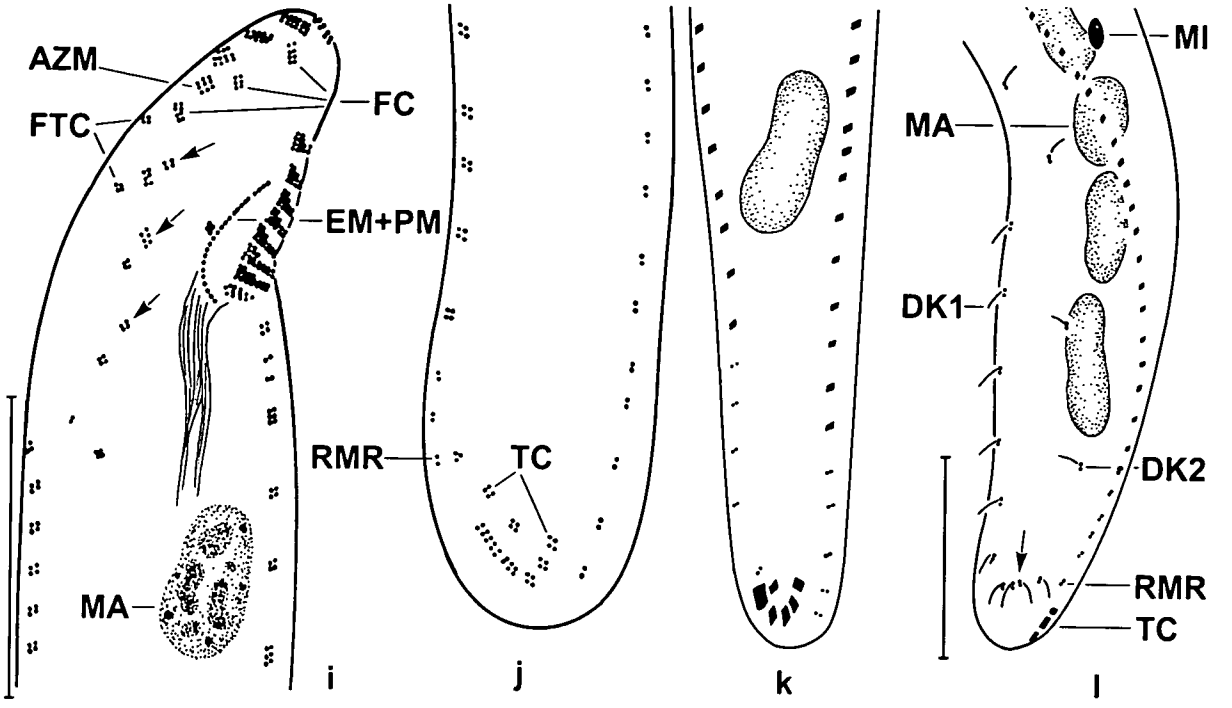


Fig. 134i–l. *Afrothrix multinucleata* after protargol impregnation. **i**: Detailed structure of oral and somatic infraciliature of a specimen with three midventral pairs (arrows). The paroral membrane is upon the endoral in this view. **j–l**: Detailed structure of ventral and dorsal infraciliature of posterior body portion. Arrow in (l) denotes tightly spaced bristles, possibly remnants of caudal cirri. AZM – distalmost membranelle of frontal portion of adoral zone, DK1, 2 – dorsal kineties, EM – endoral membrane, FC – frontal cirri, FTC – frontoterminal cirri, MA – macronuclear nodule, MI – micronucleus, PM – paroral membrane, RMR – last right marginal cirrus, TC – transverse cirri. Scale bars 20 μm.

on ventral side; right body margin with inconspicuous but rather typical indentation at level of buccal vertex (Fig. 134d, arrow), causing indistinct cephalization. Macronuclear nodules form strand left of midline, rather variable in number and shape, that is, globular, ellipsoidal (2–3:1) or dumb-bell-shaped; nucleoli small to large. Micronuclei globular to ellipsoidal, attached to macronuclear figure in variable positions. Contractile vacuole with two collecting canals extending to body ends near mid-body at left margin of cell. Cortical granules found only around bases of cirri and dorsal bristles, ellipsoidal, inconspicuous because of moderate size (1.2 × 0.8 μm) and colourless (Fig. 134b, c); do not stain with methyl green-pyronin and protargol. Cytoplasm colourless, contains many fat globules about 3 μm across. Feeds on bacteria and heterotrophic flagellates digested in vacuoles 5–7 μm across. Glides slowly on microscope slide and soil particles.

Cirral pattern and number of cirri of usual variability, except for number of transverse cirri which varies strongly (Fig. 134a, f, g, i–k; Table 116). Marginal cirri about 10 μm long in vivo, fine, that is, usually composed of only four cilia, in posterior body portion often even of only two cilia (Fig. 134i–l); left and right row end slightly subterminally, anterior portion of right row extends onto dorsolateral surface. Three slightly enlarged frontal cirri in usual position. Buccal cirrus at summit of curves formed by paroral and endoral membrane. Five to ten, usually seven (including frontoterminal cirri) frontoventral cirri composed and arranged

as shown in figures 134f, i: four, rarely six of them form two or three midventral pairs, producing short, inconspicuous midventral row; behind last midventral pair usually a single cirrus. Transverse cirri protrude distinctly beyond body and thus rather conspicuous in vivo, although not or only slightly enlarged and longer than marginal cirri (12 μm vs. 10 μm); form U- or hooked-shaped row near posterior body end; often one or two cirri ahead of transverse cirri, possibly pretransverse cirri.

Dorsal cilia about 3 μm long in vivo, arranged in two rows almost as long as body; bristles in kinety 2 rather widely spaced. Usually some tightly spaced and transversely arranged bristles near posterior end of rows, possibly remnants of caudal cirri (Fig. 134h, l).

Adoral zone of membranelles very short, that is, on average only 15% of body length, with distinct break in upper half dividing zone in a frontal and ventral portion (Fig. 134a, g, i; Table 116): frontal portion at upper and right anterior margin of cell, composed of five (rarely of four or six) minute membranelles; ventral portion begins about 7 μm back from anterior body end and extends along left body margin, composed of eight membranelles with usual fine structure. Buccal cavity strikingly small and flat, without lip. Endoral membrane slightly, paroral distinctly shorter than ventral portion of adoral zone, both curved and likely composed of closely spaced dikinetids, intersect optically in mid-portion at level of buccal cirrus; cilia of paroral about 8 μm long in vivo. Pharyngeal fibres prominent in vivo and after protargol impregnation, of ordinary length and structure, extend obliquely backwards.

Occurrence and ecology: To date found only at type location, that is, the margin of the Namib Desert. The species was numerous in the non-flooded Petri dish culture, indicating that many resting cysts were present. The vermiform body indicates that it is a true terrestrial ciliate, well-adapted to live in sand. The type species occurred in grassland soil near the Sheldrick waterfalls in the Shimba Hills Nature Reserve, Kenya (FOISSNER 1999b). Thus, this genus might be restricted to Africa.

Generic classification and comparison with similar species: The most prominent feature of the present species is the bipartited adoral zone of membranelles. Three genera with this curious feature are known: *Afrothrix* FOISSNER, 1999b; *Erniella* FOISSNER, 1987; → *Etoschothrix*. The present species is assigned to *Afrothrix* because the frontoventral cirri form, as in the type species, a midventral-like pattern, and the ventral membranelles show the usual fine structure, that is, are composed of two long ciliary rows, one short row, and one very short row (Fig. 134f, i). By contrast, *Erniella* has two long ventral cirral rows and → *Etoschothrix* has an *Oxytricha*-like frontoventral cirral pattern. Furthermore, both in *Erniella* and *Etoschothrix*, the ventral adoral membranelles are composed of three ciliary rows only, namely two long rows and one very short row.

Afrothrix multinucleata differs from the type species, *Afrothrix darbyshirei* FOISSNER, 1999b, by the smaller size (110–200 × 15–30 μm vs. 230–330 × 40–60 μm), the lower number of midventral pairs (usually 2 vs. usually 4) and dorsal kineties (2 vs. 3), and the higher number of macronuclear nodules (usually 9 vs. 2). *Erniella filiformis* FOISSNER, 1987 and → *Etoschothrix terricola* are easily distinguished from *A. multinucleata* by the arrangement and higher number of macronuclear nodules (17–61 scattered nodules in *Erniella filiformis* and *Etoschothrix terricola* vs. 4–15 nodules forming a strand). In vivo, *Afrothrix multinucleata* is thus easily recognized by the vermiform shape, the bipartited adoral zone of membranelles, and the macronuclear nodules forming a strand left of midline.

Table 116. Morphometric data on *Afrothrix multinucleata*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	129.3	130.0	24.1	5.0	18.6	84.0	186.0	23
Body, width	16.6	16.0	2.8	0.6	17.0	13.0	25.0	23
Body length:body width, ratio	7.9	7.7	1.4	0.3	17.2	5.5	11.1	23
Anterior body end to proximal end of adoral zone, distance	18.5	18.0	1.8	0.4	9.5	14.0	21.0	23
Body length:length of adoral zone, ratio	7.0	6.9	1.3	0.3	19.2	4.4	10.3	23
Anterior body end to ventral portion of adoral zone, distance	7.1	7.0	1.0	0.2	14.7	5.0	9.0	23
Anterior body end to last frontoventral cirrus, distance (arrow in Fig. 134f)	24.4	24.0	3.4	0.7	13.9	18.0	31.0	23
Anterior macronuclear nodule, length	11.1	10.0	4.6	1.0	41.5	6.0	26.0	23
Anterior macronuclear nodule, width	5.3	5.0	0.9	0.2	17.5	4.0	7.0	23
Anterior body end to first macronuclear nodule, distance	23.2	23.0	7.2	1.5	30.8	11.0	37.0	23
Posterior body end to last macronuclear nodule, distance	28.1	26.0	10.2	2.1	36.2	13.0	53.0	23
Macronuclear nodules, number [b]	9.9	9.0	2.7	0.6	27.2	4.0	15.0	23
Anterior micronucleus, length	2.4	2.4	0.7	0.2	27.8	1.6	4.0	13
Anterior micronucleus, width	1.7	1.6	0.4	0.1	22.7	1.6	3.0	13
Micronuclei, number [c]	1.1	1.0	–	–	–	0.0	4.0	21
Frontal adoral membranelles, number	5.0	5.0	–	–	–	4.0	6.0	23
Ventral adoral membranelles, number	8.1	8.0	0.7	0.2	9.1	7.0	10.0	23
Frontal cirri, number	3.0	3.0	–	–	–	3.0	4.0	21
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Frontoterminal cirri, number	2.2	2.0	–	–	–	2.0	3.0	20
Anterior body end to last frontoterminal cirrus, distance	14.0	14.0	1.3	0.3	9.3	10.0	16.0	20
Frontoventral cirri, number [d]	7.5	7.0	1.1	0.2	14.7	5.0	10.0	20
Midventral pairs, number	2.2	2.0	–	–	–	2.0	3.0	19
Anterior body end to first right marginal cirrus, distance	9.6	10.0	1.3	0.3	14.0	7.0	12.0	23
Right marginal cirri, number	43.2	44.0	5.6	1.2	13.0	32.0	53.0	23
Left marginal cirri, number	44.4	46.0	7.6	1.6	17.0	23.0	57.0	23
Uppermost transverse cirrus to posterior end, distance	3.8	4.0	1.1	0.3	29.6	1.0	5.0	17
Transverse cirri, number [e]	4.4	5.0	2.1	0.5	47.1	0.0	7.0	18
Dorsal kineties, number	2.0	2.0	–	–	–	1.0	2.0	23
Dorsal kinety 1, number of kinetids	14.3	14.0	1.8	0.4	12.4	11.0	16.0	18
Dorsal kinety 2, number of kinetids	9.3	9.0	3.1	0.7	33.0	5.0	15.0	19

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] The specimen with only four nodules appears otherwise normal.

[c] Difficult to count because faintly impregnated and of similar size as cell inclusions.

[d] All cirri except buccal cirrus and frontal cirri.

[e] Including ventral cirri possibly present ahead of transverse cirri.

Etoschothrix nov. gen.

Diagnosis: Hypotrichida with bipartited adoral zone of membranelles, 1 right and left marginal row, frontoventral cirri in *Oxytricha*-like pattern, and transverse cirri.

Type species: *Etoschothrix terricola* nov. spec.

Etymology: Composite of *Etoscha* (large, white place) and the Greek noun *thrix* (hair = ciliate s.l.), meaning "a ciliate occurring in the Etosha Pan". Feminine gender.

Systematic position and comparison with related genera: → *Etoschothrix terricola* has, like *Erniella filiformis* FOISSNER, 1987c and *Afrothrix darbyshirei* FOISSNER, 1999b, a very distinctive oral apparatus which, however, probably evolved convergently, as indicated by the different nuclear and cirral pattern of the three (type) species mentioned (Fig. 135f–i): many (→ *Etoschothrix terricola, Erniella filiformis*) vs. two (*A. darbyshirei*) macronuclear nodules; frontoventral cirri in *Oxytricha*-like pattern (→ *Etoschothrix terricola*) vs. two long, separate ventral rows (*Erniella filiformis*) or in mid-ventral pattern (*A. darbyshirei*); one buccal cirrus (→ *Etoschothrix terricola, A. darbyshirei*) vs. many buccal cirri (*Erniella filiformis*); one row of dorsal bristles (→ *Etoschothrix terricola, Erniella filiformis*) vs. three rows (*A. darbyshirei*); ventral adoral membranelles each composed of two long rows and one very short row of cilia (→ *Etoschothrix terricola, Erniella filiformis*) vs. of ordinary structure, that is, two long rows, one slightly shortened row and one strongly shortened row (*A. darbyshirei*). The last mentioned feature shows that *Etoschothrix* and *Erniella* must be far from other hypotrichs because the fine structure of the adoral membranelles is very conservative.

The right side oral ciliature of → *E. terricola* is unique in being composed of a row of very widely spaced (paroral?) cilia close to a line of very closely spaced (endoral?) kinetids (Fig. 135 l). We never saw such a pattern in any of the 500 hypotrichs we analyzed. However, details are difficult to recognize and possibly not entirely correct; thus, we did not include this feature in the genus diagnosis. These peculiarities and the differences detailed above indicate that *Etoschothrix*, *Afrothrix* and *Erniella* are not confamiliar, in spite of their overall similarity, especially regarding the bipartited adoral zone of membranelles. Ontogenetic data are required for a proper classification.

Some early dividers of → *E. terricola* showed that the oral primordium develops apokinetally underneath the parental oral apparatus and then elongates to the transverse cirri in midline of body, where a strand of fine fibres extends in morphostatic specimens (Fig. 135f, m; 383h), very much like in excysting cells of *Onychodromus acuminatus* (JAREÑO & TUFFRAU 1979). Furthermore, 3–4 frontoventral cirral anlagen develop and two of the rightmost frontoventral cirri are morphogenetically inactive, producing a pattern reminiscent of that found in oxytrichid hypotrichs, for instance, *Urosoma macrostyla* (FOISSNER 1983a). A very late divider showed that the macronuclear nodules fuse and the dorsal kinety divides without anlagen formation.

Etoschothrix, *Afrothrix*, and *Erniella* prefer saline habitats. Likely, they are related to several marine genera, such as *Notocephalus parvulus* CORLISS & SNYDER (see redescription by PETZ et al. 1995) and *Holosticha discocephalus* KAHL, 1932.

Etoschothrix terricola nov. spec. (Fig. 135a–m; 383a–h; Table 117)

Diagnosis: Size about 180 × 30 µm in vivo, contractile by about 20% of body length; very elongate elliptical. Cortical granules minute, yellowish, around cirral bases and dorsal bristles. On average 25 scattered macronuclear nodules, 6 frontal and 21 ventral adoral membranelles, 33 cirri in left and 40 in right marginal row, 3 frontal cirri, 5 frontoventral cirri, 1 buccal cirrus, 2 (4?) transverse cirri, and 1 dorsal kinety.

Type location: Highly saline soil from margin of Etosha Pan, Namibia, 19°10'S 15°55'E (site 61 in figures 2, 3 and chapter 2.1.2).

Etymology: The Latin *terricola* (living in soil) refers to the habitat the species was discovered.

Description: Size 130–220 × 20–40 µm in vivo, usually near 180 × 30 µm, length:width ratio 6:1 on average, contractile by about 20% of body length, prepared specimens thus stouter (about 5:1; Table 117). Slender and occasionally slightly curved, widest from underneath oral apparatus to mid-body, posterior third more distinctly narrowed than anterior, slightly to distinctly (contracted specimens) twisted about main body axis, dorsoventrally flattened up to 2:1 (Fig. 135a, d, f; 383a); narrowed body ends inflated and thus indistinct in prepared specimens, in contrast to spiral body twist, which is maintained. Anterior body end obliquely truncate and with minute process at upper end of buccal overture. Macronuclear nodules highly variable in number and shape, globular to distinctly ellipsoidal (3:1), each usually with a single, large nucleolus; occasionally, some nodules connected by fine strands. Micronuclei slightly ellipsoidal, usually one each in anterior and posterior third of cell, compact and thus easy to recognize in vivo. Contractile vacuole with two collecting canals at left body margin in anterior third of cell, that is, rather close to adoral zone of membranelles. Cortex bright and thickened in oral area. Cortical granules about 0.7 × 0.4 µm, but distinct because compact and yellowish; cells, however, colourless because granules restricted to bases of marginal cirri and dorsal bristles; stain black with protargol, sparse or lacking around frontal and ventral cirri (Fig. 135b, c, k). Middle third of cell usually packed with colourless fat globules 1–4 µm across and food vacuoles containing mainly → *Euplotopsis incisa* (about 40 × 30 µm) and *Homalogastra setosa*, which are ingested whole, showing that the narrow oral opening can considerably extend. Glides rapidly on microscope slide and soil particles.

Cirral pattern of usual variability, while cirral numbers more variable than average (Fig. 135a, f, i, k; 383a–c; Table 117). All cirri rather thin and short and thus inconspicuous, except for the slightly enlarged and up to 15 µm long frontal and transverse cirri. Marginal cirri about 12 µm long in vivo, each composed of two ciliary rows. Marginal rows follow spiral twist of body, right row commences subapically on dorsal side and extends obliquely to transverse cirri, last cirrus distinctly reduced in size; left marginal row anteriorly more or less distinctly curved approaching proximal buccal vertex, extends to midline of posterior end, last cirrus easily misinterpreted as caudal cirrus because distinctly set off from other marginal cirri and very near to posterior group of dorsal bristles. Three frontal cirri in usual position. Four to eight, usually six (including buccal cirrus) frontoventral cirri composed and arranged as shown in figures 135i, k, that is, in *Oxytricha*-like pattern, do not usually extend beyond proximal buccal vertex, except for those specimens which have seven or eight cirri (Fig. 135j;

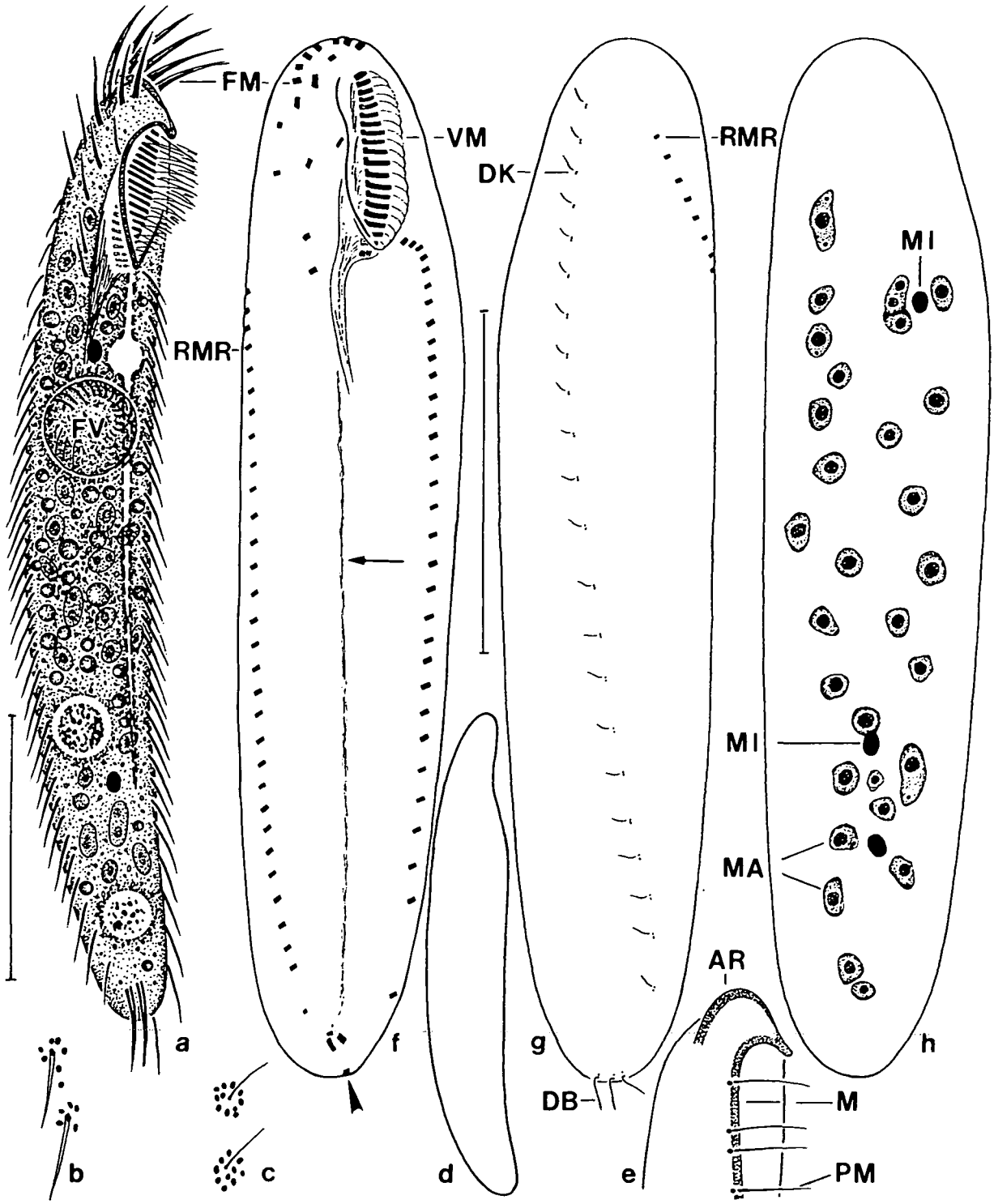


Fig. 135a–h. *Etoschothrix terricola* from life (a–e) and after protargol impregnation (f–h). **a:** Ventral view of a slender specimen. **b, c:** Yellowish granules occur around the cirri and dorsal bristles. **d:** Lateral view. **e:** Anterior body portion showing cortical ridges and widely spaced paroral (?) cilia. **f–h:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrow marks strand of fibres guiding oral primordium. Arrowhead denotes last cirrus of left marginal row. AR – anterior ridge covering bases of frontal membranelles, DB – dorsal bristles, DK – dorsal kinety, FM – frontal membranelles, FV – food vacuole with *Euplotes*, M – right margin of buccal opening, MA – macronuclear nodules, MI – micronuclei, PM – paroral (?) membrane, RMR – right marginal row, VM – ventral membranelles. Scale bars 50 μm.

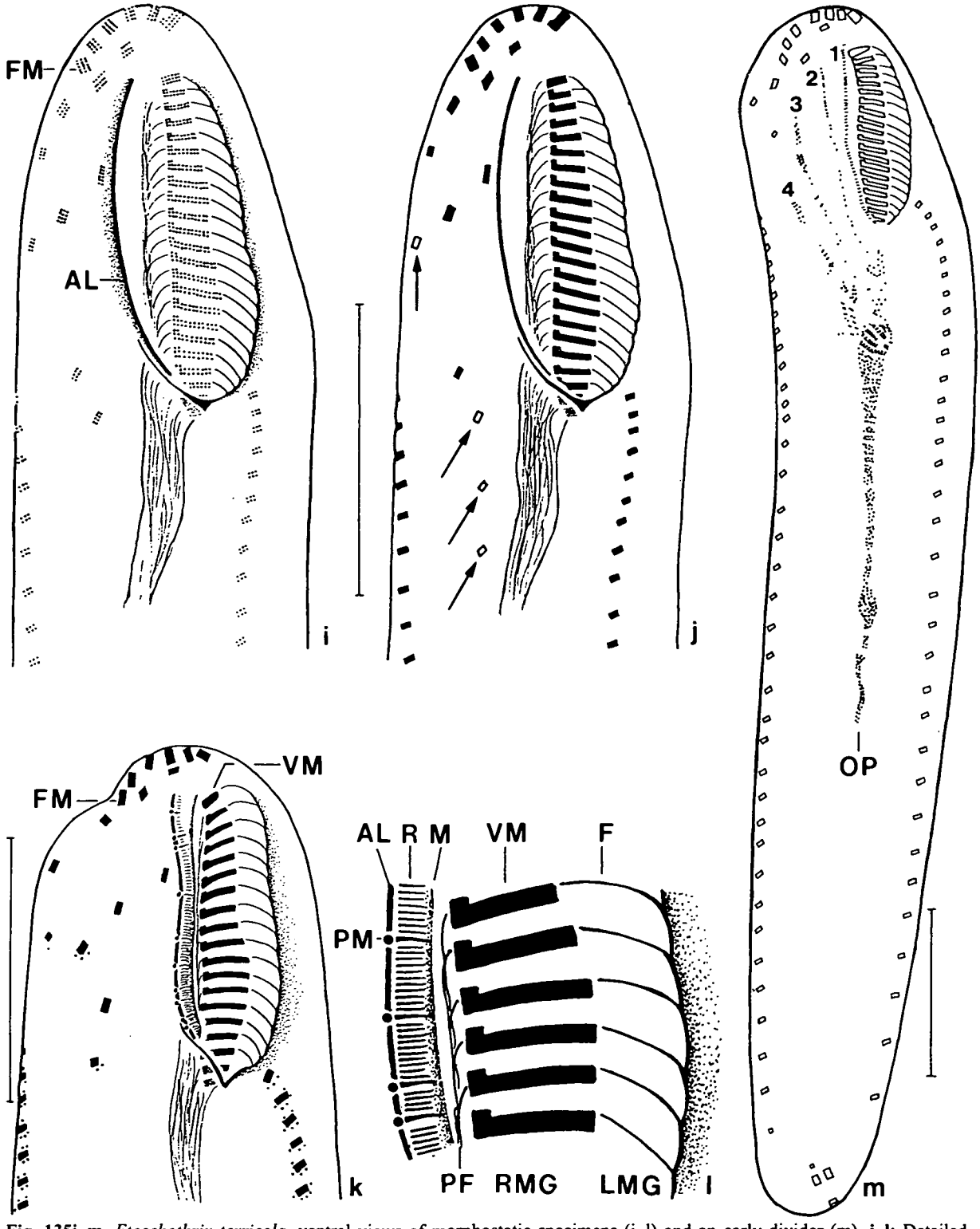


Fig. 135i–m. *Etoschothrix terricola*, ventral views of morphostatic specimens (i–l) and an early divider (m). **i–l:** Detailed structure of somatic and oral infraciliature. Arrows (j) mark cirri not occurring in all specimens. Note cortical granules, mainly around marginal cirri (k). **m:** Early divider showing oral primordium and four cirral anlagen (numbers 1–4). AL – argyrophilic line (endoral?), F – fibres, FM – frontal membranelles, LMG – left half of membranellar groove, M – right margin of buccal opening, OP – oral primordium, PF – pharyngeal fibres, PM – paroral membrane, R – rods, RMG – right half of membranellar groove, VM – ventral membranelles. Scale bars 25 μm.

Table 117). Transverse cirri about 15 µm long in vivo, project above posterior body end, usually form two distinct groups, each possibly composed of two closely spaced cirri.

Dorsal cilia about 4 µm long in vivo, arranged in single row commencing subapically near left body margin and obliquely extending to right posterior body margin, terminating in midline of posterior body end with two to five, usually four closely spaced, 5–6 µm long bristles (Fig. 135g; 383e).

Oral area slightly flattened, conspicuous, though occupying only about 20% of body length, because of its particular organization (Fig. 135a, e, f; 383a–d, f, g; Table 117). Adoral zone of membranelles with distinct break in upper third, dividing zone into a short frontal and a long ventral portion. Frontal adoral zone at upper and right anterior margin of cell, ventrally covered by a flat ridge, usually composed of six short membranelles occasionally forming two indistinct groups with three membranelles each, cilia about 20 µm long and thus forming distinct tuft. Ventral adoral zone rather distant from left body margin, extends longitudinally in right half of flat groove, composed of 21 membranelles on average, elongate elliptical because widest (about 8 µm in vivo) membranelles near centre of zone, left margin of zone irregular because neighbouring membranelles of slightly different length; individual membranelles composed of two long ciliary rows and one very short row attached to right anterior end. Two distinct fibre systems associated with ventral portion of adoral zone of membranelles (Fig. 135e, f, i, k, l; 383b, f): at right many fine, irregularly curved fibres extending posteriorly to form conspicuous pharyngeal bundle; at left a stiff fibre originates from the anterior ciliary row of each membranelle and traverses the left half of the membranellar groove, at the margin of which it curves backwards and overlaps with the neighbouring fibres to form a distinct strand extending into the proximal buccal vertex. Buccal cavity pocket-like, dorsal margin very near to right end of adoral membranelles; right margin thickened, forming short process anteriorly and acute vertex posteriorly merging into left margin of membranellar groove, covers proximal portion of adoral zone more or less completely, depending on orientation of cell (Fig. 135e).

Right side oral ciliature difficult to analyze. The following details are recognizable in some excellently impregnated specimens (Fig. 135e, k, l; 383e, g): near the right margin of the buccal overture extends a heavily impregnated, more or less distinctly curved line, which is unstructured in morphostatic cells but composed of closely spaced granules in early dividers (Fig. 135m), indicating that it consists of very closely spaced dikinetids; short, faintly impregnated rods extend horizontally from this line. On or very near to this line are 5–15 widely spaced, sharply impregnated granules, which are ciliated, as evident from live observations and protargol impregnation; these granules are well-recognizable only in excellently prepared specimens and if the buccal roof, on which they are located, is parallel to the focal plane.

Occurrence and ecology: To date found only in soils from the margin of the Etosha Pan (Table 4). Obviously tolerates very saline conditions and pH up to 9.

Comparison with related species: There are three species which are very similar to *E. terricola* in body size and shape as well as the structure of the adoral zone of membranelles. *Erniella filiformis* FOISSNER, 1987c, which also inhabits saline soils, has two long ventral cirral rows and three to six buccal cirri. *Afrothrix darbyshirei* FOISSNER, 1999b has only two macronuclear nodules, three dorsal kineties, and a short midventral row composed of four pairs of cirri. → *Afrothrix multinucleata* has the about ten macronuclear nodules

arranged in a series and the cortical granules are colourless. Thus, *Etoschothrix*, *Erniella*, and *Afrothrix* cannot be confused, even in vivo, because the features are very distinct and easy to recognize.

Table 117. Morphometric data on *Etoschothrix terricola*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	146.1	145.0	18.6	3.4	12.8	113.0	186.0	30
Body, width	27.7	27.0	4.9	0.9	17.8	17.0	36.0	29
Anterior body end to proximal end of adoral zone, distance	29.8	30.0	3.9	0.7	13.1	24.0	36.0	29
Anterior body end to last frontoventral cirrus, distance	35.1	34.0	5.3	1.2	15.2	24.0	48.0	21
Macronuclear nodules, length	6.1	6.0	1.0	0.2	16.1	4.0	8.0	23
Macronuclear nodules, width	4.3	4.0	0.9	0.2	20.7	2.0	6.0	23
Macronuclear nodules, number	35.0	35.0	10.2	2.1	29.0	17.0	59.0	23
Micronuclei, length	3.6	4.0	0.7	0.2	18.2	2.0	5.0	21
Micronuclei, width	2.6	3.0	0.4	0.1	14.5	2.0	4.0	21
Micronuclei, number	2.0	2.0	–	–	–	1.0	3.0	25
Frontal adoral membranelles, number	6.1	6.0	–	–	–	6.0	7.0	21
Ventral adoral membranelles, number	20.7	21.0	1.5	0.3	7.2	19.0	24.0	21
Frontal cirri, number	3.0	3.0	–	–	–	2.0	4.0	22
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	22
Frontoventral cirri, number	5.2	5.0	1.0	0.2	20.0	3.0	7.0	23
Right marginal cirri, number	39.4	40.0	6.6	1.4	16.7	24.0	51.0	23
Left marginal cirri, number	33.3	33.0	6.1	1.3	18.3	17.0	48.0	22
Transverse cirri, number				see text				
Dorsal kineties, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	22

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Parakahliella halophila nov. spec. (Fig. 136a–u; 384a–i; Table 118)

Diagnosis: Size about 90–100 × 35–55 µm in vivo. Ellipsoidal, slightly tapering posteriorly. 4–8, usually 4–5 macronuclear nodules; 18–48, usually 22–27 adoral membranelles; 1 buccal cirrus; 4–13 (usually 5–7) cirri in right frontoventral row and 2–13 (usually 6–9) cirri in left (postoral) frontoventral row; 2–5, usually 3 caudal cirri; and 4 dorsal kineties. 1 right and 1 left marginal cirral row.

Type location: Highly saline soil from the coast of the Great Salt Lake in Utah, USA, near the town of Brigham, 41°30'N 112°W.

Etymology: Composite of the Greek words *halós* (salt) and *philos* (preferring), referring to the saline habitats the species occurs in.

Description: The three populations studied are fairly similar (Fig. 136m–t; Table 118). However, it cannot be excluded that they are different species or subspecies. Thus, the data are kept separate, and the formal diagnosis contains only the American type population which, however, embraces the major part of the total variability encountered because some sort of macrostomes developed six days after rewetting the sample (Fig. 136o; Table 118); accordingly, coefficients of variation are unusually high. The "macrostomes" have, on average, slightly more adoral membranelles (27 vs. 22) and macronuclear nodules (5 vs. 4). Furthermore, remnants of marginal rows from the previous generation are more frequent.

Size 80–150 × 30–80 µm in vivo, usually about 90–100 × 35–55 µm, length:width ratio 1.9–2.4:1 on average in protargol preparations. Shape also highly variable in all populations, usually ellipsoidal and slightly tapering posteriorly, occasionally fusiform or narrowed tail-like. Dorsoventrally flattened up to 2:1, ventral side flat or concave, dorsal more or less distinctly vaulted in middle third and with rather conspicuous furrow between kineties 3 and 5 (Fig. 136c, e, f, h; 384a–c, k, l; Table 118); highly flexible but acontractile. Nuclear apparatus left of midline. Macronuclear nodules in series, usually broadly ellipsoidal (1.6:1 on average), outline often irregular, nucleoli small to large. Micronuclei near or attached to macronuclear nodules, about 3 µm across in vivo and thus inconspicuous. Contractile vacuole with conspicuous collecting canals slightly above mid-body. Cortex colourless and very flexible, without specific granules. Cytoplasm with some fat globules 2–4 µm across and few to many colourless crystals concentrated in posterior third of cell (Fig. 136a, k; 384j). Omnivorous, feeds on bacteria, brown fungal conidia, flagellates, ciliates (*Pseudocohnilembus*, *Vorticella astyliformis*, and even small specimens its own species), and wheat starch digested in vacuoles 10-20 µm across. Movement without peculiarities, glides rather rapidly on microscope slide and organic debris, showing great flexibility.

Cirral pattern and number of cirri highly variable. Cirri about 13 µm long in vivo, arranged as shown in figures 136m, o, q, s and 384a–c, k, l; pattern somewhat population-specific, but transitions occur, and some specimens of population IV, which have only three postoral cirri, look similar to an ordinary *Oxytricha*, except for the absent transverse cirri. Frontoventral cirri sparse compared to congeners, left of right frontoventral row usually two cirri; invariably one buccal cirrus right of anterior end of paroral membrane. Remnants of parental marginal rows occur only in populations II and III and mainly in posterior half of cell. Lack of transverse cirri confirmed by ontogenesis in all populations.

Dorsal bristles about 4 µm long in vivo, arranged in four rows, the rightmost of which ends above mid-body; rarely a parental kinety fragment occurs between rows 3 and 5 (= row 4; Fig. 136r). Caudal cirri conspicuous, usually two to three associated with kinety 1 and one cirrus with kinety 2 (Fig. 136n, p, r, t; Table 118).

Adoral zone inconspicuous because occupying only 25–36%, on average 31% of body length; composed of an average of 22–27 membranelles of conventional fine structure, bases of largest membranelles about 8 µm wide in vivo. Buccal cavity narrow but deep, abuts on adoral zone of membranelles anteriorly, producing fairly characteristic pattern (Fig. 136a, c, d, i). Buccal lip projects angularly to cover right half of buccal cavity. Paroral and endoral membrane slightly curved, in parallel but somewhat diverging posteriorly, both possibly composed of single line of tightly spaced cilia (Fig. 136i, m, o, q, s; 384k, l; Table 118). Pharyngeal fibres of ordinary length and structure.

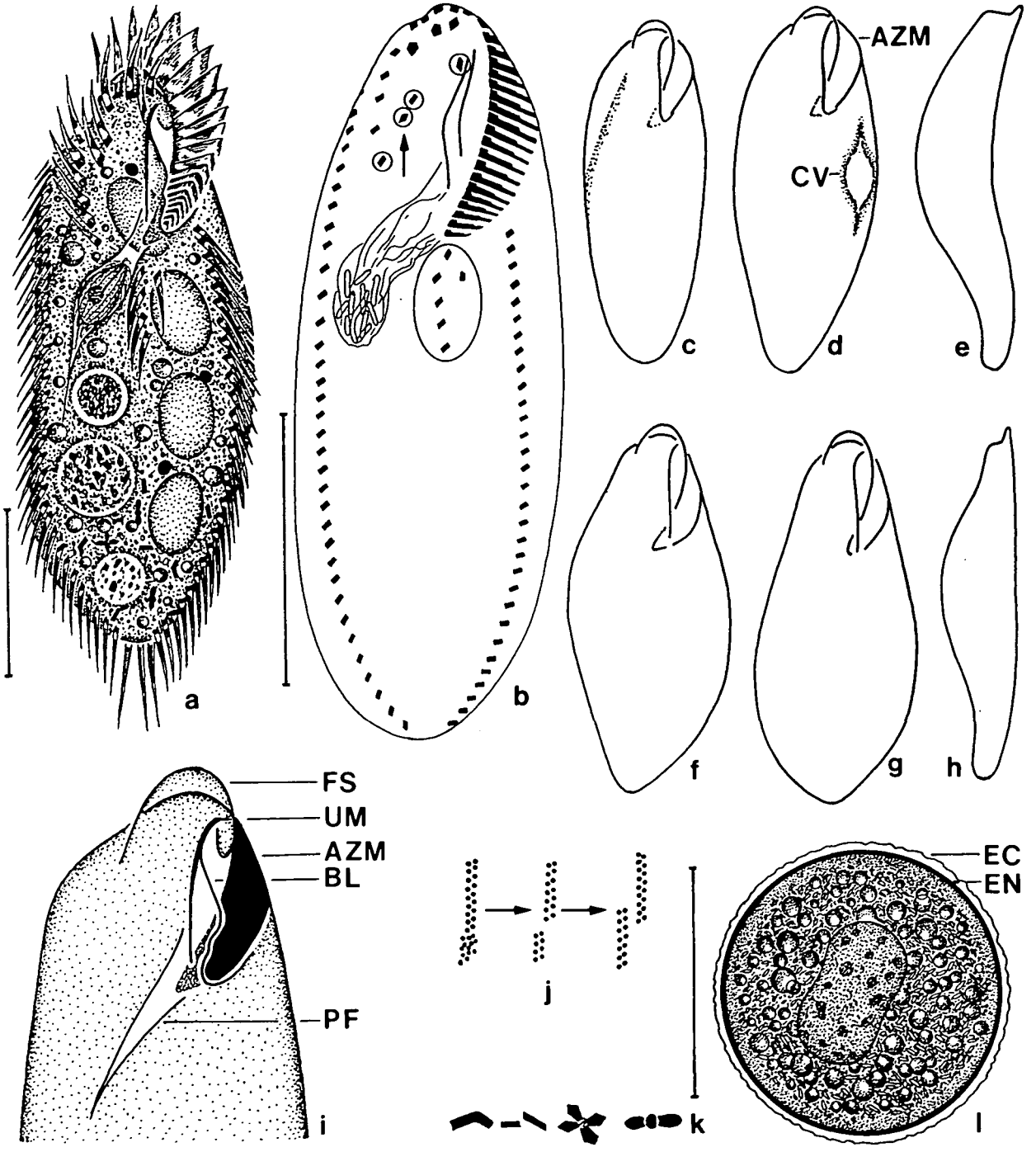


Fig. 136a–l. *Parakahliella halophila* from life (a, c–i, k, l) and after protargol impregnation (b, j). **a:** Ventral view of a representative specimen just ingesting a *Pseudocohnilembus*. **b, j:** Ventral view with ontogenetically active cirri encircled. In the proter frontal field, four cirri produce an anlage each, except for the posterior cirrus (arrow) of the cirri left of the right frontoventral row which produces two anlagen by posterior splitting (j). The postoral cirri generate the oral apparatus and the frontoventral cirri of the opisthe. **c, d, f, g:** Shape variability. Note that the right margin of the buccal cavity abuts on the adoral zone of membranelles anteriorly, a feature which makes the species easily recognizable in vivo. **e, h:** *Parakahliella halophila* is flattened dorsoventrally up to 2:1. **i:** Oral apparatus. **k:** Cytoplasmic crystals. **l:** Resting cyst with dumb-bell-shaped macronuclear mass. AZM – adoral zone of membranelles, BL – buccal lip, CV – contractile vacuole, EC – ectocyst, EN – endocyst, FS – frontal scutum, PF – pharyngeal fibres, UM – undulating membranes. Scale bars 30 µm.

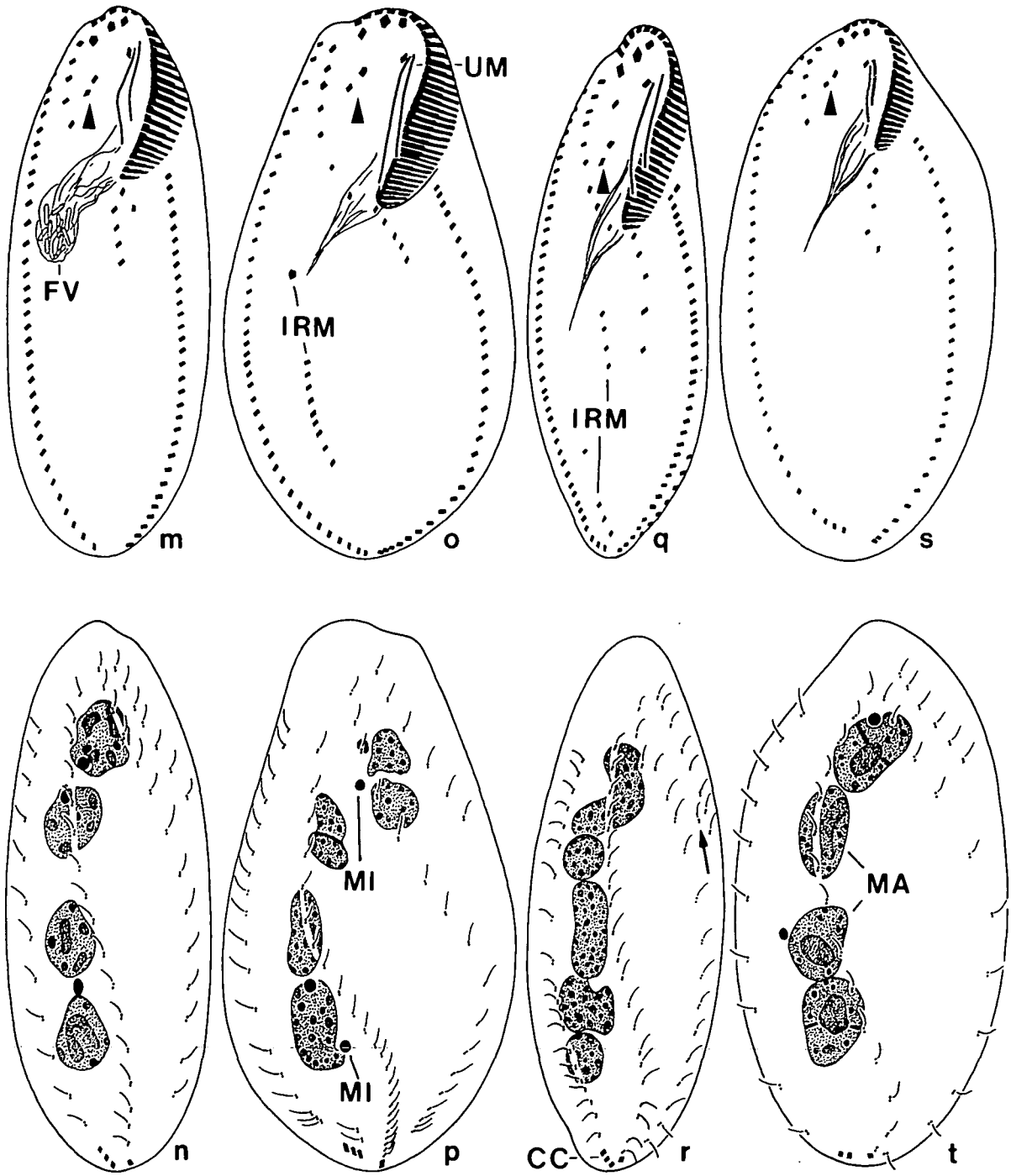


Fig. 136m–t. *Parakahliella halophila* populations, infraciliature of ventral (m, o, q, s) and dorsal (n, p, r, t) side after protargol impregnation. See table 118 for detailed morphometric data. Arrowheads mark cirri left of the right frontoventral row. Note that the undulating membranes have the same pattern in all populations. **m, n:** USA type population two days after rewetting the sample, length 82 µm. **o, p:** USA type population six days after rewetting the sample, length 98 µm. **q, r:** Namibian site (59) population, which is rather similar to the type population six days after rewetting the sample (o, p), length 80 µm. Arrow marks single kinetid comprising dorsal kinety 4. **s, t:** Namibian site (18) population, which is similar to the type population two days after rewetting the sample (m, n), length 81 µm. CC – caudal cirri, FV – descending food vacuole, IRM – inner right marginal row, MA – macronuclear nodules, MI – micronuclei, UM – undulating membranes.

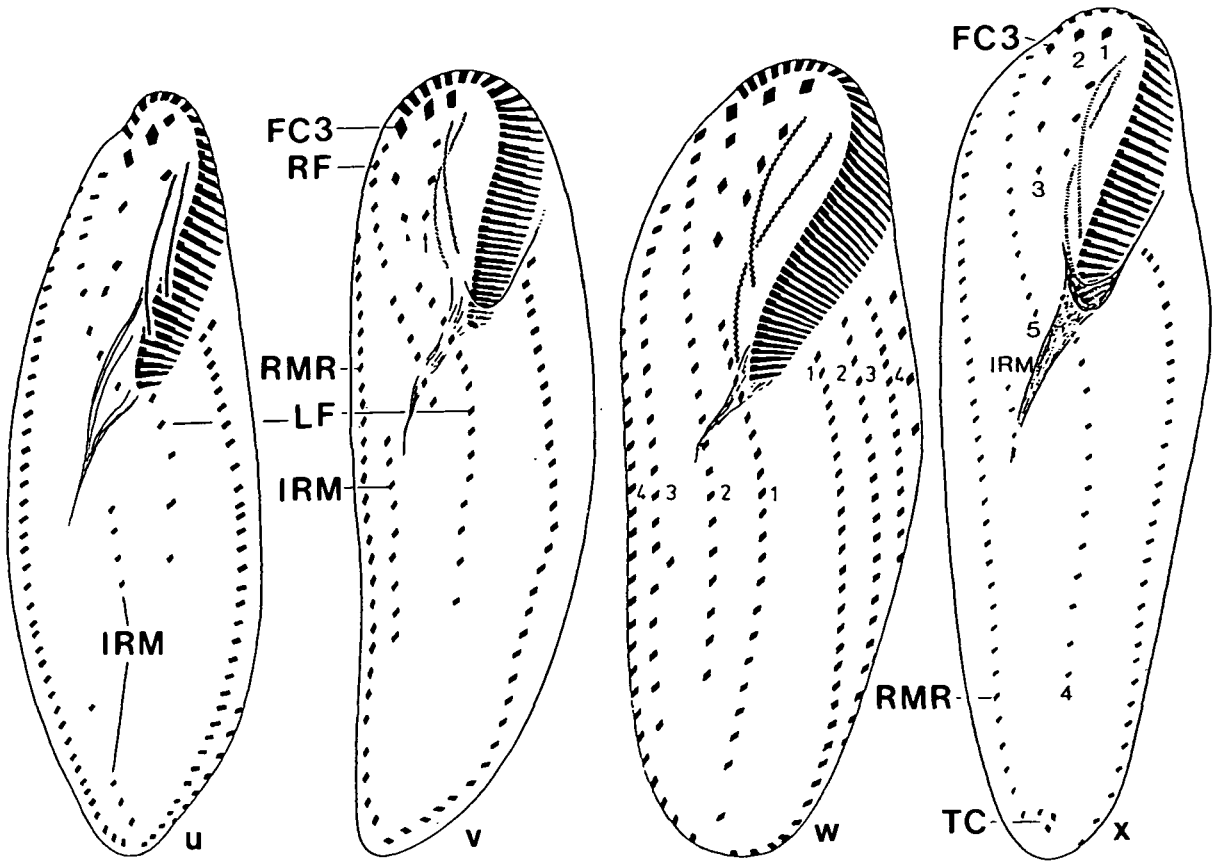


Fig. 136u–x. Comparison of the ventral cirral pattern of *Parakahliella halophila* (**u**; length 80 µm), *P. haideri* (**v**; length 130 µm; from BERGER & FOISSNER 1989b), *P. macrostoma* (**w**; length 100 µm; from FOISSNER 1982), and *Fragmocirrus espeletiae* (x; length 160 µm; from FOISSNER 2000b). All from protargol-impregnated specimens. Numbers denote cirral rows. See text for comparison of species. FC3 – frontal cirrus 3, IRM – inner right marginal row, LF – left frontoventral row, RF – right frontoventral row, RMR – (outer) right marginal row, TC – transverse cirri.

Resting cysts globular and colourless, 36–43 µm across in vivo ($\bar{x}$ = 39.5 µm, SD = 2.3 µm, CV = 5.9%, n = 15). Ectocyst about 1 µm thick, hyaline and wrinkled (Fig. 136 l; 384e–g). Meso- and endocyst also about 1 µm thick, very compact and thus refractive, smooth; followed by an about 2 µm wide, opaque, finely granulated zone indistinctly separate from main cyst content. Cytoplasm packed with bright fat globules 2–4 µm across and about 1 µm-sized, ellipsoidal inclusions. Macronuclear nodules fused to dumb-bell-shaped or globular mass in ripe cysts (Fig. 136 l; 384h, i). Cyst wall up to 4 µm thick and often distinctly faceted in protargol preparations, very likely due to considerable shrinkage (Fig. 384i).

Ontogenesis: Division of *Parakahliella halophila* is very similar to that of *P. haideri* BERGER & FOISSNER, 1989b, and will thus not be described in detail. The oral primordium develops along the postoral cirri (Fig. 384d), which are incorporated in the opisthe's frontoventral anlagen. Usually, six or seven frontoventral anlagen each develop in proter and opisthe, including anlage 1, which, as is usual, originates from the primordium for the undulating membranes. The posterior cirrus of the cirri left of the right frontoventral row develops two, rarely three anlagen by splitting a primary primordium in the posterior third

(Fig. 136b, j). In *P. haideri*, this cirrus generates only one anlage, while the right frontoventral row produces two streaks (BERGER & FOISSNER 1989b). Only one row of right and left marginal cirri are generated, as well as one dorsomarginal kinety. No transverse cirri are produced. Most parental cirri and dorsal kinetids, which are not involved in anlagen formation, are resorbed. Remnants of the parental marginal cirral rows occur only in populations II and III, forming the inner right, respectively, outer left marginal row (Fig. 136o, q; Table 118). Parental dorsal kinetids are preserved in populations I, II, and III, albeit rarely, forming dorsal kinety 4, as in *P. macrostoma* and *P. haideri* (BERGER et al. 1985, BERGER & FOISSNER 1989b).

Table 118. Morphometric data on *Parakahliella halophila* and comparison with *P. haideri*.

Characteristics [a]	Pop [b]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	I	87.6	88.0	9.2	2.2	10.5	72.0	104.0	17
	II	94.9	89.0	16.5	4.0	17.4	76.0	136.0	17
	III	84.9	87.0	10.1	2.9	11.8	67.0	108.0	21
	IV	77.1	78.0	7.8	1.9	10.1	61.0	88.0	17
	V	86.0	85.0	12.7	1.5	14.8	61.0	136.0	72
	VI	127.1	125.0	12.5	2.0	9.8	105.0	160.0	40
Body, width	I	36.3	37.0	4.1	1.0	11.3	29.0	44.0	17
	II	49.5	50.0	9.5	2.3	19.1	34.0	75.0	17
	III	32.8	32.0	4.1	0.9	12.4	27.0	42.0	21
	IV	37.5	37.0	3.9	1.0	10.5	30.0	44.0	17
	V	38.7	37.0	8.5	1.0	22.0	27.0	75.0	72
	VI	52.5	51.0	8.4	1.3	15.9	35.0	73.0	37
Anterior body end to proximal end of	I	23.9	24.0	2.0	0.5	8.4	19.0	27.0	17
adoral zone of membranelles, distance	II	30.8	27.0	8.9	2.2	28.8	22.0	57.0	17
	III	30.7	31.0	4.6	1.0	15.1	22.0	40.0	21
	IV	19.2	19.0	2.2	0.5	11.6	14.0	23.0	17
	V	26.4	25.0	7.1	0.8	26.8	14.0	57.0	72
	VI	48.3	48.0	6.6	1.1	13.8	33.0	60.0	40
Posterior macronuclear nodule, length	I	14.8	15.0	3.2	0.8	21.5	10.0	22.0	17
	II	12.6	12.0	4.1	1.0	32.9	7.0	20.0	17
	III	11.3	12.0	2.8	0.6	24.9	6.0	15.0	21
	IV	13.5	13.0	2.4	0.6	17.6	10.0	18.0	17
	V	12.9	13.0	3.4	0.4	26.1	6.0	22.0	72
	VI	11.6	10.0	4.6	0.8	39.5	7.0	25.0	40
Posterior macronuclear nodule, width	I	8.9	9.0	1.3	0.3	14.3	7.0	11.0	17
	II	6.8	7.0	1.7	0.4	25.4	4.0	10.0	17
	III	6.4	6.0	0.9	0.2	13.5	5.0	8.0	21
	IV	10.8	10.0	1.8	0.4	16.7	8.0	15.0	17
	V	8.1	8.0	2.3	0.3	27.9	4.0	15.0	72
	VI	8.2	8.0	1.4	0.2	17.3	6.0	12.0	40
Posterior micronucleus, largest diameter	I	2.2	2.0	–	–	–	2.0	3.0	17
	II	2.3	3.0	–	–	–	2.0	3.0	17
	III	2.1	2.0	–	–	–	2.0	3.0	21
	IV	2.1	2.0	–	–	–	2.0	3.0	17

(continued)

Characteristics [a]	Pop [b]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	V	2.2	2.0	–	–	–	2.0	3.0	72
	VI	2.6	3.0	–	–	–	2.0	3.0	40
Adoral membranelles, number	I	22.4	22.0	1.8	0.5	8.2	18.0	25.0	17
	II	29.3	27.0	7.1	1.7	24.3	22.0	48.0	17
	III	33.5	34.0	4.2	0.9	12.5	25.0	44.0	21
	IV	20.8	21.0	1.7	0.4	8.3	17.0	24.0	17
	V	26.9	24.0	6.8	0.8	25.2	17.0	48.0	72
	VI	47.7	47.0	6.8	1.1	14.2	34.0	62.0	37
Macronuclear nodules, number	I	4.1	4.0	0.5	0.1	11.8	4.0	6.0	17
	II	5.9	5.0	1.6	0.4	26.3	4.0	8.0	17
	III	4.8	4.0	1.2	0.3	24.8	3.0	8.0	21
	IV	3.8	4.0	0.6	0.1	14.9	2.0	4.0	17
	V	4.7	4.0	1.3	0.2	28.2	2.0	8.0	72
	VI	6.2	6.0	0.6	0.1	10.5	5.0	9.0	40
Micronuclei, number	I	2.7	3.0	0.7	0.2	26.5	2.0	4.0	17
	II	2.8	2.0	1.2	0.3	43.4	1.0	5.0	17
	III	4.1	4.0	1.0	0.2	25.5	2.0	6.0	21
	IV	2.5	2.0	0.9	0.2	34.6	2.0	4.0	17
	V	3.1	3.0	1.2	0.1	38.0	1.0	6.0	72
	VI	4.0	4.0	1.3	0.2	31.9	2.0	7.0	40
Enlarged frontal cirri, number	I	3.0	3.0	0.0	0.0	0.0	3.0	3.0	17
	II	3.1	3.0	–	–	–	3.0	4.0	17
	III	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	IV	3.0	3.0	0.0	0.0	0.0	3.0	3.0	17
	V	3.0	3.0	–	–	–	3.0	4.0	72
	VI	3.0	3.0	0.4	0.1	13.2	2.0	5.0	39
Buccal cirri, number	I	1.0	1.0	0.0	0.0	0.0	1.0	1.0	17
	II	1.0	1.0	0.0	0.0	0.0	1.0	1.0	17
	III	1.1	1.0	–	–	–	1.0	2.0	21
	IV	1.0	1.0	0.0	0.0	0.0	1.0	1.0	17
	V	1.0	1.0	–	–	–	1.0	2.0	72
	VI	3.0	3.0	0.7	0.1	22.2	1.0	4.0	40
Cirri left of frontoventral row, number	I	2.0	2.0	0.0	0.0	0.0	2.0	2.0	17
	II	2.1	2.0	–	–	–	2.0	3.0	17
	III	2.5	2.0	0.8	0.2	32.2	1.0	4.0	21
	IV	2.0	2.0	0.0	0.0	0.0	2.0	2.0	17
	V	2.2	2.0	0.5	0.1	23.5	1.0	4.0	72
	VI	2.2	2.0	0.4	0.1	19.8	1.0	3.0	40
Left frontoventral row, number of cirri	I	5.8	6.0	1.6	0.4	27.3	2.0	8.0	17
	II	8.2	9.0	2.2	0.5	26.4	5.0	13.0	17
	III	8.0	7.0	2.2	0.5	27.7	5.0	12.0	21
	IV	4.0	4.0	2.1	0.5	51.5	1.0	11.0	17
	V	6.6	6.0	2.6	0.3	39.8	1.0	13.0	72
	VI	13.6	13.0	3.4	0.6	25.2	4.0	20.0	37
Right frontoventral row, number of cirri [c]	I	5.4	5.0	1.0	0.2	18.6	4.0	7.0	17
	II	7.1	7.0	1.7	0.4	23.8	5.0	12.0	17
	III	7.3	7.0	1.5	0.3	20.0	5.0	11.0	21
	IV	4.1	4.0	0.6	0.1	13.7	3.0	5.0	17

(continued)

Characteristics [a]	Pop [b]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	V	6.0	6.0	1.8	0.2	30.2	3.0	12.0	72
	VI	16.3	16.0	2.7	0.4	16.6	10.0	22.0	37
Left marginal row, number of cirri	I	26.9	28.0	2.6	0.6	9.7	22.0	31.0	17
	II	30.6	31.0	3.8	0.9	12.4	23.0	37.0	17
	III	32.1	32.0	4.1	0.9	12.9	23.0	39.0	21
	IV	26.2	26.0	2.7	0.7	10.4	21.0	33.0	17
	V	29.1	29.0	4.2	0.5	14.4	21.0	39.0	72
	VI	32.3	32.0	3.9	0.6	12.0	23.0	40.0	40
Outer right marginal row, number of cirri	I	33.7	35.0	3.0	0.7	8.8	29.0	39.0	17
	II	37.2	36.0	6.6	1.6	17.9	26.0	50.0	17
	III	38.2	39.0	4.3	0.9	11.3	27.0	45.0	21
	IV	31.0	30.0	3.1	0.8	9.9	27.0	40.0	17
	V	35.2	35.0	5.3	0.6	15.0	26.0	50.0	72
	VI	32.6	33.0	4.0	0.7	12.4	25.0	43.0	38
Inner right marginal row, number of cirri	I	0.0	0.0	0.0	0.0	0.0	0.0	0.0	17
	II	4.1	0.0	–	–	–	0.0	22.0	17
	III	3.0	2.0	3.1	0.7	102	0.0	10.0	21
	IV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	17
	V	1.9	0.0	–	–	–	0.0	22.0	72
	VI	9.3	8.0	4.7	0.8	50.9	2.0	18.0	35
Additional cirral rows (pieces of right or	I	0.0	0.0	0.0	0.0	0.0	0.0	0.0	17
left marginal rows), number	II	0.5	0.0	–	–	–	0.0	1.0	17
	III	0.6	1.0	–	–	–	0.0	2.0	21
	IV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	17
	V	0.3	0.0	–	–	–	0.0	2.0	72
	VI	1.1	1.0	–	–	–	0.0	3.0	33
Dorsal kineties, number	I	4.1	4.0	–	–	–	4.0	5.0	17
	II	4.1	4.0	–	–	–	4.0	5.0	17
	III	4.3	4.0	–	–	–	4.0	5.0	21
	IV	4.0	4.0	0.0	0.0	0.0	4.0	4.0	17
	V	4.1	4.0	–	–	–	4.0	5.0	72
	VI	5.0	5.0	0.0	0.0	0.0	5.0	5.0	24
Dorsal kinety 1, number of kinetids	I	11.7	12.0	1.8	0.4	15.2	9.0	17.0	17
	II	17.3	16.0	5.1	1.2	29.5	12.0	32.0	17
	III	14.7	15.0	1.7	0.4	11.4	12.0	18.0	21
	IV	9.5	9.0	1.2	0.3	12.4	8.0	12.0	17
	V	13.4	13.0	4.0	0.5	30.0	8.0	32.0	72
	VI	28.5	28.0	3.5	0.7	12.4	21.0	34.0	29
Dorsal kinety 2, number of kinetids	I	15.1	15.0	1.4	0.3	9.3	13.0	17.0	17
	II	20.6	20.0	5.3	1.3	25.9	11.0	31.0	17
	III	16.3	16.0	2.4	0.5	14.4	13.0	20.0	21
	IV	11.9	12.0	1.4	0.3	11.7	10.0	15.0	17
	V	16.0	15.0	4.3	0.5	26.5	10.0	31.0	72
	VI	29.7	30.0	3.6	0.7	12.3	22.0	38.0	25
Dorsal kinety 3, number of kinetids	I	12.7	13.0	1.3	0.3	9.9	11.0	15.0	17
	II	17.4	17.0	4.1	1.0	23.8	12.0	29.0	17
	III	15.2	15.0	3.0	0.7	19.5	11.0	23.0	21
	IV	9.9	9.0	1.4	0.3	13.8	8.0	13.0	17

(continued)

Characteristics [a]	Pop [b]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	V	13.9	14.0	3.9	0.5	27.7	8.0	29.0	72
	VI	26.4	27.0	3.4	0.7	12.7	19.0	33.0	24
Dorsal kinety 4, number of kinetids	I	0.1	0.0	–	–	–	0.0	1.0	17
	II	0.6	0.0	–	–	–	0.0	7.0	17
	III	1.1	0.0	–	–	–	0.0	9.0	21
	IV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	17
	V	0.9	0.0	–	–	–	0.0	9.0	72
	VI	8.2	8.0	1.9	0.4	22.7	4.0	11.0	18
Dorsal kinety 5, number of kinetids	I	5.5	6.0	1.2	0.3	22.5	3.0	8.0	17
	II	8.5	8.0	2.4	0.6	28.0	5.0	15.0	17
	III	8.6	9.0	2.1	0.4	23.8	5.0	12.0	21
	IV	4.8	5.0	0.8	0.2	17.5	3.0	6.0	17
	V	6.9	6.0	2.4	0.3	35.2	3.0	15.0	72
	VI	12.1	12.0	1.9	0.4	15.4	9.0	16.0	27
Caudal cirri associated with dorsal kinety 1, number	I	2.1	2.0	0.4	0.1	20.8	1.0	3.0	17
	II	2.1	2.0	0.9	0.2	40.5	1.0	4.0	17
	III	2.7	3.0	0.7	0.1	24.7	1.0	4.0	21
	IV	1.9	2.0	–	–	–	1.0	2.0	17
	V	2.2	2.0	0.7	0.1	29.5	1.0	4.0	72
	VI	2.7	3.0	0.5	0.1	19.7	2.0	4.0	35
Caudal cirri associated with dorsal kinety 2, number	I	1.2	1.0	–	–	–	1.0	2.0	17
	II	1.1	1.0	–	–	–	1.0	2.0	17
	III	1.4	1.0	–	–	–	1.0	3.0	21
	IV	1.1	1.0	–	–	–	1.0	2.0	17
	V	1.2	1.0	–	–	–	1.0	3.0	72
	VI	1.1	1.0	–	–	–	1.0	2.0	34

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Populations (all in exponential growth phase as evident from many dividers contained in the slides): I – type population from USA two days after rewetting the sample; II – type population from USA six days after rewetting the sample; III – Namibian site (59) population; IV – Namibian site (18) population; V – populations I–IV pooled; VI – *Parakahliella haideri* (from BERGER & FOISSNER 1989b).

[c] Includes all postoral cirri that do not belong to the marginal cirral rows.

Occurrence and ecology: The type population was discovered in a soil sample from a flat, dry puddle at the coast of the Great Salt Lake in Utah (USA). The puddle bottom was overgrown with halophytes and covered with a salt crust. The sample contained much litter and plant roots and had pH 8.0. In Namibia, *P. halophila* occurred at sites (18), (59), and (61), which are also highly saline. Thus, *P. halophila* is a euryhaline and very likely cosmopolitan species.

Comparison of populations and with related species: We studied three

populations (I, III, IV in Table 118) of *P. halophila* from two widely separated regions (USA, Namibia), and the same population (I, II in Table 118) two and six days after rewetting the sample. The data show high variability between and within the populations, as evident from a comparison of the specimens two and six days after rewetting. The two-day-specimens are rather similar to the Namibian site (18) population (Fig. 136m, s), while the six-day-specimens are highly reminiscent of the Namibian site (59) population (Fig. 136o, q). Thus, we do not split *P. halophila* into subspecies, although molecular methods might show that it is a complex of sibling species.

Parakahliella haideri BERGER & FOISSNER, 1989b (Fig. 136v) differs morphometrically rather distinctly from *P. halophila*, although the extreme values often overlap (Table 118). The best morphometric feature for distinguishing these species is the buccal ciliature: *P. haideri* has 1–4, usually 3 buccal cirri, whereas P. *halophila* has 1–2, usually 1 buccal cirrus. A much more important feature are the undulating membranes, which optically cross in *P. haideri*, while they are invariably side by side in *P. halophila* (cp. Fig. 136v with Fig. 136u). This conspicuous difference indicates that *P. halophila* and → *P. namibicola*, described below, could even be not congeneric with *P. haideri* and *P. macrostoma*. This will have to be proved by sequence data. *Parakahliella macrostoma* (FOISSNER, 1982) BERGER et al., 1985 (Fig. 136w) is much more densely cirrated than *P. halophila* and has, like *P. haideri*, crossed undulating membranes. Furthermore, ontogenesis shows that it has two left marginal rows (BERGER et al. 1985). → *Parakahliella binucleata* is also more densely cirrated than *P. halophila* and has only two macronuclear beads. Furthermore, it has conspicuous cortical granules. Likewise, → *P. namibicola* has only two macronuclear nodules. *Fragmocirrus espeletiae* FOISSNER, 2000b (Fig. 136x) also resembles *P. halophila*, but has (inconspicuous) transverse cirri and, like *P. haideri*, usually three buccal cirri.

***Parakahliella binucleata* nov. spec.** (Fig. 137a–j, 382d; Table 119)

Diagnosis: Size about 140 × 50 µm in vivo; ellipsoidal. 2 macronuclear nodules. Cortical granules in dense rows, colourless, about 1 µm across. 27–57, usually 37 adoral membranelles; 1 or 2, rarely 3 buccal cirri; 3–9, usually 5 frontoventral rows; 2–12, usually 4 caudal cirri on dorsal kinety 1, 1–7, usually 3 on kinety 2, and 1–3, usually 2 on kinety 3; 4 dorsal kineties. 1 right and 1–6, usually 2 left marginal cirral rows.

Type location: Soil from Etosha National Park, Namibia, 19°10'S 16°10'E (site 64 in figures 2, 3 and chapter 2.1.2).

Etymology: The Latin adjective *binucleata* (two nuclei) refers to the two macronuclear nodules, a main feature of the species.

Description: Size 120–190 × 35–65 µm in vivo, usually near 140 × 50 µm, length:width ratio about 2.6–3.4:1 in vivo and 1.7–3.3:1 in protargol preparations, where specimens tend to become inflated; very flexible but acontractile. Ellipsoidal to slightly fusiform; dorsoventrally flattened up to 1.5:1, ventral side flat, dorsal distinctly vaulted in posterior half (Fig. 137a, c). Macronuclear nodules in middle third of cell slightly left of midline, ellipsoidal to elongate ellipsoidal, with numerous globular nucleoli 1–2 µm across; rather small compared to size of

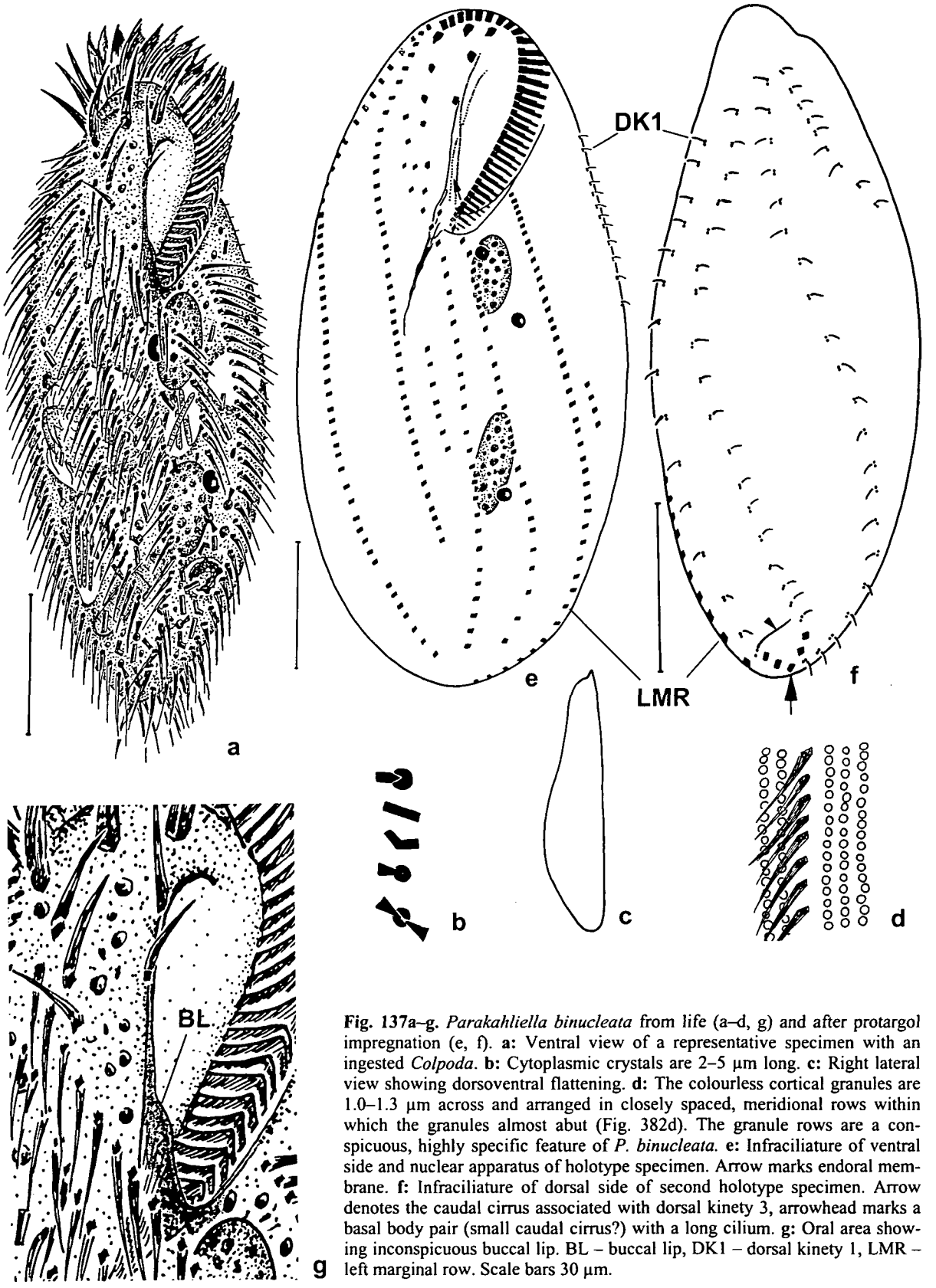


Fig. 137a–g. *Parakahliella binucleata* from life (a–d, g) and after protargol impregnation (e, f). **a:** Ventral view of a representative specimen with an ingested *Colpoda*. **b:** Cytoplasmic crystals are 2–5 µm long. **c:** Right lateral view showing dorsoventral flattening. **d:** The colourless cortical granules are 1.0–1.3 µm across and arranged in closely spaced, meridional rows within which the granules almost abut (Fig. 382d). The granule rows are a conspicuous, highly specific feature of *P. binucleata*. **e:** Infraciliature of ventral side and nuclear apparatus of holotype specimen. Arrow marks endoral membrane. **f:** Infraciliature of dorsal side of second holotype specimen. Arrow denotes the caudal cirrus associated with dorsal kinety 3, arrowhead marks a basal body pair (small caudal cirrus?) with a long cilium. **g:** Oral area showing inconspicuous buccal lip. BL – buccal lip, DK1 – dorsal kinety 1, LMR – left marginal row. Scale bars 30 µm.

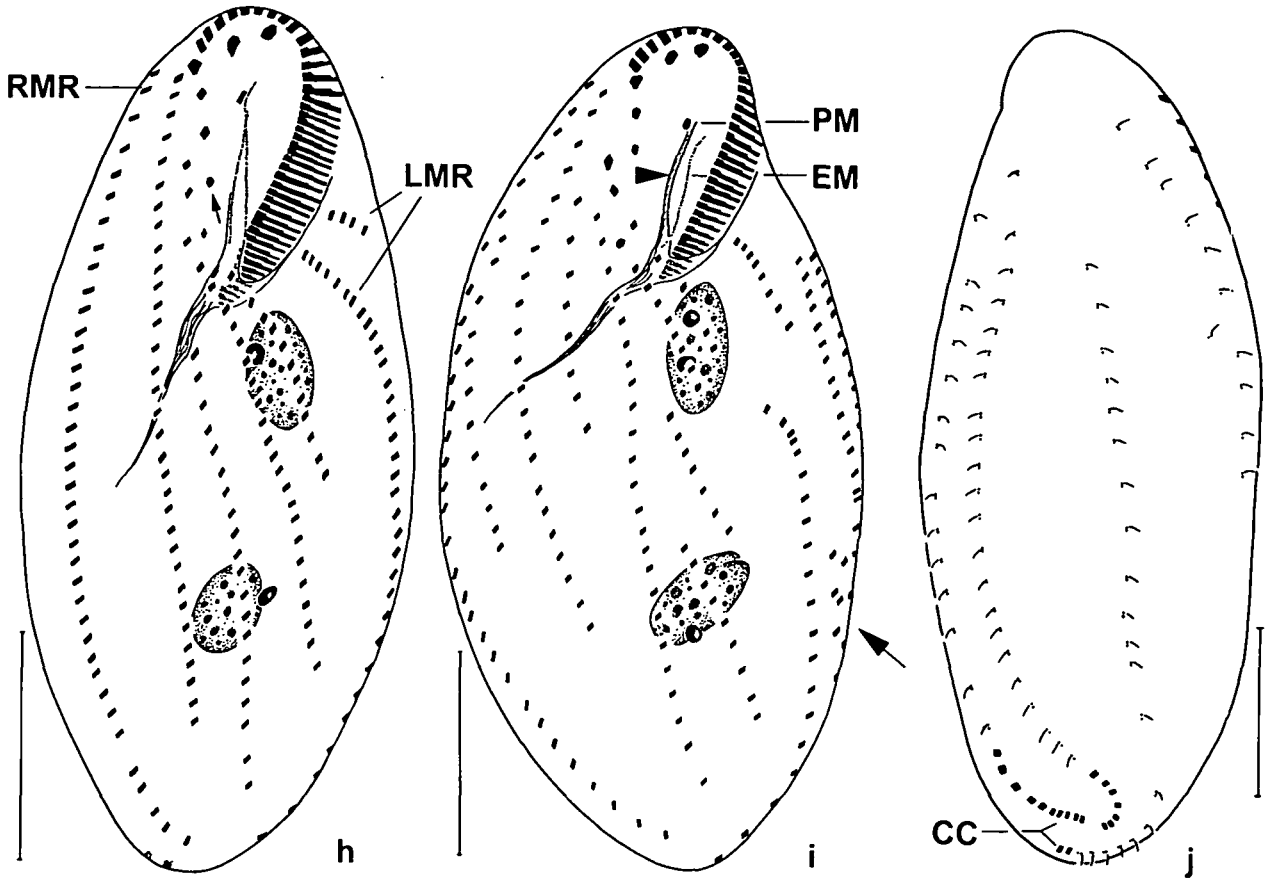


Fig. 137h–j. *Parakahliella binucleata*, infraciliature and nuclear apparatus after protargol impregnation. **h, i:** The ventral cirral pattern of *P. binucleata* is, as in congeners, highly variable. Arrow in (h) marks the short cirral row behind the right frontal cirrus. Arrow in (i) denotes region with widely spaced marginal cirri, likely remnants of parental rows; arrowhead marks line formed by pharyngeal fibres. **j:** Dorsal side of a specimen with many caudal cirri. CC – caudal cirri, EM – endoral membrane, LMR – left marginal rows, PM – paroral membrane, RMR – right marginal row. Scale bars 30 µm.

cell (Fig. 137e). Micronuclei usually attached or near macronuclear nodules, globular, about 5 × 4 µm in vivo. Contractile vacuole in mid-body at left margin. Cortical granules in closely spaced meridional rows (Fig. 137d, 382d); individual granules inconspicuous because only 1.0–1.3 µm in diameter and colourless, impregnate more or less intensely with protargol and become bright red, but not released when methyl green-pyronin is added. Cytoplasm colourless, with many small crystals concentrated in posterior third of cell. Omnivorous, feeds on long bacterial rods, filamentous cyanobacteria, flagellates (*Polytomella*), amoebas, and ciliates (small *Colpoda* species) digested in vacuoles up to 30 µm across. Movement without peculiarities, that is, glides moderately quickly on microscope slide and debris showing great flexibility.

Cirral pattern and number of cirri highly variable, as is usual in this genus (Table 119). Frontoventral and marginal cirri about 12–15 µm long in vivo. Right marginal row commences at level of right frontal cirrus and ends subterminally. Left marginal ciliature variable, that is, usually one long row commences slightly above buccal vertex and terminates at posterior end of cell, plus one or two short to long rows at variable positions left of long row; some specimens with more than three left marginal rows of rather different length,

arrangement, and distances between cirri, possibly remnants of parental left marginal rows (Fig. 137e, h, i). Frontal cirri distinctly, cirri behind right frontal cirrus slightly enlarged. One buccal cirrus right of anterior end of paroral membrane, in about 50% of specimens a second, rarely a third, buccal cirrus occurs in mid-region of buccal cavity. Number, length, and arrangement of frontoventral cirral rows highly variable, as in congeners, that is, none of the patterns can be considered as "representative" (Fig. 137e, h, i).

Dorsal bristles about 3 µm long in vivo, arranged in four rows of which the rightmost ends at or above mid-body[25]; dorsal ciliary pattern often difficult to recognize due to the cortical granules. Caudal cirri, although present in considerable number (6–18), inconspicuous in vivo because of similar size as marginal cirri (Fig. 137f, j; Table 119).

Table 119. Morphometric data on *Parakahliella binucleata*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	132.8	128.0	19.3	3.6	14.5	106.0	173.0	29
Body, width	59.8	57.0	14.0	2.6	23.4	36.0	100.0	29
Anterior body end to proximal end of adoral zone, distance	41.5	38.0	9.8	1.8	23.7	29.0	64.0	29
Length of adoral zone:body length, ratio in %	31.1	31.0	4.2	0.8	13.6	21.0	40.0	29
Anterior macronuclear nodule, length	19.8	19.0	3.7	0.7	18.8	15.0	30.0	29
Anterior macronuclear nodule, width	8.2	8.0	1.1	0.2	13.2	7.0	11.0	29
Anterior micronucleus, length	3.0	3.0	–	–	–	3.0	4.0	29
Anterior micronucleus, width	2.6	2.5	0.4	0.1	14.1	2.0	4.0	29
Adoral membranelles, number	38.7	37.0	8.5	1.6	22.0	27.0	57.0	29
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	29
Micronuclei, number	3.2	3.0	1.3	0.2	40.3	1.0	7.0	29
Enlarged frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	29
Buccal cirri, number	1.5	1.0	0.6	0.1	37.9	1.0	3.0	29
Cirri behind right frontal cirrus, number	3.1	3.0	0.4	0.1	13.0	2.0	4.0	25
Frontoventral rows, number [b]	5.4	5.0	1.7	0.4	31.5	3.0	9.0	19
Left marginal rows, number (including short fragments)	2.0	2.0	1.0	0.2	51.9	1.0	6.0	27
Right marginal rows, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	27
Left marginal cirri, number (from long, innermost row)	37.4	36.0	8.2	1.5	21.9	20.0	54.0	29
Right marginal cirri, number	43.0	43.0	6.3	1.2	14.6	31.0	57.0	27
Dorsal kineties, number	4.1	4.0	–	–	–	4.0	5.0	13
Caudal cirri associated with dorsal kinety 1, number	5.1	4.0	2.3	0.5	44.9	2.0	12.0	25
Caudal cirri associated with dorsal kinety 2, number	3.2	3.0	1.4	0.3	44.9	1.0	7.0	20
Caudal cirri associated with dorsal kinety 3, number	1.9	2.0	0.5	0.1	26.5	1.0	3.0	20

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Short row behind right frontal cirrus not included.

[25] A late divider showed that dorsal kineties do not fragmentate and one dorsomarginal kinety (= kinety 4) is generated.

Adoral zone occupies 21–40%, on average 31% of body length, composed of an average of 37 membranelles, bases of largest membranelles about 7 µm wide in vivo. Buccal cavity narrow and flat. Buccal lip inconspicuous, covers only proximal portion of adoral zone. Paroral and endoral membrane usually slightly curved and optically crossed in mid-portion (Fig. 137a, e); exact arrangement of undulating membranes, however, difficult to recognize in many specimens; both membranes likely composed of a single line of tightly spaced cilia, paroral cilia about 7 µm long in vivo. Pharyngeal fibres of ordinary length and structure.

Occurrence and ecology: To date found at type location and Namibian site (50), where it showed exactly the same features.

Comparison with related species: The new species is the sole *Parakahliella* with cortical granules. Only one other species has two macronuclear nodules, viz., → *Parakahliella namibicola*. *Parakahliella macrostoma* (FOISSNER, 1982) BERGER et al., 1985 has 5–13, usually 7–11 nodules (Fig. 136w); *Parakahliella haideri* BERGER & FOISSNER, 1989b has 5–9, usually 6 nodules (Fig. 136v); and → *P. halophila* has 2–8, usually 4 nodules (Table 118). → *Parakahliella halophila* specimens with two macronuclear nodules can be easily distinguished from *P. binucleata* by the sparse ventral ciliature. Furthermore, *P. binucleata* is the sole species with caudal cirri on dorsal kinety 3 (Fig. 137f, j). *Paraurostyla weissei* (STEIN, 1859) BORROR, 1972a and *P. granulifera* BERGER & FOISSNER, 1989a, which have a very similar general appearance, possess transverse cirri (BERGER 1999).

Parakahliella namibicola **nov. spec.** (Fig. 138a–j; Table 120)

Diagnosis: Size about 100 × 35 µm in vivo; elongate ellipsoidal. On average 2 macronuclear nodules, 25 adoral membranelles, 1 buccal cirrus, 4 cirri in left frontoventral row, 20 cirri each in middle and right frontoventral row, 5 caudal cirri, and 4 dorsal kineties. 1 right and 1 left marginal row, and 3 frontoventral rows, of which the middle and right extend beyond mid-body.

Type location: Sandy bark from an *Acacia erioloba* (Camel thorn) tree in the Sossus Vlei, Southern Namib Desert, 24°50'S 15°20'E (site 25 in figure 2 and chapter 2.1.2).

Etymology: The Latin composite *namibicola* (living in the Namib Desert) refers to the region the species was discovered.

Description: Size 70–120 × 25–45 µm in vivo, usually near 100 × 35 µm, length:width ratio 1.8–3.9:1, on average 2.7:1 in protargol preparations; very flexible but acontractile (Table 120). Shape highly variable as shown by figures 138a–g, basically elongate ellipsoidal with posterior quarter often rather distinctly narrowed and indented at right side, providing cells with a somewhat sigmoidal outline; dorsoventrally flattened up to 2:1, invariably slightly to distinctly twisted about main body axis, marginal cirral rows thus only partially recognizable when specimens are viewed ventrally. Nuclear apparatus in middle third of body left of midline. Number of macronuclear nodules varies from one to four, but 85% of the 113 specimens investigated have two nodules; individual nodules broadly to elongate ellipsoidal, on average near 2:1, outline often irregular, contain many small and some medium-sized

nucleoli. Micronuclei not unequivocally recognizable in vivo and protargol preparations, not even in dividers, one micronucleus is possibly present in some specimens. Contractile vacuole without distinct collecting canals, in or slightly above mid-body. Cortex colourless and very flexible, without specific granules. Cytoplasm densely granulated providing cells with a brownish shimmer at low magnification ($\leq \times 100$), contains rather many ordinary crystals mainly in posterior third, and food vacuoles up to 15 µm across. Benin specimens fed on naked amoebae and, especially, a *Polytoma*-like flagellate with a size of about 10 × 6 µm and a red eye-spot. Glides slowly on microscope slide and between soil particles.

Cirral pattern and number of cirri less variable than in congeners, that is, of almost ordinary variability (Fig. 138a, e, h, i; Table 120). Cirri 10–15 µm long in vivo, become smaller and more widely spaced in posterior quarter of all rows. Right marginal row commences dorsally at level of right frontal cirrus and ends, like left row, subterminally; very rarely specimens with a short, second left marginal row occur. Frontal cirri slightly enlarged and close together. Usually one, rarely two or no, buccal cirrus right of anterior end of paroral membrane, that is, only about 5 µm away from anterior body end. Number, length, and arrangement of frontoventral rows rather stable, usually as shown in figure 138e. Left frontoventral row commences underneath right frontal cirrus and ends at level of oral vertex, composed of an average of only four cirri; rarely some supernumerary cirri occur left of the row. Middle frontoventral row commences at same level as left row and extends obliquely beyond mid-body, composed of an average of 20 cirri. Right frontoventral row commences right and at level of right frontal cirrus and extends obliquely beyond mid-body ending some micrometers above middle row, composed of an average of 20 cirri. Transverse cirri lacking.

Dorsal bristles about 3 µm long in vivo, arranged in four rows (five in one out of 30 specimens), of which the two middle rows extend diagonally, mainly due to the spiralization of the body. Rows 1 and 2 distinctly shortened anteriorly and posteriorly associated with an average of three caudal cirri, respectively, one caudal cirrus. Row 3 usually distinctly shortened posteriorly, in 5 out of 23 specimens associated with one or two caudal cirri; row 4 (and 5 occasionally present) near anterior right corner of cell, consists of only few kinetids (Fig. 138i; Table 120).

Adoral zone of ordinary shape and structure, inconspicuous because occupying only 22–32%, on average 27% of body length, composed of an average of 25 membranelles, bases of largest membranelles about 7 µm wide in vivo (Fig. 138a, e, h; Table 120). Buccal cavity narrow compared to size of species and moderately deep; buccal lip rather conspicuous, bears paroral membrane and projects angularly to cover proximal portion of adoral zone. Paroral and endoral membrane almost straight and side by side, paroral commences slightly ahead of endoral and ends a few micrometers above endoral; paroral cilia tightly spaced, about 7 µm long in vivo. Pharyngeal fibres inconspicuous both in vivo and protargol preparations.

Ontogenesis: The slides from the type location contain several dividers showing the main ontogenetic events and the generic home of the species. Ontogenesis commences with the production of an oral primordium close to the postoral portion of the long ventral cirral row 2. Two cirral streaks and a primordium for the undulating membranes are produced by the oral primordium and one streak each by within-row proliferation of the long ventral rows 2 and 3. Thus five anlagen streaks are recognizable in middle dividers (Fig. 138j). No transverse cirri are produced. Caudal cirri are generated at the end of dorsal kineties 1 and 2, which divide as is usual, while kinety 4 originates dorsomarginally.

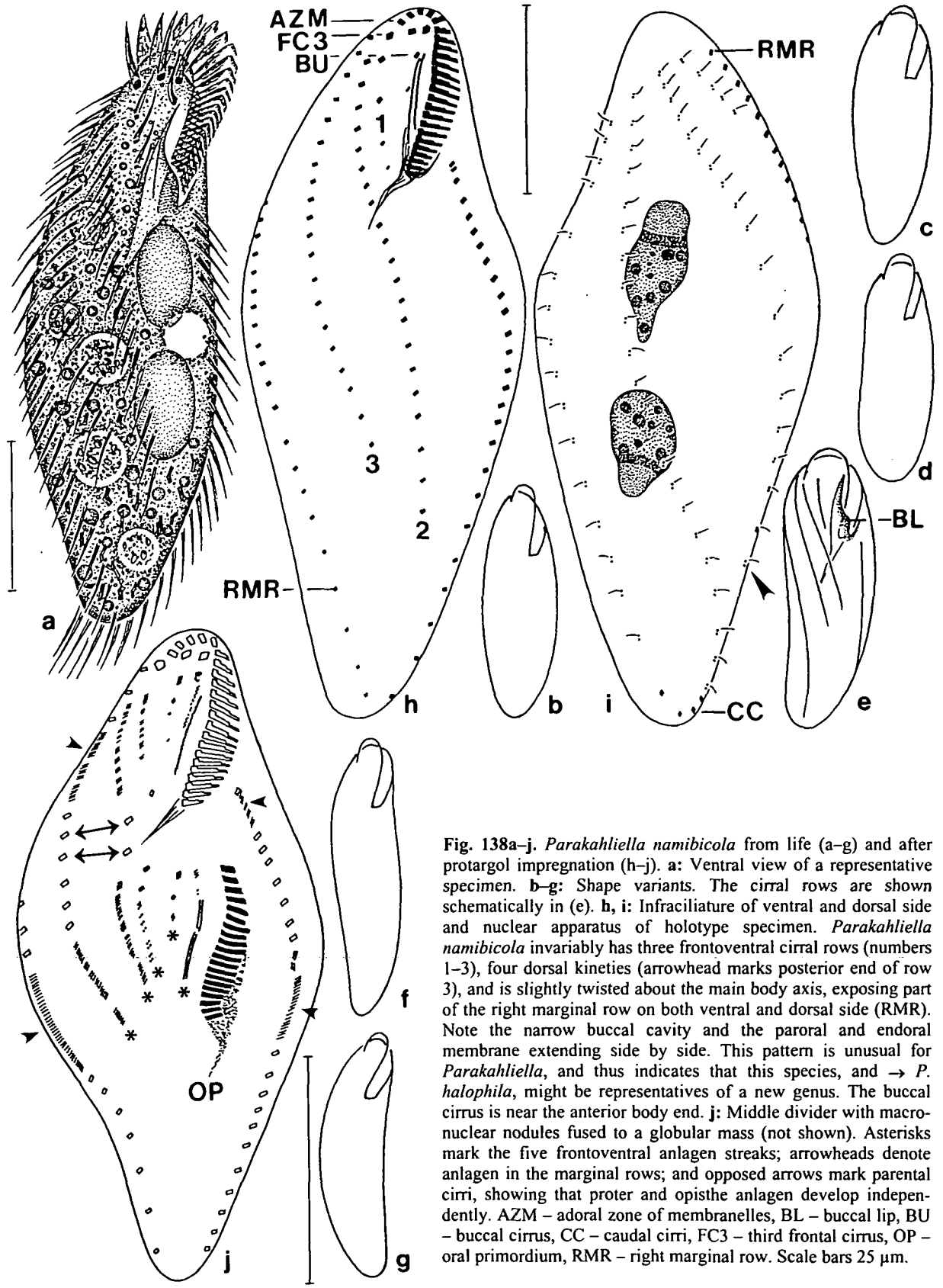


Fig. 138a–j. *Parakahliella namibicola* from life (a–g) and after protargol impregnation (h–j). **a:** Ventral view of a representative specimen. **b–g:** Shape variants. The cirral rows are shown schematically in (e). **h, i:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. *Parakahliella namibicola* invariably has three frontoventral cirral rows (numbers 1–3), four dorsal kineties (arrowhead marks posterior end of row 3), and is slightly twisted about the main body axis, exposing part of the right marginal row on both ventral and dorsal side (RMR). Note the narrow buccal cavity and the paroral and endoral membrane extending side by side. This pattern is unusual for *Parakahliella*, and thus indicates that this species, and → *P. halophila*, might be representatives of a new genus. The buccal cirrus is near the anterior body end. **j:** Middle divider with macronuclear nodules fused to a globular mass (not shown). Asterisks mark the five frontoventral anlagen streaks; arrowheads denote anlagen in the marginal rows; and opposed arrows mark parental cirri, showing that proter and opisthe anlagen develop independently. AZM – adoral zone of membranelles, BL – buccal lip, BU – buccal cirrus, CC – caudal cirri, FC3 – third frontal cirrus, OP – oral primordium, RMR – right marginal row. Scale bars 25 µm.

Occurrence and ecology: *Parakahliella namibicola* was almost the only, but very abundant species in the sandy bark sample from an *Acacia* tree in the dunes of the Namib Desert, demonstrating the highly clumped distribution. No other species of the genus is twisted about the main body axis, indicating that body spiralling might be advantageous in sandy environments. Indeed, *Circinella arenicola*, a very slender, cephalized hypotrich discovered in a dune of North America, is also distinctly spiralized (FOISSNER 1994a). Likewise, → *Erimophrya arenicola*, another hypotrich living in the sand dunes of the Namib Desert, is twisted about the main body axis.

Comparison with related species: The new species is possibly the sister of → *Parakahliella binucleata*, which also has two macronuclear nodules, but possesses conspicuous cortical granules and several short and long frontoventral cirral rows. Thus, *Parakahliella namibicola* and *P. binucleata* are easily distinguished, even in vivo. No other species of the genus is twisted about the main body axis. Generally, the cirral pattern of *P. namibicola* is less complicated and variable than that of the congeners. The lack of micronuclei is remarkable, but must be substantiated by further investigations.

There are quite a lot of similar soil hypotrichs, especially amphisiellids, which are easily confused with *P. namibicola*. Thus, combined live observation (lack of cortical granules) and silver impregnation is indispensable for reliable identification. However, if a species has the following combination of features in vivo, it is likely *P. namibicola*: body slightly spiralized and about 100 × 35 µm in size, two macronuclear nodules, no cortical granules, two ventral cirral rows extending beyond mid-body, several caudal cirri, narrow buccal cavity, and a short (quarter of body length) adoral zone composed of about 25 membranelles.

Table 120. Morphometric data on *Parakahliella namibicola*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	80.8	82.0	10.7	2.2	13.2	57.0	105.0	23
Body, width	30.8	30.0	5.2	1.1	16.8	20.0	45.0	23
Body length:width, ratio	2.7	2.5	0.5	0.1	17.1	1.8	3.9	23
Anterior body end to proximal end of adoral zone of membranelles, distance	21.8	22.0	1.8	0.4	8.4	18.0	26.0	23
Body length:length of adoral zone, ratio	3.7	3.6	0.4	0.1	11.9	3.0	4.8	23
Anterior body end to right marginal row, distance	6.8	6.0	2.3	0.5	33.5	4.0	12.0	23
Posterior body end to right marginal row, distance	3.1	3.0	1.5	0.3	49.7	1.0	7.0	23
Posterior body end to left marginal row, distance	3.4	3.0	1.9	0.4	54.0	1.0	9.0	23
Anterior body end to end of frontoventral row 1, distance	17.8	20.0	4.6	1.0	26.0	11.0	26.0	23
Anterior body end to end of frontoventral row 2, distance	55.3	57.0	9.1	1.9	16.5	38.0	69.0	23
Anterior body end to end of frontoventral row 3, distance	50.8	51.0	8.3	1.7	16.3	35.0	69.0	23
Anterior body end to buccal cirrus, distance	4.9	5.0	0.8	0.2	16.7	3.0	6.0	23
Anterior body end to paroral membrane, distance	4.7	5.0	0.8	0.2	17.9	3.0	6.0	23
Paroral membrane, length	9.1	9.0	1.7	0.4	18.2	7.0	14.0	23
Anterior body end to endoral membrane, distance	5.1	5.0	0.9	0.2	16.9	4.0	6.0	23
Endoral membrane, length	12.4	12.0	2.0	0.4	15.9	9.0	18.0	23
Anterior end to first macronuclear nodule, distance	23.8	24.0	3.4	0.7	14.1	17.0	32.0	23

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Macronuclear nodules, distance in between	5.8	7.0	3.6	0.8	61.8	0.0	12.0	23
Macronuclear figure, length	34.4	35.0	7.3	1.5	21.3	21.0	48.0	23
Anterior macronuclear nodule, length	14.5	15.0	3.1	0.6	21.1	9.0	21.0	23
Anterior macronuclear nodule, width	8.0	8.0	1.1	0.2	13.4	6.0	10.0	23
Macronuclear nodules, number	2.1	2.0	0.4	0.1	19.6	1.0	4.0	113
Adoral membranelles, number	24.7	24.0	2.2	0.5	9.0	21.0	31.0	23
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	23
Buccal cirri, number	1.2	1.0	–	–	–	0.0	2.0	23
Cirri left of frontoventral row 1, number	0.7	0.0	–	–	–	0.0	3.0	23
Frontoventral cirral rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	23
Frontoventral row 1, number of cirri	3.9	4.0	1.5	0.3	37.7	2.0	8.0	23
Frontoventral row 2, number of cirri	20.2	20.0	2.9	0.6	14.5	15.0	25.0	23
Frontoventral row 3, number of cirri	20.0	20.0	2.5	0.5	12.5	15.0	24.0	23
Left marginal cirral rows, number	1.1	1.0	–	–	–	1.0	2.0	23
Left marginal cirri, number	26.4	26.0	3.5	0.7	13.4	21.0	33.0	23
Right marginal cirral rows, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	23
Right marginal cirri, number	30.5	30.0	3.4	0.7	11.0	24.0	38.0	23
Dorsal kineties, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	23
Caudal cirri on dorsal kinety 1, number	3.1	3.0	1.2	0.3	37.7	1.0	6.0	23
Caudal cirri on dorsal kinety 2, number	1.4	1.0	0.6	0.1	41.1	1.0	3.0	23
Caudal cirri on dorsal kinety 3, number	0.3	0.0	–	–	–	0.0	2.0	23
Caudal cirri, total number	4.8	5.0	1.6	0.3	32.4	3.0	9.0	23

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Anatoliocirrus ÖZBEK & FOISSNER nov. gen.[26]

Diagnosis: Parakahliellidae or Oxytrichidae with transverse, caudal and frontoterminal cirri. Two or more rows each of right and left marginal cirri. All fronto-ventral-transverse cirral anlagen of proter and opisthe originate by transverse splitting of long primary primordia. Dorsal kineties generated by within anlagen and dorsomarginally.

Type species: *Anatoliocirrus capari* nov. spec.

[26] This ciliate was discovered by FOISSNER in Namibia and in a Mangrove swamp in Costa Rica. Later, FOISSNER found it in a saline wetland soil from Turkey. The Turkish population was cultivated and investigated by Miss Sirma ÖZBEK during a stay in Salzburg. Unfortunately, she could not finish the work. Thus and because the species occurs in Namibia, we include it in the present monograph, with ÖZBEK & FOISSNER as authors. Most illustrations were made by ÖZBEK, while the text was written by FOISSNER.

Etymology: Composite of the Latin nouns Anatolia (Turkey) and cirrus (hair, curl ~ compound cilia typical for hypotrichs), meaning a hypotrichous ciliate from Anatolia.

Family classification and comparison with related genera: At first glance, *Anatoliocirrus* has distinct morphological and ontogenetical similarities with *Paraurostyla*, an oxytrichid sensu lato (WIRNSBERGER, FOISSNER, ADAM 1985), and *Parentocirrus*, *Parakahliella* and *Fragmocirrus,* which EIGNER (1997) classified in the new family Parakahliellidae together with *Paraurostyla*. All these genera have so-called "neokinetal 1" anlagen development in which a V-shaped anlage *each* develops in proter and opisthe and produces the rightmost two cirral streaks. In contrast, *Anatoliocirrus* develops "neokinetal 3" anlagen, in which a *single* V-shaped anlage is produced in early dividers; this anlage grows and splits transversely to produce the two rightmost cirral streaks in both proter and opisthe (Fig. 139m, p, r, s; 385j–n).

Neokinetal 3 anlagen development is characteristic for the Oxytrichidae (EIGNER 1997), suggesting that *Anatoliocirrus* belongs to this family, and the great interphase similarities with parakahliellids developed convergently. However, there is no soft-bodied oxytrichid genus, except of *Paraurostyla,* which looks similar to *Anatoliocirrus* (for a review, see BERGER 1999). Thus, and for general reasons we cannot exclude that "neokinetal 3" anlagen originated convergently in a parakahliellid line, such as *Anatoliocirrus*. Accordingly, it is impossible to assign *Anatoliocirrus* to a certain family, which shows that it is a very distinct genus.

Table 121. Distinguishing features between *Anatoliocirrus* and similar genera. Sources see table 123.

Features	*Anatoliocirrus*	*Fragmocirrus*	*Parentocirrus*	*Parakahliella*	*Paraurostyla*
Transverse cirri	present	present	present	absent	present
Frontoterminal cirri	present	present	absent	present	present
Right marginal rows, number	several	several	one	several	one
Left marginal rows, number	several	several	one	one to several	one
Dorsal kinety fragmentation	absent	absent	present	absent	present
Primary primordia	present	absent	absent	absent	absent
Anterior/posterior migration of last two anlagen	present	present	absent	absent	present
Origin of last anlage in proter and opisthe	within same row	within different rows	within same row	within same row	within same row

As explained above, the Turkish ciliate seemingly belongs to a group of genera which are characterized by rather sophisticated features recognizable mainly during cell division, namely *Paraurostyla* BORROR, 1972a; *Parakahliella* BERGER, FOISSNER & ADAM, 1985; *Parentocirrus* VOSS, 1997; and *Fragmocirrus* FOISSNER, 2000b. Thus, the correct assignment of a new species needs ontogenetic data. *Anatoliocirrus* differs from the above mentioned genera mainly by the occurrence of primary primordia (Table 121), a conspicuous feature used to define families and genera (BERGER 1999, EIGNER 1997). The existence of primary

primordia in *Anatoliocirrus* is proven not only by the general appearance of the cirral streaks, but also by the lack of any ontogenetically inactive ventral cirri, except of the frontoterminal cirri (Fig. 139o, p, r, s; 385n). The last mentioned feature is very important because other genera, especially *Paraurostyla*, look rather similar in certain division stages, but invariably have some morphogenetically inactive parental cirri between the proter and opisthe cirral streaks, even in late dividers (FOISSNER 2000b, WIRNSBERGER et al. 1985). Besides the primary primordia, *Anatoliocirrus* differs from the above mentioned genera also in other features, all compiled in table 121.

Anatoliocirrus capari ÖZBEK & FOISSNER **nov. spec.** (Fig. 139a–z, 385a–n ; Tables 122–124)

Diagnosis: Size about 130 × 50 µm in vivo; elongate ellipsoidal. Two macronuclear nodules. Cortical granules in narrowly spaced rows, colourless, about 1 µm across. On average 36 adoral membranelles, three enlarged frontal cirri, one buccal cirrus, one frontoventral cirrus, seven frontoterminal and five transverse cirri, one pretransverse cirrus, two right and four left marginal rows, and a highly variable number (12–50) of ventral cirri arranged in three to four oblique, staggering rows. Paroral membrane composed of many short kineties each comprising three basal bodies. Four dorsal kineties, rows 1–3 bipolar and with an average of eight caudal cirri, row four terminates near mid-body.

Type location: Highly saline soil from Turkey, Mersin, Silifke, Göksu Delta, Cirba Region, 36°20'N 33°59'E.

Etymology: Named in honour of the parents of the junior author, viz., Sunay and İzzet ÇAPAR for the diligence in bringing up their children.

Description (Fig. 139a–h; 385a–i; Table 122): Size 100–150 × 30–55 µm in vivo, usually about 120 × 50 µm, length:width ratio 2.4–4:1, on average near 3:1 in vivo, slightly stouter in protargol preparations; dorsoventrally flattened up to 2:1, ventral side flat, dorsal more or less distinctly vaulted and with rather conspicuous furrow along dorsal kinety four; very flexible but acontractile. Shape inconspicuous, that is, elongate ellipsoidal, left margin less convex than right, both ends moderately broadly rounded; well-fed specimens ellipsoidal or ovoidal with posterior half inflated and broadly rounded posteriorly (Fig. 139a, d, h; 385b). Macronuclear nodules almost abutting in middle third of cell left of midline, elongate ellipsoidal on average, with numerous globular and oblong nucleoli. Micronuclei ellipsoidal, near or attached to macronuclear nodules in various positions. Contractile vacuole near mid-body at left margin of cell, with two collecting canals extending anteriad and posteriad, pulsates rarely because of the saline medium. Cortex very flexible, contains many granules in rather narrowly spaced, somewhat staggering rows; individual granules almost colourless, at best a yellowish shimmer is recognizable, about 0.8–1 µm across, a row of slightly enlarged granules along each cirral row (Fig. 139e, h; 385a, c). Cytoplasm colourless, well-fed specimens dark in posterior half at low magnification due to food inclusions and many up to 6 µm-sized crystals. Food vacuoles up to 20 µm across when feeding on bacteria, ingests also small naked amoeba and ciliates, such as *Pseudocohnilembus* sp. and *Euplotes* sp. Moves moderately fast on microscope slide and soil particles showing great flexibility.

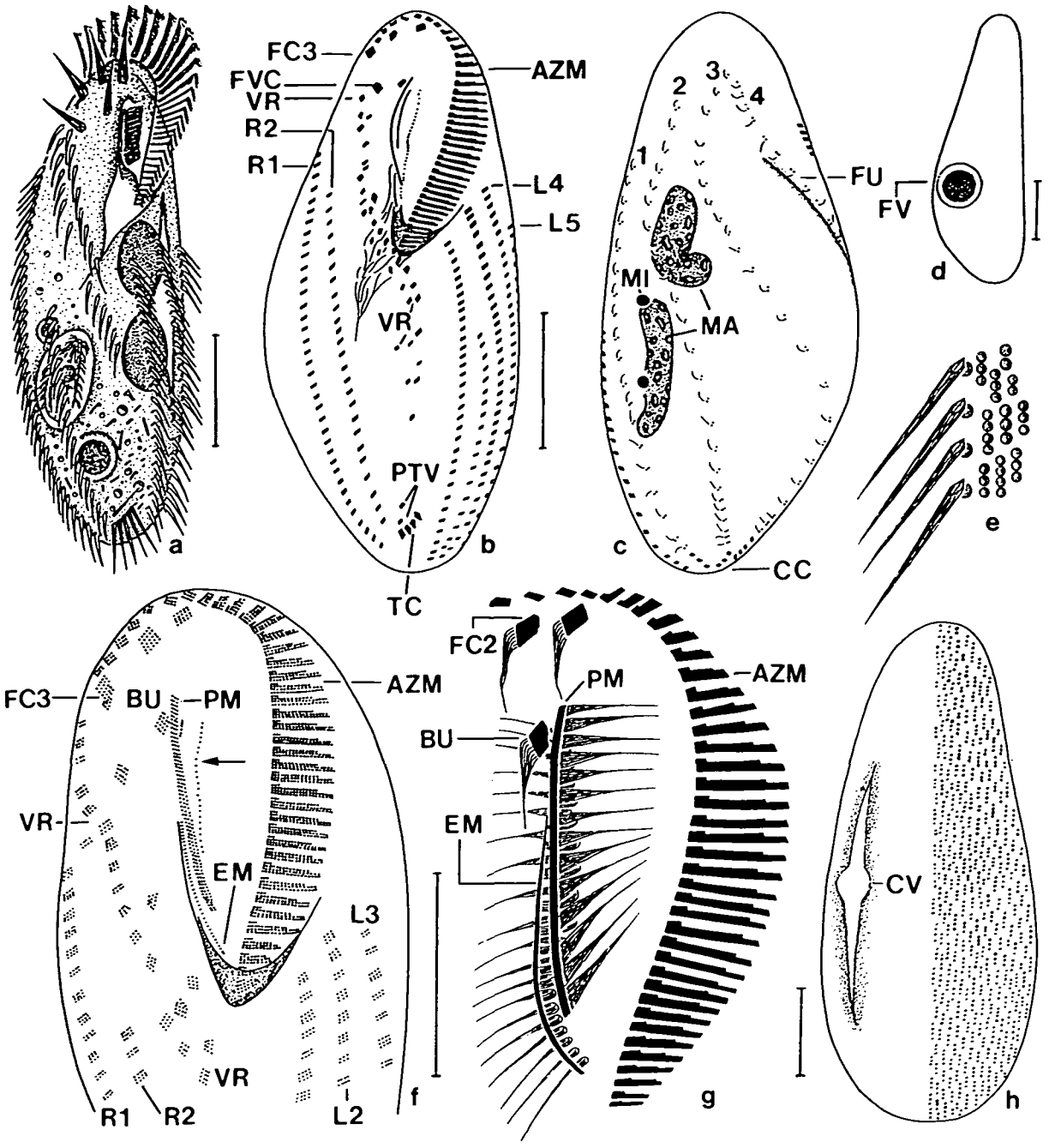


Fig. 139a–h. *Anatoliocirrus capari* from life (a, d, e, h) and after protargol impregnation (b, c, f, g). **a:** Ventral view of a representative specimen. **b, c:** Ciliary pattern of ventral and dorsal side of a specimen with many ventral cirri. The ventral cirri are arranged in three to four rows which, however, are recognizable only in late dividers. **d:** Lateral view of a specimen having just ingested large prey. **e, h:** Arrangement of the colourless cortical granules and shape of a well-fed specimen. **f:** Somatic and oral infraciliature of anterior ventral third. Arrowhead marks the "third undulating membrane" produced either by the curved endoral cilia or, more likely, by the vertices of curved buccal fibres. The paroral is composed of many short kineties each comprising three basal bodies, an important feature of this species. **g:** Fibrillar associates of oral structures. 1-4 – dorsal ciliary rows, AZM – adoral zone of membranelles, BU – buccal cirrus, CC – caudal cirri, CV – contractile vacuole, EM – endoral membrane, FC2, 3 – second and third frontal cirrus, FU – furrow along dorsal kinety 4, FV – food vacuole, FVC – frontoventral cirrus, L2-5 – left marginal rows, MA – macronuclear nodules, MI – micronucleus, PM – paroral membrane, PTV – pretransverse cirri, R1, 2 – first and second right marginal row, TC – transverse cirri, VR – ventral cirri. Scale bars 30 μm (a–d) and 20 μm (f, h).

Cirri about 11 µm long, except for transverse cirri and cilia of adoral membranelles, being 15 µm long in vivo. Composition of cirri rather variable, a representative example is shown in figure 139f. Cirral pattern highly variable, mainly due to the strongly varying number of ventral cirri and left marginal rows (Fig. 139a, b, f, i; 385b, d–f; Table 122). Usually seven, sometimes eight ventral cirral rows, according to the ontogenetic data: row 1 consists of first frontal cirrus; row 2 of second frontal cirrus and buccal cirrus; row 3 composed of third frontal cirrus plus mostly one, rarely two distinctly enlarged frontoventral cirri underneath; rows 4–7 (8), which occupy the midline region of the cell and contain most of the ventral cirri, are difficult to number in morphostatic specimens because they are short and staggering. Usually two right marginal rows: first row commences subapically at level of buccal cirrus and extends to level of posteriormost transverse cirrus; second row parallel to first row, of variable length, that is, commences near level of buccal vertex and extends up to level of pretransverse cirrus; rarely occurs a third, short right marginal row. On average four left marginal rows usually commencing slightly above buccal vertex and terminating near rear body end; occasionally one or two anteriorly shortened rows interspersed. Usually one, rarely two buccal cirri slightly underneath anterior end of paroral. Transverse cirri form oblique row in midline, slightly enlarged, project from body proper; one to two pretransverse cirri.

Dorsal bristles about 4 µm long in vivo, arranged in four, very rarely five rows (Fig. 139c). Rows 1 to 3 extend in and left of cell's midline, all slightly shortened anteriorly and associated with an average of eight caudal cirri posteriorly. Row 4 near right margin of cell, terminates at mid-body. Row five, if present, left of row four, consist of only few kinetids.

Oral apparatus with two peculiarities described below. Adoral zone of usual structure, comprises an average of 36 membranelles and occupies 30% of body length in vivo, while 43% in prepared specimens, obviously due to some shrinkage of postoral body portion. Buccal cavity of ordinary width and deepness, distinctly curved anteriorly in vivo; buccal lip narrow in anterior half, broad and angularly projecting in posterior (Fig. 139a, b, f, g, i; 385b, e–i; Table 122). Paroral membrane at right wall of buccal cavity, slightly curved, terminates distinctly above buccal vertex, extraordinary because composed of oblique rows each comprising three about 7 µm long cilia (Fig. 139f). Endoral with 10 µm long cilia, commences slightly underneath paroral and extends to near buccal vertex. Left of endoral a row of comparatively widely spaced and slightly scattered granules, seemingly representing basal bodies of a third undulating membrane, just as described by GROLIÈRE in *Opisthotricha monspessulana* (now *Sterkiella cavicola*, see BERGER 1999 for detailed review). However, careful analysis shows that this row is produced either by the curved endoral cilia or, more likely, by curved buccal fibres (possibly postciliary microtubule ribbons; see BAKOWSKA & JERKA-DZIADOSZ 1978), the curve vertices of which appear as granules (Fig. 139f, g; 385g–i). Pharyngeal fibres distinct, extend obliquely to mid-body.

Occurrence and ecology: The sample which contained *A. capari* was collected on 23 July 1999 in the Göksu Delta at the Mediterranean coast of Turkey (36°20'N 33°59'E). The area is at sea-level and flooded by the Göksu River mainly in winter time. Minimum precipitation is in August, maximum in December, annual mean amounts 637 mm. Mean annual temperature is 19° C with a difference of 20° C between the coldest and warmest month. Vegetation is sparse and dominated by *Phragmites* sp., *Archonomum* sp., *Juncus* sp. and *Inula chritmoides* leaving large spots of bare or grassland soil. The soil of this region are highly saline brown earths.

Table 122. Morphometric data on *Anatoliocirrus capari.*

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	95.3	95.0	8.0	1.5	8.4	80.0	110.0	29
Body, length in vivo	129.4	120.0	21.3	5.5	16.4	100.0	151.0	15
Body, width	38.6	38.0	5.0	0.9	12.9	30.0	48.0	29
Body, width in vivo	45.7	50.0	6.8	1.8	14.8	30.0	55.0	15
Body lenght:width, ratio	2.5	2.4	0.4	0.1	16.5	1.1	3.2	29
Body lenght:width, ratio in vivo	2.9	3.0	0.4	0.1	14.2	2.4	4.0	15
Anterior somatic end to end of adoral zone, distance	41.2	42.0	2.8	0.5	6.9	37.0	49.0	29
Anterior somatic end to end of adoral zone, distance in vivo	39.3	39.5	4.2	1.2	10.7	35.0	47.0	12
Anterior macronuclear nodule, length	20.8	20.0	4.8	0.9	23.0	15.0	38.0	29
Anterior macronuclear nodule, width	7.8	8.0	1.0	0.2	13.3	6.0	9.0	29
Posterior macronuclear nodule, length	22.0	22.0	3.1	0.6	14.2	17.0	29.0	29
Posterior macronuclear nodule, width	7.6	7.0	1.4	0.3	18.0	5.0	12.0	29
Anterior micronucleus, minimum width	2.1	2.0	–	–	–	2.0	3.0	21
Micronuclei attached to anterior macronuclear nodule, number	1.2	1.0	–	–	–	1.0	2.0	21
Posterior micronucleus, minimum width	2.0	2.0	0.0	0.0	0.0	2.0	2.0	27
Micronuclei attached to posterior macronuclear nodule, number	1.1	1.0	–	–	–	1.0	2.0	27
Macronuclear nodules, distance in between	5.3	5.0	3.0	0.5	55.3	1.0	11.0	29
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	29
Micronuclei, total number	2.3	2.0	–	–	–	2.0	3.0	19
Adoral membranelles, number	36.5	36.0	2.4	0.4	6.5	33.0	41.0	29
Enlarged frontal cirri, number [b]	3.0	3.0	0.0	0.0	0.0	3.0	3.0	29
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	29
Frontoventral cirri, number	1.4	1.0	0.6	0.1	45.1	1.0	3.0	29
Frontoterminal cirri, number [c]	7.2	7.0	1.0	0.3	13.5	5.0	8.0	9
Ventral cirral rows, number	5.7	6.0	0.9	0.2	16.0	5.0	9.0	27
First ventral row, cirri number [d, e]	1.0	1.0	0.0	0.0	0.0	1.0	1.0	29
Second ventral row, cirri number [d, e]	2.0	2.0	0.0	0.0	0.0	2.0	2.0	29
Third ventral row, cirri number [d, e]	2.4	2.0	–	–	–	2.0	4.0	29
Further ventral rows, cirri number [d, e]	26.1	27.0	7.8	1.5	29.7	12.0	50.0	27
Transverse cirri, number	4.7	5.0	0.7	0.2	15.2	4.0	6.0	21
Pretransverse cirri, number	1.4	1.0	0.6	0.1	41.8	1.0	3.0	21
Left marginal rows, number	3.9	4.0	0.9	0.2	22.9	2.0	6.0	27
Left marginal row 1, cirri number	25.4	25.0	4.1	0.8	16.1	18.0	34.0	27
Left marginal row 2, cirri number	30.5	31.0	3.3	0.6	10.7	25.0	38.0	27
Left marginal row 3, cirri number	26.8	27.0	5.4	1.1	20.2	10.0	36.0	25
Left marginal row 4, cirri number	22.5	26.0	7.9	1.9	35.4	7.0	33.0	17
Left marginal row 5, cirri number	22.4	22.0	6.5	2.4	28.9	15.0	32.0	7
Right marginal rows, number	2.1	2.0	–	–	–	2.0	3.0	28
Right marginal row 1, cirri number	36.9	38.0	4.1	0.8	11.2	27.0	43.0	29
Right marginal row 2, cirri number	19	19.0	5.5	1.0	28.8	7.0	28.0	29
Right marginal row 3, cirri number	8.0	9.0	2.6	1.5	33.1	5.0	10.0	3
Dorsal kineties, number	4.2	4.0	–	–	–	4.0	5.0	21
Dorsal kinety 1, kinetid number	18.3	19.0	3.3	0.7	18.0	8.0	24.0	21
Dorsal kinety 2, kinetid number	22.4	22.0	4.0	0.9	18.0	15.0	31.0	21
Dorsal kinety 3, kinetid number	22.4	23.0	3.1	0.7	14.0	16.0	28.0	19

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Dorsal kinety 4, kinetid number	11.9	12.0	2.4	0.5	19.8	8.0	16.0	19
Dorsal kinety 5, kinetid number	3.2	3.0	1.6	0.7	51.3	2.0	6.0	5
Caudal cirri in dorsal kinety 1, number	2.9	3.0	0.8	0.2	26.5	2.0	5.0	19
Caudal cirri in dorsal kinety 2, number	2.2	2.0	1.1	0.3	48.8	1.0	5.0	17
Caudal cirri in dorsal kinety 3, number	3.1	3.0	1.0	0.3	33.7	2.0	5.0	15

[a] Data based, if not stated otherwise, on cultivated, protargol-impregnated (FOISSNER's method), and randomly selected specimens. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard deviation of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Four in one out of 29 species investigated.

[c] Counted in middle and late dividers, where they become recognizable because they do not disintegrate into cirral anlagen.

[d] Note that the upper cirri are differentiated as "frontal cirri". First ventral row = first frontal cirrus; second ventral row = second frontal cirrus plus buccal cirrus; third ventral row = third frontal cirrus plus frontoventral cirrus; further ventral rows = all cirri on ventral side, except of transverse and pretransverse cirri.

[e] For designation of ventral rows, see figures 139b, i, z.

Table 123. Comparison of *Anatoliocirrus capari* with similar species.

Species/Authorities	Macronuclear nodules, number	Transverse cirri, number	Caudal cirri, number	Buccal cirri, number	Right marginal rows, number	Left marginal rows, number	Paroral membrane of conventional structure [a]	Cortical granules [b]
Anatoliocirrus capari	2	5	8	1	2	4	no	present
Fragmocirrus espeletiae [c]	4	3	3	3	2	2	yes	absent
Fragmocirrus terricola [c]	8	2	3	3	2	3	yes	not known
Parentocirrus hortualis [d]	7	4	3	3	1	1	yes	present
Parakahliella macrostoma [e]	11	0	5	4	2	4	yes	not known
Parakahliella haideri [f]	6	0	4	3	2	1	yes	absent
Paraurostyla weissei [g]	2	8	13	1	1	1	no	present
Paraurostyla granulifera [h]	2	7	3	1	1	1	no	present
Paraurostyla pulchra [c]	≥ 20	6	0	4	1	1	yes	not known
Paraurostyla buitkampi [e]	4	6–15	0	4	1	1	yes	absent
Paraurostyla polynucleata [i]	9	9	0	4	?	1	not known	not known
Paraurostyla coronata [j]	2	8	16	1	1	1	not known	present

[a] Conventional structure = composed of dikinetids, unconventional structure = composed of short, oblique kineties each comprising at least three basal bodies.

[b] Detailed explanation of cortical granules, see BERGER (1999).

[c] FOISSNER (2000b) and BUITKAMP (1977b).

[d] VOSS (1997).

[e] FOISSNER (1982) and BERGER et al. (1985).

[f] BERGER & FOISSNER (1989b).

[g] WIRNSBERGER et al. (1985).

[h] BERGER & FOISSNER (1989a).

[i] ALEKPEROV (1993).

[j] ARORA et al. (1999).

The sample consisted of five sub-samples taken in an area of about 100 m^2 and a depth of up to 10 cm, including the leaf and grass litter; the aqueous soil extract had a salinity of 15‰. The sample was air-dried for about four weeks and than treated with the non-flood Petri dish method, as described by FOISSNER (1987d). *Anatoliocirrus capari* appeared about one week after rewetting the sample. Some cells were isolated with a fine pipette and cultivated in 15‰ artificial sea water enriched with pieces of larva of the meal beetle (*Tenebrio molitar*). This provided flourishing cultures with many dividers.

Anatoliocirrus capari likely is a cosmopolitan and rather frequent in saline soils because we found it also in a highly saline mud sample from a river in Namibia and in a Mangrove swamp in Costa Rica. Some experiments showed that it can be grown at salinities between 0‰ and 35‰, that is, in tap water and ordinary sea water. When transferred to new culture medium, the specimens grow very fast obviously ingesting cells of the meal worms. In contrast, growth is poor in medium containing squashed wheat grains, that is, bacteria. Forms globular, smooth-walled resting cysts in old cultures.

Comparison with related species: *Anatoliocirrus capari* is difficult to identify in vivo because it belongs to a rather large group of hypotrichs having a very similar size and overall appearance as well as incomplete ventral cirral rows. However, the following combination of features, easily recognizable even in live specimens, distinguishes *A. capari* from all (Table 123): two macronuclear nodules and more than one right and left row of marginal cirri each.

Ontogenesis (Fig. 139i–z; 385j–n; Table 124): *Oral apparatus*. The new oral apparatus develops as in parakahliellid and oxytrichid hypotrichs (for an overview, see BERGER 1999). Briefly, an oral primordium originates close to the leftmost transverse cirrus and unites with primordia formed by the postoral ventral cirri (Fig. 139j–l). This results in a large, fusiform oral primordium extending from the buccal vertex to the transverse cirri. Interestingly, the primordium, where new adoral membranelles develop from anterior to posterior, as usual, remains attached to the transverse cirri until mid-division (Fig. 139r, s). The anterior portion of the primordium generates (likely 3) cirral anlagen and the anterior portion of the undulating membranes, while the posterior portion of the undulating membranes is probably produced mainly by the posterior end of the cirral anlagen. The short paroral kineties of *Anatoliocirrus capari* originate as in *Paraurostyla weissei* (BAKOWSKA & JERKA-DZIADOSZ 1978, JERKA-DZIADOSZ 1981). Briefly, a row of dikinetids is formed at the left side of the undulating membrane primordium; many disorganized basal bodies remain (Fig. 139w). Then, this dikinetidal row splits longitudinally (Fig. 139x, y): the left portion becomes the endoral membrane, while the right forms short kineties together with the scattered basal bodies of the primordium. When the buccal cavity develops, the paroral optically moves over the endoral intersecting it in mid-buccal cavity. The parental adoral zone of membranelles remains unchanged, while the buccal area, the paroral and the endoral, as well as the pharyngeal fibres are reorganized completely. The origin of the "third undulating membrane", which becomes recognizable only in post-dividers, could not be clarified. However, no special anlage is formed for this structure, supporting that it is an optical artifact as described above.

Ventral cirral pattern. Anatoliocirrus capari usually generates seven cirral anlagen streaks. One or two additional streaks of varying length may occur between anlagen III–VII. Likewise, the number of cirri generated in the anlagen IV–VII is highly variable (Table 122).

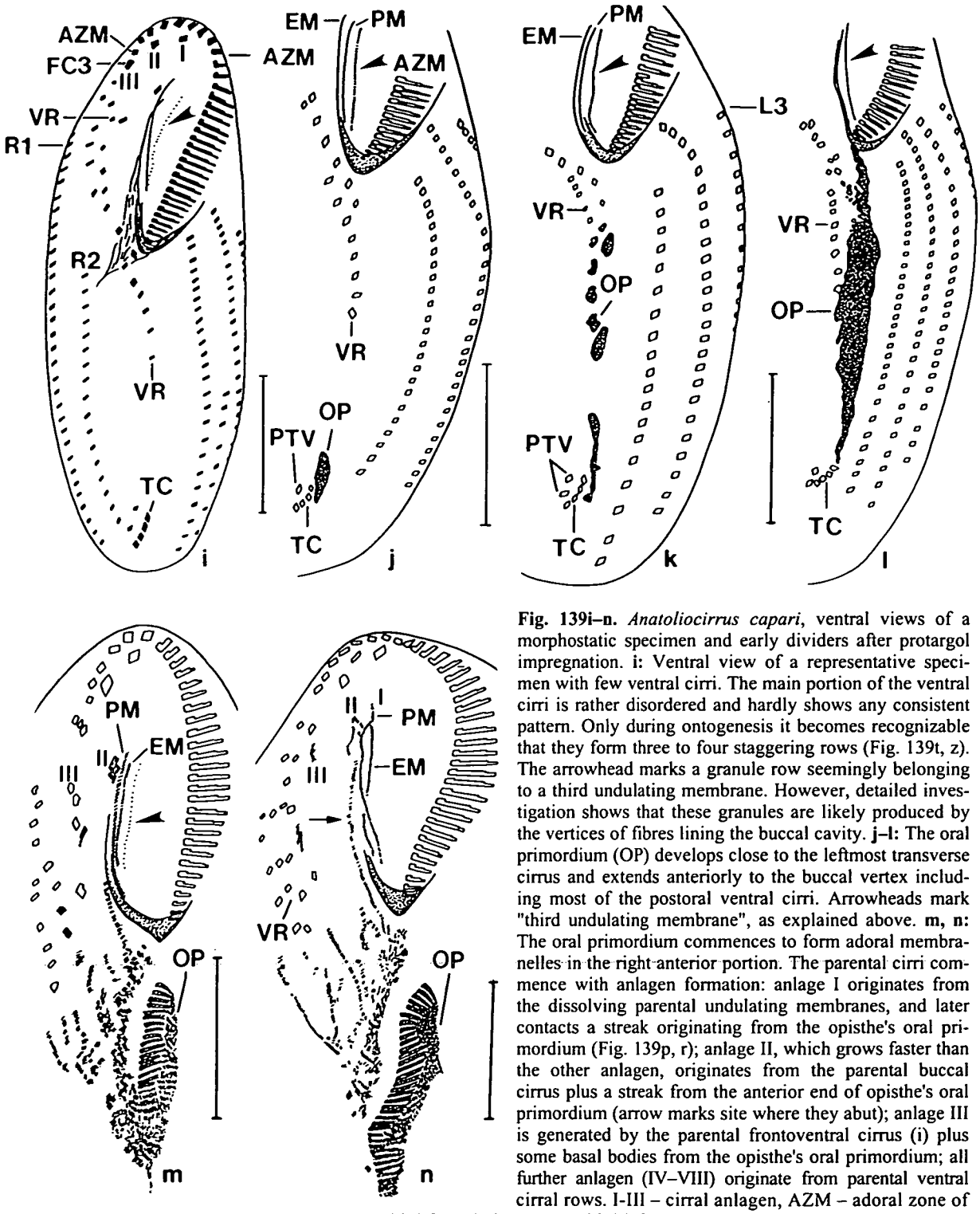
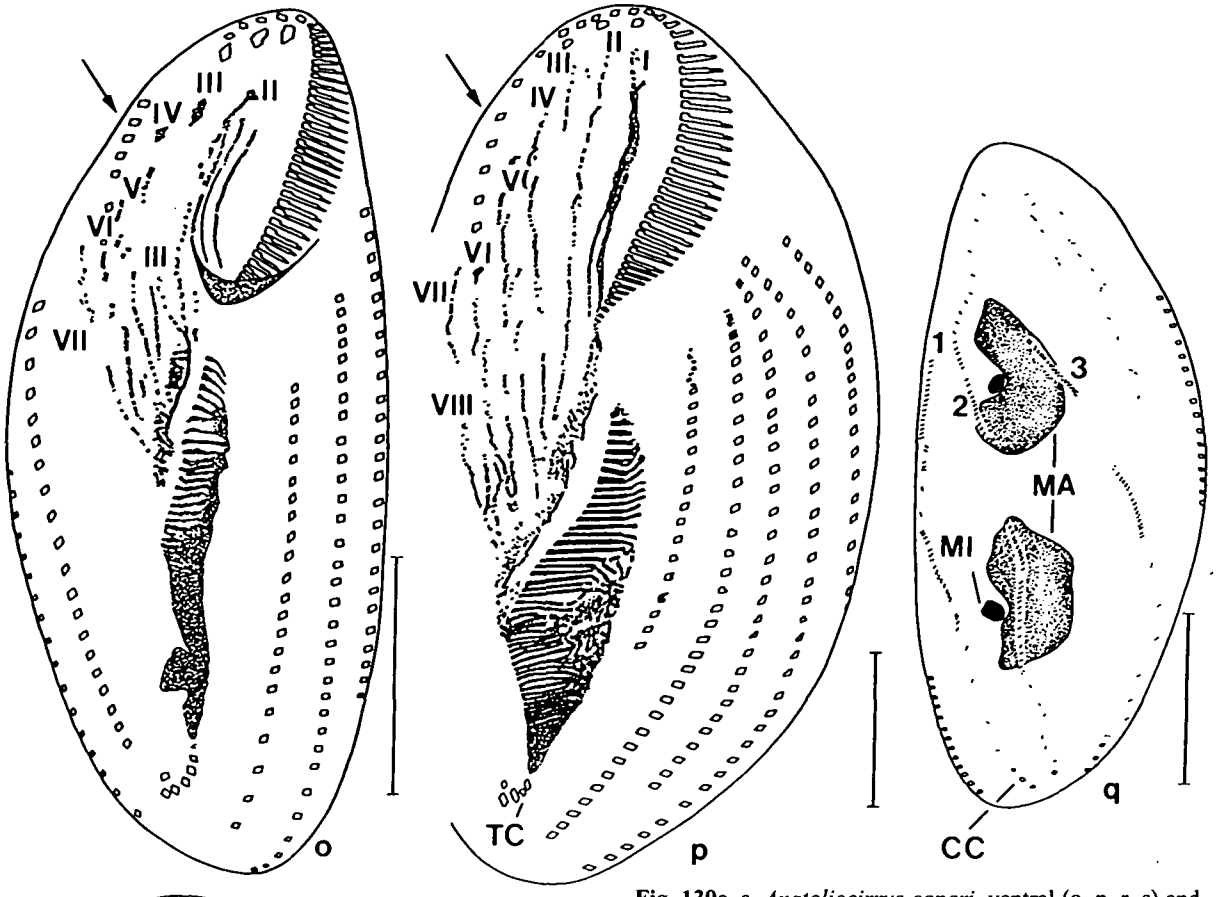


Fig. 139i–n. *Anatoliocirrus capari*, ventral views of a morphostatic specimen and early dividers after protargol impregnation. **i:** Ventral view of a representative specimen with few ventral cirri. The main portion of the ventral cirri is rather disordered and hardly shows any consistent pattern. Only during ontogenesis it becomes recognizable that they form three to four staggering rows (Fig. 139t, z). The arrowhead marks a granule row seemingly belonging to a third undulating membrane. However, detailed investigation shows that these granules are likely produced by the vertices of fibres lining the buccal cavity. **j–l:** The oral primordium (OP) develops close to the leftmost transverse cirrus and extends anteriorly to the buccal vertex including most of the postoral ventral cirri. Arrowheads mark "third undulating membrane", as explained above. **m, n:** The oral primordium commences to form adoral membranelles in the right anterior portion. The parental cirri commence with anlagen formation: anlage I originates from the dissolving parental undulating membranes, and later contacts a streak originating from the opisthe's oral primordium (Fig. 139p, r); anlage II, which grows faster than the other anlagen, originates from the parental buccal cirrus plus a streak from the anterior end of opisthe's oral primordium (arrow marks site where they abut); anlage III is generated by the parental frontoventral cirrus (i) plus some basal bodies from the opisthe's oral primordium; all further anlagen (IV–VIII) originate from parental ventral cirral rows. I-III – cirral anlagen, AZM – adoral zone of membranelles, EM – endoral membrane, FC3 – third frontal cirrus, L3 – third left marginal row, PM – paroral membrane, OP – oral primordium, PTV – pretransverse cirri, R1, 2 – first and second right marginal row, TC – transverse cirri, VR – ventral cirri. Scale bars 30 μm.



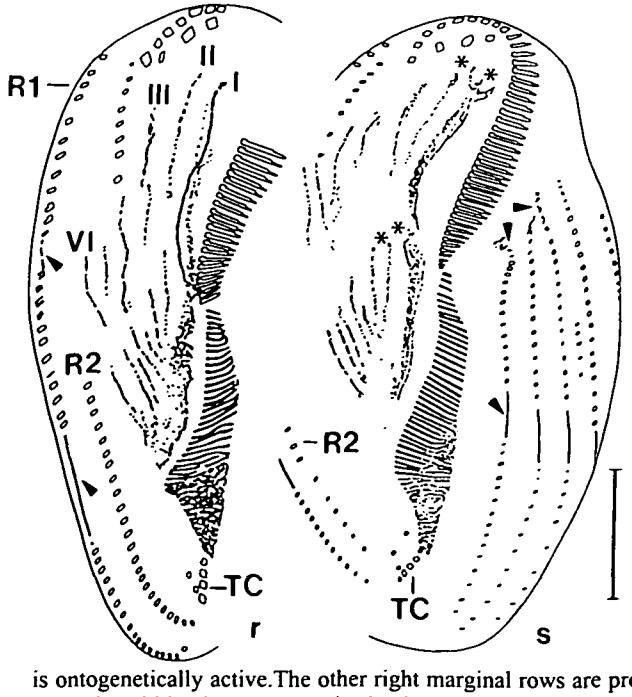
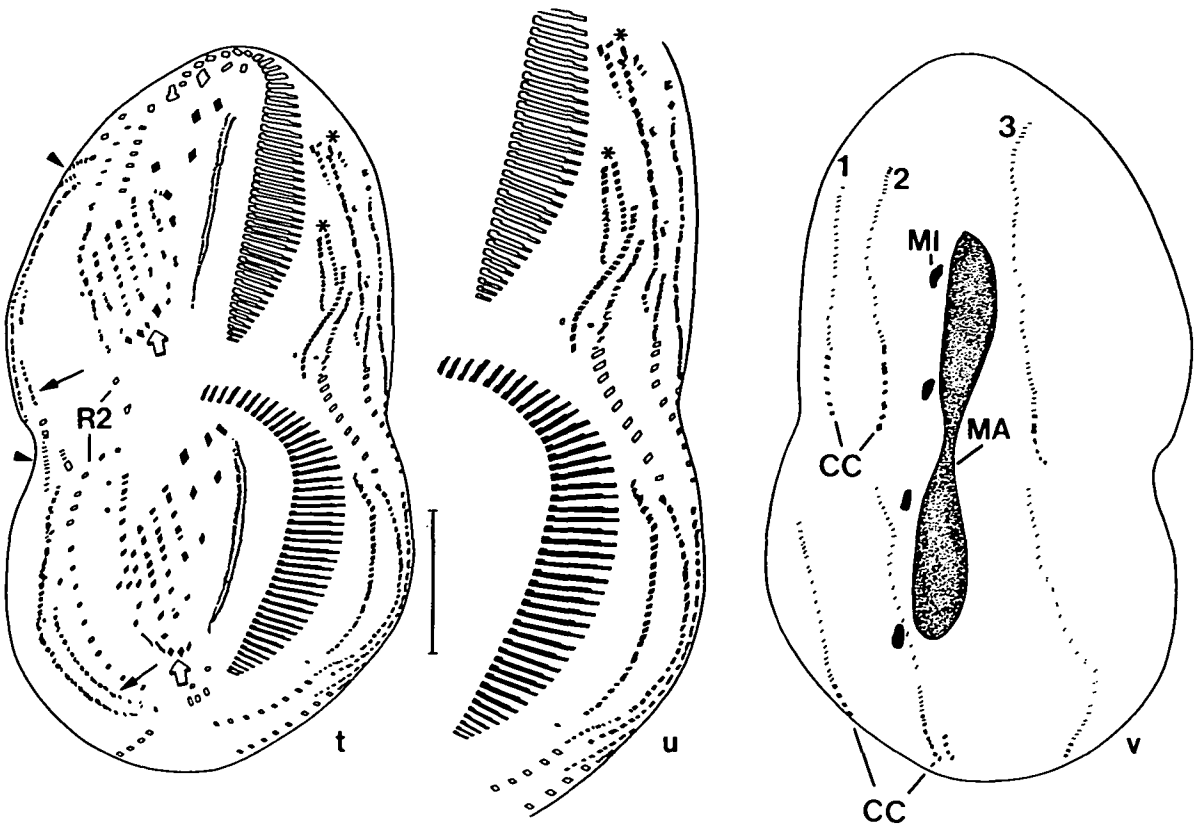


Fig. 139o–s. *Anatoliocirrus capari*, ventral (o, p, r, s) and dorsal (q) views of early-middle (o–q) and middle (r, s) dividers after protargol impregnation. Parental structures shown by contour, newly formed shaded black. The oral primordium proceeds to form adoral membranelles from anterior to posterior. **o, p:** All parental ventral cirri are modified to cirral anlagen, except of the frontoterminal cirri (arrows), forming more or less distinct, continuous streaks called primary primordia. The primary primordia are the main generic feature of *Anatoliocirrus* and are typical for neokinetal 3 (oxytrichid) anlagen development (EIGNER 1997). **q:** Dorsal ciliary rows 1–3 originate by intrakinetal proliferation of kinetids in the parental kineties. Row 4 is generated dorsomarginally (Fig. 139t). **r, s:** The opisthe's adoral zone of membranelles is almost complete. The primary primordia split transversely to form secondary primordia, that is, a set of six to eight anlagen each in proter and opisthe. Disordered basal bodies, which will become the opisthe's and proter's paroral and endoral, extend along the adoral membranellar zones; the parental adoral zone is not reorganized. New frontal cirri become visible in both daughter cells (asterisks). The marginal rows, except of the second right row, reproduce by two anlagen each within the parental rows (arrowheads). Although there are several right marginal rows, only row 1 is ontogenetically active.The other right marginal rows are produced by terminal splitting of the anlagen produced in row 1. 1-3 – dorsal kineties, I-VIII – cirral anlagen streaks, CC – caudal cirri, MA – macronuclear nodules, MI – micronucleus, R1, 2 – first and second right marginal row, TC – transverse cirri. Scale bars 30 μm.



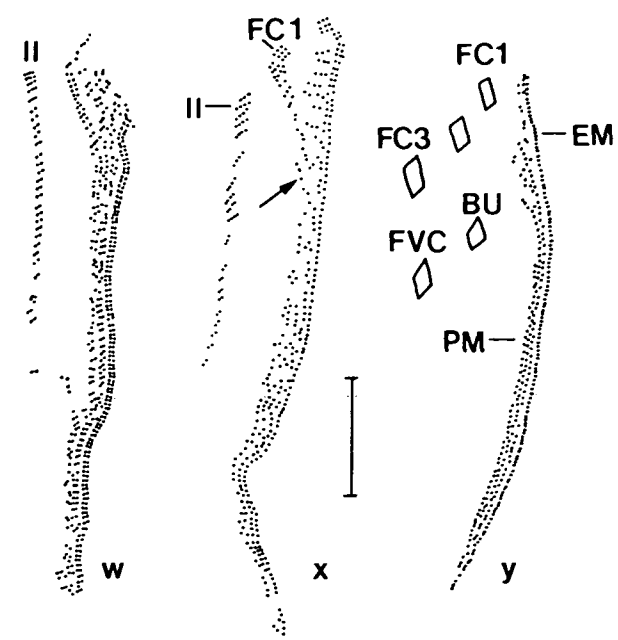


Fig. 139t–y. *Anatoliocirrus capari*, ventral (t, u) and dorsal (v) views of a late divider and formation of the paroral and endoral membrane after protargol impregnation (w–y). Figure (u) is an enlarged part of figure (t). Parental structures shown by contour, newly formed shaded black. **t, u:** The oral apparatus is almost complete in proter and opisthe. The marginal primordia split posteriorly in the first right row producing a new, shorter streak each (arrows). The parental second right marginal row (R2) is inactive and resorbed in very late dividers. Splitting of the anlagen for the left marginal rows produces the high morphostatic variability in row number (asterisks). Open arrows mark newly formed transverse cirri, which split off from anlagen IV-VII. Dorsal ciliary row 4 is generated dorsomarginally, that is, originates close to the first right marginal row (arrowheads) and then migrates dorsally. **v:** First division of the fused macronuclear mass. The micronuclei divide once. Caudal cirri are generated at posterior end of bristle rows 1-3. **w–y:** The undulating membranes (paroral and endoral) develop from an anarchic field of basal bodies, whereby the main events occur between the stages shown in figures (r) and (z), that is, middle to very late dividers. First a row of dikinetids organizes along the left margin of the anarchic field (w). This row splits longitudinally (x): the left part becomes the single-rowed endoral membrane, while the right part organizes to short, oblique paroral kineties (arrow) together with the remaining basal bodies from the anarchic field (x, y). 1-3 – dorsal ciliary rows, II – cirral anlage two, BU – buccal cirrus, CC – caudal cirri, EM – endoral membrane, FC1, 3 – first and third frontal cirrus, FVC – frontoventral cirrus, MA – macronucleus, MI – micronucleus, PM – paroral membrane, R2 – second right marginal row. Scale bars 10 μm (w–y) and 30 μm (t, v).

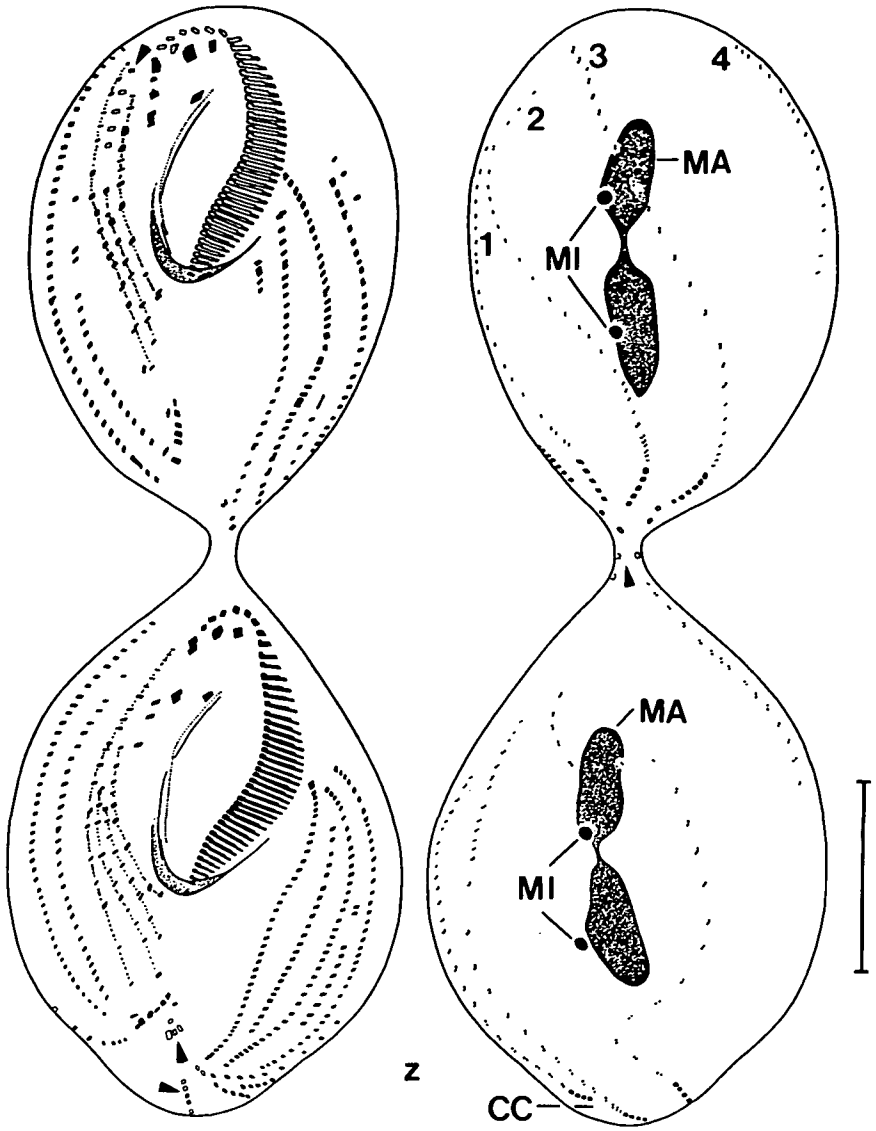


Fig. 139z. *Anatoliocirrus capari*, very late divider after protargol impregnation. Parental structures shown by contour, newly formed shaded black. All ventral cirri and the nuclear apparatus have been formed in proter and opisthe. Only now it is recognizable that the main portion of the ventral cirri forms three to four rows (connected by dots). About 30% of the newly formed ventral cirri will be reduced in post-dividers (Table 124), as are parental cirri not involved in anlagen formation (arrowheads). Note that dorsomarginal kinety 4 moved onto dorsal side. 1-4 – dorsal ciliary rows, CC – caudal cirri, MA – macronuclear nodules, MI – micronuclei. Scale bar 40 μm.

These irregularities produce part of the conspicuous variability of the cirral pattern of *Anatoliocirrus capari*. All ventral cirri are involved in anlagen formation, except of those in the anterior portion of the rightmost ventral row (Fig. 139o, p, r–t, z; 385n), which are thus highly reminiscent of oxytrichid frontoterminal cirri (BERGER 1999); they are resorbed in late dividers, and no parental cirri or dorsal bristles are transmitted to the next generation.

Anatoliocirrus is unique in developing long primary primordia (cirral anlagen), which form an extremely conspicuous, fan-like array of anlagen streaks in early and early-middle dividers (Fig. 139m–p; 385j, n). Later, the primary primordia split transversely in the middle, producing seven to eight secondary primordia, that is, cirral anlagen each in proter and opisthe (Fig. 139r, s). When ontogenesis is almost completed, cirral streaks IV–VII commence to migrate anteriorly and posteriorly, producing the irregular pattern so typical for the interphase specimens (Fig. 139t, z).

Anlage (primary primordium) I is produced by the dissolving parental undulating membranes and later contacts a streak originating from the opisthe's oral primordium. Anlage (primary

primordium) II is produced by the parental buccal cirrus and unites with an extraordinarily long streak produced from the anterior end of the oral primordium. Anlage (primary primordium) III is produced from the parental frontoventral cirrus underneath frontal cirrus 3 and a streak very likely also originating from the opisthe's oral primordium; however, we cannot exclude that this anlage also includes some ventral cirri. Anlagen (primary primordia) IV to VII all are generated from the ventral cirral rows (Fig. 139l–p; 385j–n).

When cytokinesis commences, proter and opisthe anlagen IV–VII each produce a transverse cirrus by splitting off the last cirrus of the streak; the rightmost anlage leaves 2–3 cirri to generate one to three transverse and one to two pretransverse cirri (Fig. 139t, z). Subsequently, the newly formed cirral streaks begin to migrate anteriorly and posteriorly, producing the species-specific cirral pattern. However, the final pattern is obtained only in post-dividers, where a considerable portion (about 30%) of the cirri is reduced, leaving the interphase pattern so difficult to interpret (Table 124).

Marginal cirral pattern. In middle dividers, the first right marginal row produces a primordium each in the anterior and posterior half (Fig. 139r, s). These primordia later split posteriorly, producing two streaks each, of which the longer right one becomes the new first right marginal row, while the shorter left one develops the new second right marginal row (Fig. 139t). In contrast, all left marginal rows produce an anlage each anteriorly and posteriorly. Furthermore, anlagen splitting, as described for the right row, occurs very likely too and explains the high variability in row number and number of cirri within rows (Fig. 139s–u).

Dorsal infraciliature. A primordium each develops within the proter and opisthe parental ciliary rows 1–3 (Fig. 139q, v). Row four originates dorsomarginally, that is, close to the outer marginal cirral primordium (Fig. 139t). This row migrates dorsolaterally in late dividers. Caudal cirri are produced in variable numbers only at end of rows 1–3 (Fig. 139v, z).

Nuclear apparatus. The nuclear apparatus divides as usual, that is, the macronuclear nodules first fuse to a globular mass, which later divides two times (Fig. 139v, z).

Table 124. Comparison of numbers of cirri produced by anlagen IV–VII in morphostatic and dividing specimens of *Anatoliocirrus capari*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Morphostatic specimens	30.8	27.5	8.0	1.5	26.0	17.0	56.0	28
Proter	40.9	42.0	6.6	1.7	16.1	28.0	52.0	15
Opisthe	46.6	47.0	9.8	2.5	21.0	31.0	64.0	15
Post-dividers	48.5	45.0	11.6	3.5	23.9	36.0	70.0	11

[a] Data based on protargol-impregnated specimens (WILBERT's method) from a single culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard deviation of arithmetic mean, $\bar{x}$ – arithmetic mean.

Perisincirra paucicirrata nov. spec. (Fig. 140a–g; Table 125)

Diagnosis: Size about 100 × 20 µm in vivo; elongate ellipsoidal. 2 macronuclear nodules and 1 micronucleus in between. On average 15 adoral membranelles, 9 cirri in right (marginal?) row one, and 6 in row two, 7 in left row one and 6 in row two, 1 buccal cirrus, and 2 cirri behind right frontal cirrus. 3 dorsal kineties with a caudal cirrus each.

Type location: Mud from rock-pools at the bank of the Shoalhaven River near the village of Bungonia, Australia, 35°S 149°E.

Etymology: Composite of the Latin adjectives *paucus* (few) and *cirratus* (hairy), referring to the few, widely spaced cirri.

Description: Size 70–130 × 15–30 µm, usually 90–110 µm long in vivo, only slightly flattened dorsoventrally; length:width ratio about 5:1 in vivo and 2.2–8.6, on average 4.1:1 in protargol preparations. Elongate ellipsoidal with margins slightly converging posteriorly; very flexible but acontractile (Fig. 140a–c; Table 125). Macronuclear nodules left of midline in middle body third, usually elongate ellipsoidal, rarely ellipsoidal or even globular; nucleoli small to large. Micronucleus (about 3 × 2 µm) difficult to recognize both in vivo and protargol preparations, usually one near or at posterior end of anterior macronuclear nodule and thus more or less distinctly between the two beads. Contractile vacuole without conspicuous collecting canals distinctly ahead of mid-body at left cell margin. Cortical granules lacking. Cytoplasm colourless, usually packed with highly refractive fat globules 0.5–3.0 µm across making cells dark under low magnification (×40–100) and bright field illumination; in posterior body portion usually some ordinary crystals. Feeds on fungal spores and hyphae. Swims and glides rather rapidly on microscope slide and debris, showing great flexibility.

Cirral pattern rather constant, while cirral number within rows highly variable (Fig. 140a, c; Table 125). All cirri rather long and conspicuously fine, that is, about 15 µm and composed of only two or four cilia. Invariably two rows of conspicuously widely spaced (marginal?) cirri both right and left of midline. Frontal cirri in transverse row, of about same size as other cirri. Buccal cirrus right of anterior end of paroral and ahead of endoral. Usually two, rarely three cirri or only one cirrus behind right frontal cirrus. Transverse cirri lacking. Dorsal bristles about 4 µm long in vivo, arranged in three sparsely ciliated rows each terminating with an about 22 µm long, fine caudal cirrus (Fig. 140d, f).

Adoral zone of usual shape and structure, conspicuously short occupying only 11–25%, on average 18% of body length, composed of an average of 15 membranelles about 5 µm wide in vivo and of ordinary fine structure (Fig. 140a, c, g; Table 125). Buccal cavity flat and narrow, right margin forms convex lip partially covering proximal portion of adoral zone and bearing paroral membrane composed of a 5–6 µm long, straight series of cilia decreasing in length from 5 µm anteriorly to 3 µm posteriorly; endoral membrane also more or less straight, but slightly longer than paroral, with which it forms an acute angle. Pharyngeal fibres inconspicuous, extend straight backwards.

Observations on Namibian site (64) population: The Namibian specimens are highly similar to the Australian type, but have only one (vs. two), rarely none (Fig. 140e), cirrus behind the right frontal cirrus. Furthermore, 20% of the cells have two micronuclei.

Occurrence and ecology: The type population was discovered in the black mud of rock-pools in an Australian river, where it occurred with low abundance (Fig. 140a–d, g). In Namibia, *Perisincirra paucicirrata* was rare at sites (64; Fig. 140e, f) and (70), that is, waterholes. Thus, *P. paucicirrata* probably prefers semiterrestrial habitats.

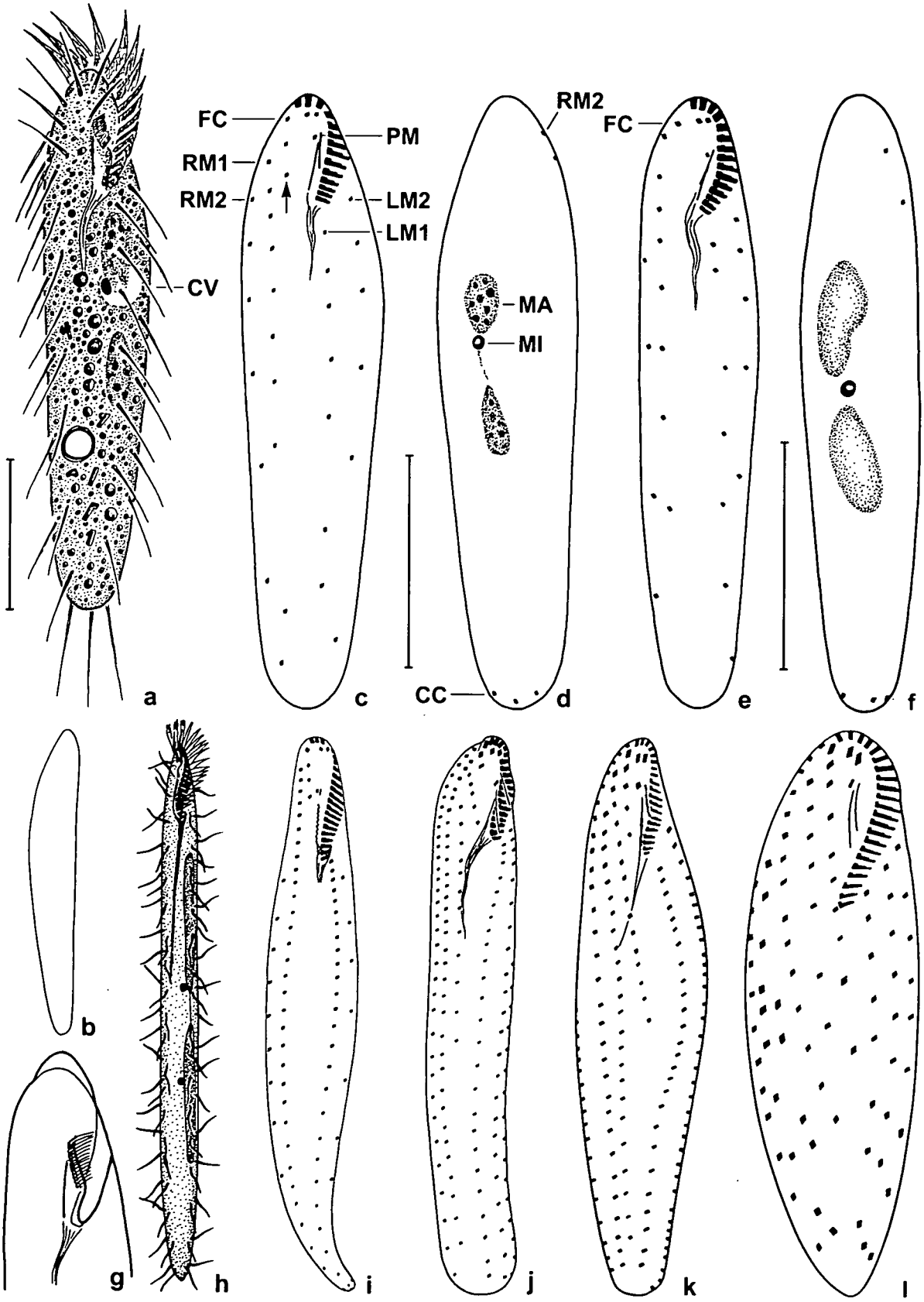
Generic classification and comparison with related species: This new species is likely related to the type of *Perisincirra*, viz., *Perisincirra kahli* (GROLIÈRE, 1975) JANKOWSKI, 1978, as indicated by the two left and right rows of rather widely spaced, long and fine cirri (Fig. 140h). Furthermore they agree in the slender shape (we also found a specimen with a length: width ratio of 8.6:1), the short adoral zone (< 20% of body length on average), the two macronuclear nodules, and the three dorsal kineties. GROLIÈRE (1975) did not mention caudal cirri; possibly he misinterpreted the posteriormost cirri of the ventral rows because the infraciliature of these slender and fragile species is difficult to analyze.

Perisincirra paucicirrata differs from the type species in body length (64–121 µm, on average 85 µm vs. 85–160 µm, on average 115 µm after protargol impregnation), length:width ratio (in protargol preparations on average 4.1:1 vs. 10:1), the lower number of adoral membranelles (13–17 vs. 18–20), and the lower number of cirri in the rows (4–12 vs. 18–20). Furthermore, the type population of *P. paucicirrata* usually has two cirri behind the right frontal cirrus; these are likely lacking in *P. kahli*, but also in the *P. paucicirrata* specimen from Namibia (Fig. 140e). → *Perisincirra longicirrata* has six (vs. four) cirral rows and a more conspicuous oral apparatus because of the higher number of adoral membranelles (21 vs. 15) and the much deeper and wider buccal cavity.

The four cirral rows and the lack of transverse and midventral cirri assign *Perisincirra* to the Kahliellidae TUFFRAU, 1979. Species of the genera *Kahliella* CORLISS, 1960 (Fig. 140j), *Engelmanniella* FOISSNER, 1982 (Fig. 140i), *Deviata* EIGNER, 1995 (Fig. 140k), and *Neogeneia* EIGNER, 1995 (Fig. 140 l) can be easily distinguished from *P. paucicirrata*, inter alia, by the higher number of cirral rows and the more tightly spaced cirri in at least some of the rows (for review, see EIGNER 1995). In vivo, *Perisincirra paucicirrata* is thus recognizable by the long, fine, widely spaced cirri; the small size (around 100 × 20 µm); and the two macronuclear nodules. Nevertheless, identifications should be checked by protargol impregnation because there are likely several other, yet undescribed species in all genera mentioned.

Fig. 140a–g. *Perisincirra paucicirrata*, Australian (a–d, g) and Namibian (e, f) specimens from life (a, b, g) and after protargol impregnation (c–f). **a:** Ventral view of a representative specimen. **b:** Right lateral view. **c, d:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrow in (c) denotes cirri behind right frontal cirrus. The dorsal bristle rows (likely three) could not be recognized unequivocally and are thus not shown (see text). **e, f:** Infraciliature of ventral and dorsal side and nuclear apparatus of two Namibian specimens, which sometimes lack cirri behind the right frontal cirrus. **g:** Oral apparatus showing paroral on buccal lip and paroral cilia decreasing in length from anterior to posterior. CC – caudal cirri, CV – contractile vacuole, FC – right frontal cirrus, LM1, 2 – left cirral rows, MA – macronuclear nodule, MI – micronucleus, PM – paroral membrane, RM1, 2 – right cirral rows. Scale bars 30 µm.

Fig. 140h–l. Ventral side of protargol-impregnated *Perisincirra kahli* (**h**; from GROLIÈRE 1975; length 130 µm), *Engelmanniella mobilis* (**i**; from FOISSNER 1982; length 98 µm), *Kahliella bacilliformis* (**j**; from BERGER & FOISSNER 1987; length 121 µm), *Deviata abbrevescens* (**k**; from EIGNER 1995; length 128 µm), and *Neogeneia hortualis* (**l**; from EIGNER 1995; length 98 µm).


FC
PM
RM1
RM2
LM2
LM1
CV
MA
MI
CC
a
b
c
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g
h
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Table 125. Morphometric data on *Perisincirra paucicirrata* (PP) and *P. longicirrata* (PL).

Characteristics[a]	Species	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	PP	84.8	87.0	13.3	3.0	15.7	64.0	121.0	20
	PL	71.2	70.0	9.1	2.3	12.8	53.0	92.0	16
Body, width	PP	21.9	22.0	3.9	0.9	17.7	14.0	32.0	19
	PL	33.0	32.0	5.8	1.4	17.5	24.0	50.0	16
Body length:width, ratio	PP	4.1	3.9	1.3	0.3	32.6	2.2	8.6	19
	PL	2.2	2.2	0.3	0.1	11.5	1.8	2.6	16
Anterior body end to rear end of adoral zone, distance	PP	14.8	15.0	1.0	0.2	7.0	13.0	16.0	19
	PL	25.9	25.5	3.3	0.8	12.8	22.0	32.0	16
Body length:length of adoral zone, ratio	PP	5.8	5.8	1.3	0.3	21.9	4.0	9.3	19
	PL	2.8	2.7	0.4	0.1	13.2	2.3	3.5	16
Anterior body end to buccal cirrus, distance	PP	5.8	6.0	0.7	0.2	12.5	5.0	7.0	17
	PL	13.2	14.0	2.2	0.6	16.7	10.0	18.0	15
Anterior body end to first macronuclear nodule, distance	PP	23.1	24.0	4.1	0.9	17.8	16.0	31.0	19
	PL	18.3	18.0	3.1	0.8	17.1	14.0	24.0	16
Macronuclear nodules, distance in between	PP	6.2	6.0	3.1	0.7	50.5	2.0	14.0	19
	PL	7.2	8.0	3.4	0.9	47.4	1.0	12.0	16
Anterior macronuclear nodule, length	PP	12.8	12.0	2.6	0.6	20.1	10.0	19.0	19
	PL	15.4	14.0	2.5	0.6	16.3	12.0	21.0	16
Anterior macronuclear nodule, width	PP	4.1	4.0	1.0	0.2	25.3	2.5	6.0	19
	PL	6.6	6.5	1.1	0.3	16.4	5.0	9.0	16
Posterior macronuclear nodule, length	PP	12.3	12.0	2.0	0.5	16.0	9.0	17.0	19
	PL	14.5	14.5	1.9	0.5	13.3	11.0	17.0	16
Posterior macronuclear nodule, width	PP	3.4	3.0	0.8	0.2	23.1	2.5	6.0	19
	PL	6.4	6.0	1.2	0.3	18.9	5.0	10.0	16
Anterior body end to paroral membrane, distance	PP	5.1	5.0	0.8	0.2	15.8	4.0	6.0	15
	PL	11.4	10.5	2.4	0.7	21.4	8.0	16.0	14
Anterior body end to endoral membrane, distance	PP	6.5	6.0	0.7	0.2	10.2	6.0	8.0	13
	PL	15.2	14.0	2.6	0.7	17.1	12.0	20.0	15
Paroral membrane, length	PP	5.5	5.0	–	–	–	5.0	6.0	11
	PL	8.3	8.0	1.5	0.4	18.7	5.0	11.0	12
Endoral membrane, length	PP	6.8	7.0	–	–	–	6.0	8.0	12
	PL	9.8	10.0	1.5	0.4	15.2	7.0	12.0	13
Macronuclear nodules, number	PP	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
	PL	2.0	2.0	0.0	0.0	0.0	2.0	2.0	16
Anterior micronucleus, length	PL	3.0	3.0	–	–	–	2.5	4.0	15
Anterior micronucleus, width	PL	2.7	2.5	–	–	–	2.0	4.0	15
Micronuclei, number	PP	1.0	1.0	0.0	0.0	0.0	1.0	1.0	5
	PL	1.9	2.0	–	–	–	1.0	2.0	16
Adoral membranelles, number	PP	15.2	15.0	1.0	0.2	6.8	13.0	17.0	19
	PL	21.0	21.0	1.0	0.3	4.9	18.0	22.0	16
Frontal cirri, number	PP	3.0	3.0	0.0	0.0	0.0	3.0	3.0	17
	PL	3.0	3.0	0.0	0.0	0.0	3.0	3.0	16
Cirri behind right frontal cirrus, number	PP	2.0	2.0	–	–	–	1.0	3.0	18
	PL	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Buccal cirri, number	PP	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
	PL	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15

(continued)

Characteristics[a]	Species	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Cirral rows right of midline, number	PP	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
	PL	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13
Cirral rows left of midline, number	PP	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
	PL	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13
Right cirral row 1, number of cirri	PP	8.9	9.0	1.8	0.4	19.7	5.0	12.0	18
	PL	10.5	11.0	1.5	0.4	14.4	7.0	12.0	13
Right cirral row 2, number of cirri	PP	6.3	7.0	1.2	0.3	19.5	4.0	8.0	18
	PL	11.9	12.0	1.3	0.4	11.1	9.0	14.0	13
Right cirral row 3, number of cirri	PL	11.6	12.0	2.3	0.6	20.0	7.0	16.0	13
Left cirral row 1, number of cirri	PP	5.7	6.0	1.5	0.4	26.7	3.0	9.0	18
	PL	7.7	7.0	2.5	0.8	33.3	5.0	14.0	9
Left cirral row 2, number of cirri	PP	6.5	7.0	1.0	0.2	15.4	5.0	8.0	17
	PL	8.1	8.0	1.7	0.5	21.0	4.0	10.0	11
Left cirral row 3, number of cirri	PL	7.2	7.0	2.0	0.6	28.4	3.0	10.0	13
Caudal cirri, number	PL	3.0	3.0	0.0	0.0	0.0	3.0	3.0	12
Dorsal kineties, number	PL	4.0	4.0	0.0	0.0	0.0	4.0	4.0	10

[a] Data based on mounted, protargol-impregnated (DIECKMANN's, respectively, FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Perisincirra longicirrata nov. spec. (Fig. 141a–e; Table 125)

Diagnosis: Size about 80 × 30 µm in vivo; elongate ellipsoidal to bluntly fusiform. 2 macronuclear nodules with a micronucleus each. On average 21 adoral membranelles, about 12 cirri each in the three (marginal?) rows right of midline and about 8 cirri each in the three rows left of midline, 1 buccal cirrus, 1 cirrus behind right frontal cirrus, and 3 caudal cirri. Cirri widely spaced and fine, but up to 30 µm long.

Type location: Red, hard, sandy soil (pH 7.3) with some litter and roots from the University Campus in Abomey-Calavi, Benin, 06°27'N 02°21'E.

Etymology: Composite of the Latin adjectives *longus* (long) and *cirratus* (hairy), referring to the long cirri.

Description: Size 60–100 × 20–40 µm in vivo, usually around 80 × 30 µm, only slightly flattened dorsoventrally; length:width ratio about 2.8:1 in vivo and 1.8–2.6:1, on average 2.2:1 in protargol preparations, where specimens are usually slightly inflated. Outline elongate elliptical to bluntly fusiform with anterior region slightly more narrowed than indistinctly pointed posterior; very flexible but acontractile (Fig. 141a–c; Table 125). Macronuclear nodules left of midline in central quarters of cell, usually ellipsoidal, rarely almost globular or elongate ellipsoidal; nucleoli small and globular. Usually one globular, compact micronucleus attached to each macronuclear nodule at various positions. Contractile vacuole without distinct collecting canals near mid-body at left cell margin. Cortical granules lacking. Cytoplasm colourless, usually packed with highly refractive fat globules 1–6 µm

across, except in buccal field, making cells dark under low magnification and bright field illumination; crystals sparse or lacking. Feeds on about 10 × 6 µm-sized heterotrophic flagellates (*Polytoma* sp.). Rotates and glides rather rapidly on microscope slide and debris showing great flexibility.

Cirral pattern rather constant, while cirral number within rows highly variable (Fig. 141a, d; Table 125). Invariably three posteriorly more or less distinctly curved rows of conspicuously widely spaced (marginal?) cirri both right and left of midline. Frontal cirri 20–30 µm long in vivo and composed of up to 3 × 4 basal bodies, that is, slightly longer and distinctly larger than other cirri, which are 15–25 µm (posteriorly also up to 30 µm) long and likely composed of 2 × 2 or 2 × 3 basal bodies only. Buccal cirrus ahead of endoral and slightly behind anterior end of paroral membrane. Invariably one cirrus behind right frontal cirrus. Transverse cirri lacking.

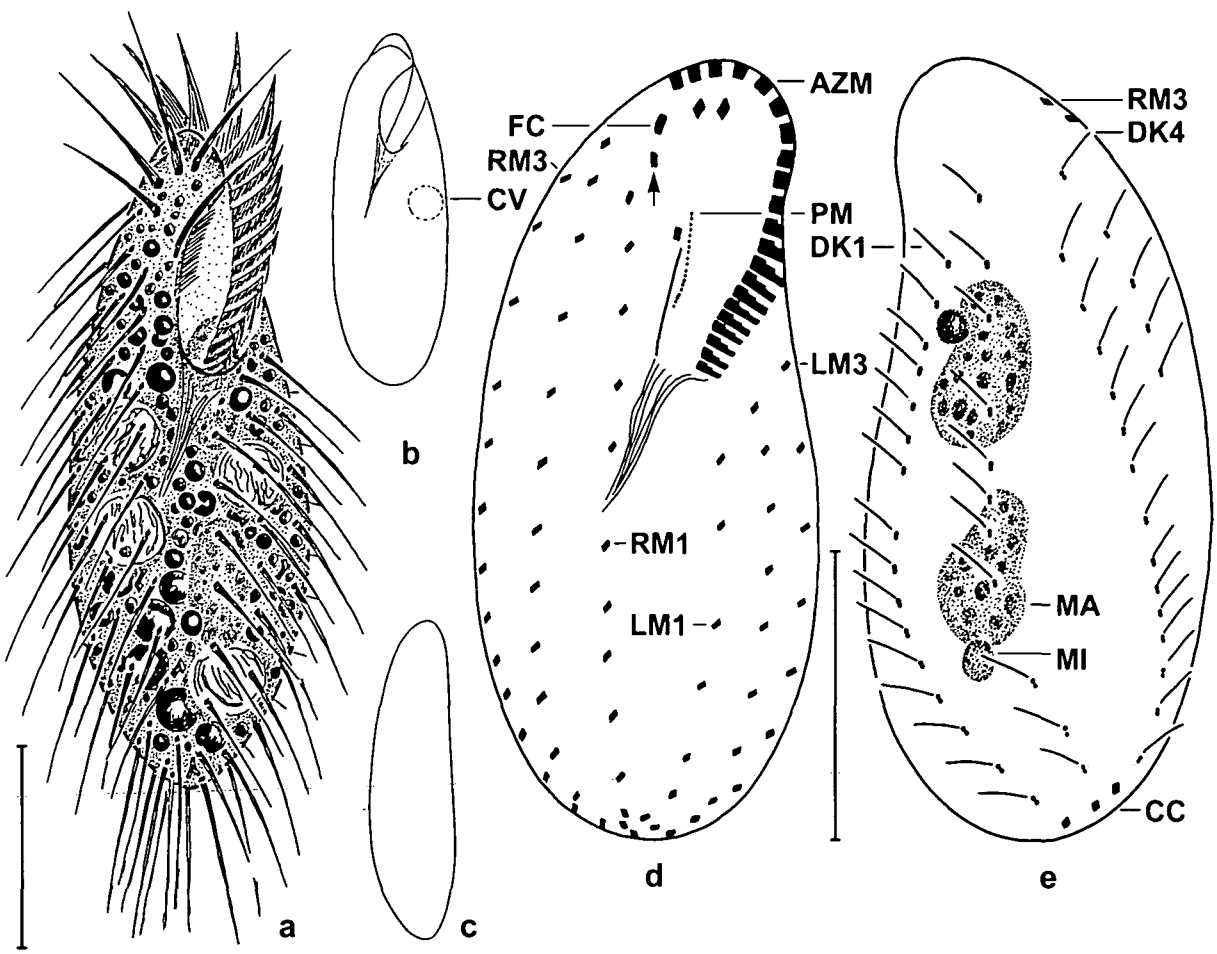

Fig. 141a–e. *Perisincirra longicirrata* from life (a–c) and after protargol impregnation (d, e). **a:** Ventral view of a representative, bluntly fusiform specimen. **b:** Ventral view of an ellipsoidal specimen showing the contractile vacuole and the wide buccal field. **c:** Lateral view showing that *P. longicirrata* is only slightly flattened dorsoventrally. **d, e:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrow in (d) denotes cirrus behind right frontal cirrus. AZM – adoral zone of membranelles, CC – caudal cirri, CV – contractile vacuole, DK1, DK4 – dorsal kineties, FC – right frontal cirrus, LM1, LM3 – cirral rows left of midline, MA – macronuclear nodule, MI – micronucleus, PM – paroral membrane, RM1, RM3 – cirral rows right of midline. Scale bars 25 µm.

Dorsal bristles about 5 µm long in vivo, arranged in four rows (Fig. 141e). All rows more or less distinctly shortened anteriorly, rows 1–3 each terminating with a 20–30 µm long caudal cirrus; row 4 likely a dorsomarginal kinety because ending above mid-body.

Oral apparatus gonostomoid, that is, adoral zone extends straight along left body margin, performing right bend and slight clockwise rotation to plunge into buccal cavity slightly above mid-body. Adoral zone occupies 29–44%, on average 37% of body length, composed of an average of 21 membranelles with bases of largest membranelles up to 5 µm wide and of ordinary fine structure (Fig. 141a, d). Buccal cavity rather deep and wide and conspicuously soft; right margin without lip, distinctly curved, extends from left end of frontal scutum to near proximal end of adoral zone of membranelles. Paroral on right margin of buccal cavity, almost straight or slightly curved, composed of an 8 µm long series of about 20, in vivo circa 5 µm long cilia; endoral about 10 µm long, begins about 4 µm ahead of paroral and extends to mid of buccal cavity. Pharyngeal fibres extend obliquely backwards.

Occurrence and ecology: To date found at type location and at Namibian site (73). The species was rare at both sites. The meaning of the extremely long cirri, compared to body size, is obscure, especially when considering that only 8 µm long cirri are obviously sufficient for the large → *Amphisiella multinucleata*.

Generic classification and comparison with related species: This species is likely closely related to → *Perisincirra paucicirrata*, as indicated by the rows of widely spaced, long and fine cirri and the caudal cirri at the end of dorsal kineties 1–3. It differs from both congeners, *Perisincirra kahli* (GROLIÈRE, 1975) JANKOWSKI, 1978 (type of *Perisincirra*) and → *P. paucicirrata*, inter alia, in body shape (ratio of body length to width about 2.8:1 vs. 4.1–10:1), the number of cirral rows (six vs. four), and the much deeper and wider buccal cavity making the oral apparatus conspicuous.

The overall appearance of *P. longicirrata* is reminiscent of *Kahliella* spp. because of the rather high number of cirral rows and the gonostomoid oral apparatus. However, *Kahliella* species have more closely spaced cirri in at least two of the rows and lack caudal cirri (BERGER & FOISSNER 1987, EIGNER 1995, HORVÁTH 1932). *Neogeneia hortualis* EIGNER, 1995 has also rather widely spaced cirri in most rows; however, it possesses a distinctly higher number of cirral rows (11–13 vs. 6), only two dorsal kineties (vs. four), and only one caudal cirrus (vs. three; Fig. 140 l). *Parastrongylidium* species, which also have a rather similar size and overall appearance, possess a moniliform macronucleus, more cirral rows (11–13 vs. 6) and cirri per row, one dorsal kinety, and lack caudal cirri (AESCHT & FOISSNER 1992, FLEURY & FRYD-VERSAVEL 1984). In vivo, *Perisincirra longicirrata* is recognizable by the small size (≤ 100 µm), the rather conspicuous buccal cavity and, especially, the six rows of widely spaced, long and fine cirri. Identifications should be checked by protargol impregnation because there are several, as yet undescribed similar species and the species is easily confused with → *Perisincirra paucicirrata*.

In Venezuela, we found a rather similar species. However, its cirri and dorsal bristles are shorter (about 12 µm, respectively, 2.5 µm vs. 15–30 µm, respectively, 5 µm), the paroral is shorter and composed of slightly wider spaced cilia, and the buccal field is more narrow and flat. These differences indicate that the African and South American populations are different at, at least, subspecies level.

Wallackia bujoreani (LEPSI, 1951) BERGER & FOISSNER, 1989 (Fig. 142a–g, 143a–p; 398 l)

The Namibian site (71) population of *W. bujoreani* is highly similar to the original description (LEPSI 1951; Fig. 142d; 398 l) and the redescription by BERGER & FOISSNER (1989a), who neotypified the species (Fig. 142b, c). Even minor features, such as the slight posterior shortening of the right marginal row, the anterior shortening of cirral row 4, and the irregularly shaped cytoplasmic crystals are found in the Namibian specimens. Thus, a redescription is not necessary. There are, however, a few differences and additional observations, which should be mentioned.

Shape highly variable, as shown in figures 142a, e, f and indistinguishable from that of *Gonostomum affine*. Cortex glassy and distinctly crenated along cirral rows; dorsal bristles about 4 µm long and originating in conspicuous pits (vacuoles?) about 2 µm across (Fig. 142f). Both features are very likely caused by the highly saline environment, as indicated by the dorsal bristles, which appear as is usual in protargol preparations. A further peculiarity caused by the high salinity, respectively, the glassy cortex, concerns the cortical granules, which are, although rather large, almost invisible in live specimens. Fortunately, they impregnate strongly with protargol. However, in the specimens from the non-saline site (49), they do not impregnate but stand out as white rods from the brownish cytoplasm. Food vacuoles 4–5 µm across, contain bacterial residues. Cilia of paroral membrane and most cirri about 10 µm long in vivo, anterior frontal cirri and caudal cirri about 15 µm long. Transverse cirri as indistinct as in Corsican neotype population. No elongated dorsal bristles at posterior body end, which is an important difference to the freshwater species *W. schiffmanni* FOISSNER, 1976 (Fig. 142g).

Occurrence and ecology: LEPSI (1951) discovered *W. bujoreani* in arable soil from Romania. The neotype population occurred in a sandy, brown soil (pH 4.1) near a stream in Corsica (BERGER & FOISSNER 1989a). In Namibia, *Wallackia bujoreani* was found at the highly saline sites 54, 59, 60, 71, having pH values between 8 and 9, but also in the non-saline sample from site (49). Thus, *Wallackia bujoreani* is euryhaline and very likely cosmopolitan, inhabiting such different biotopes as arable soils and saline steppes.

Ontogenesis: Ontogenesis was studied in the excellently prepared specimens from site (54). For designation of cirral rows, see figure 143a. As is usual, parental structures are shown by contour, newly formed ones are shaded black. All stages depicted were seen in at least two specimens.

Ontogenesis commences with the production of an oral primordium in the barren postoral area between the left marginal row and frontoventral cirral row 4. No parental cirri are involved (Fig. 143b). Next, adoral membranelles develop within the oral primordium from anterior to posterior and two anlagen streaks originate from the right anterior end of the oral primordium; these streaks, which still consist of few dikinetids, extend up to the level of proter's paroral membrane. The left streak is opisthe's anlage I, while the right is anlage III; anlage II is later produced from anlage I, which transforms into a long primary primordium. Concomitantly, scattered basal bodies appear between the mid-portion of the adoral zone of membranelles and frontoventral cirral row 2. These basal bodies contact neither the parental

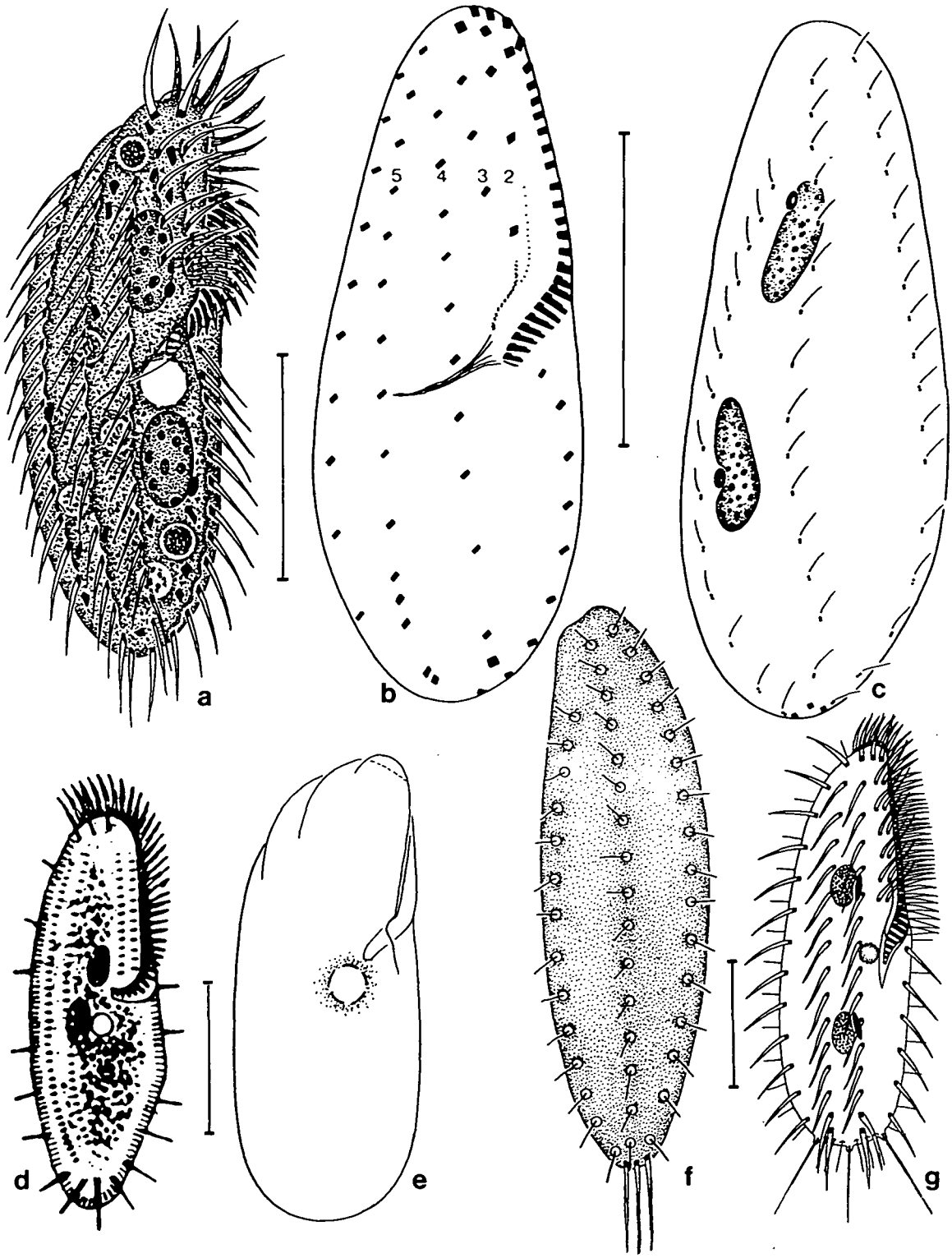

Fig. 142a–f. *Wallackia bujoreani* from life (a, d–f) and after protargol impregnation (b, c). **a:** Ventral view of a representative specimen from Namibian site (71). **b, c:** Infraciliature of ventral and dorsal side of neotype specimen from Corsica (from BERGER & FOISSNER 1989a). Numerals denote cirral rows. **d:** Figure of original description (from LEPSI 1951). **e, f:** Broad and slender shape variant from Namibia (video records). Note deep pits around dorsal bristles. **g:** *Wallackia schiffmanni* FOISSNER, 1976 differs from *W. bujoreani* mainly by the long posterior dorsal bristles. Scale bars 30 µm.

cirri nor undulating membranes and thus develop de novo (Fig. 143c). Their number increases rapidly to form a conspicuous streak, which organizes to a long row of oblique dikinetids becoming proter's anlage I (Fig. 143d–f).

The next stage is characterized by the occurrence of primordia in cirral rows 2 and 3, which change as a whole to dikinetidal anlagen streaks, and rows 4 and 5, which commence anlagen formation subequatorially and near anterior end, respectively. Furthermore, the two anlagen produced by the oral primordium organize to distinct, dikinetidal streaks, of which the left is a very long primary primordium extending into the proter oral area. Adoral membranelle formation is almost complete in the oral primordium, and the parental oral structures appear unchanged (Fig. 143e, f), although the oral area flattens and thus slightly dislocates the undulating membranes (Fig. 143g, h). The de novo-produced proter anlage 1 separates frontal cirrus 1 at its anterior end. Anlagen appear intrakinetally in the marginal rows and dorsal kineties (Fig. 143h, i). Between this and the next stage (Fig. 143j), the very long primordium (anlage 1) of the opisthe splits: the anterior third becomes opisthe's cirral streak (anlage) II, while the posterior portion will produce the opisthe's undulating membranes and frontal cirrus 1 (Fig. 143g, h, j, l).

In early-middle dividers, all cirral anlagen are recognizable, while the parental undulating membranes are still unchanged (Fig. 143j). Proter's anlagen are generated as follows: anlage I de novo; anlagen II and III develop from parental cirral rows 2 and 3, which change to cirral primordia as a whole; anlagen IV and V develop intrakinetally in parental cirral rows 4 and 5. The opisthe anlagen originate differently: anlagen I, II, and III are produced by the oral primordium, whereby anlage II is generated from a primary primordium splitting transversely[27]; anlagen IV and V develop intrakinetally in parental cirral rows 4 and 5. Marginal rows originate as is usual.

In middle dividers, the macronuclear nodules fuse to a globular mass and the parental undulating membranes disorganize. Most cirri transformed into anlagen, leaving only a few parental cirri each at anterior and posterior end of the frontoventral cirral rows and in mid body (Fig. 143k). Next, cirri commence to organize within the anlagen, and the opisthe's anlage for the undulating membranes splits longitudinally: the right row, which will become the paroral membrane, produces frontal cirrus 1 (Fig. 143 l). In the proter, new undulating membranes begin to organize: the endoral very likely develops from parental basal bodies, while the paroral originates from the posterior part of anlage I, whose anterior portion produces proter's frontal cirrus 1. Finally, two rows of slightly scattered basal bodies are recognizable in both proter and opisthe: the left row is the endoral membrane, the right the paroral (Fig. 143 l, m).

Late and very late dividers show few peculiarities (Fig. 143m–p). However, two important events occur: (i) the parental adoral zone reorganizes internally because the adoral membranelles lose row 4 and increase length of row 3 (Fig. 143m); (ii) the paroral moves over the endoral and thus the left row is now the paroral, while the right is the endoral (Fig. 143m, n). A caudal cirrus is produced at the end of each dorsal kinety (Fig. 143o). Transverse cirri are not unequivocally identifiable, but, if present, are produced by cirral rows 4 and 5 (Fig. 143n, p).

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[27] Possibly, a new term should be created because this primary primordium does not produce an anlagen streak each for proter and opisthe, as is usual, but both parts remain in the opisthe. On the other hand, the second main feature of a primary primordium, viz., that it splits transversely, is found also in *Wallackia*.

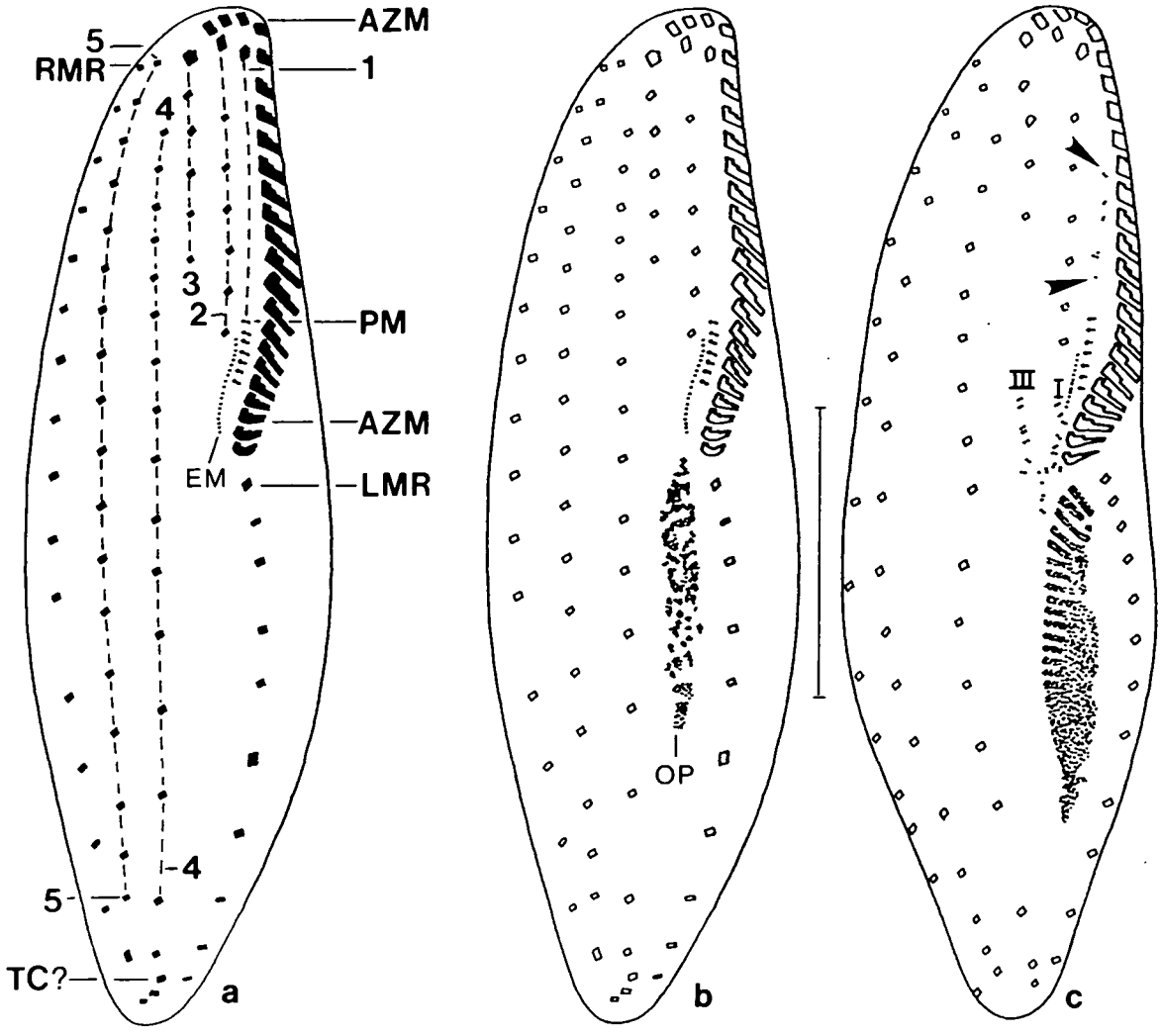

Fig. 143a–c. *Wallackia bujoreani*, ventral views of very early dividers after protargol impregnation. **a:** Terminology. The figure is the same as (b), but with the oral primordium removed. **b:** The oral primordium originates postorally in the barren area between frontoventral cirral row 4 and the left marginal row. **c:** Two anlagen streaks are produced from the right anterior end of the oral primordium, where adoral membranelles are forming. Arrowheads mark proter's anlage I, which originates de novo between the adoral zone of membranelles and frontoventral cirral row 2. AZM – adoral zone of membranelles, EM – endoral membrane, LMR – left marginal row, OP – oral primordium, PM – paroral membrane, RMR – right marginal row, TC – transverse cirri, 1–5 – frontoventral cirral rows, I, III – opisthe anlagen streaks. Scale bar 20 μm.

Ontogenetic comparison and familiar assignment: No previous data are available on the ontogenesis of *Wallackia*. Our investigations show several outstanding features. (i) The adoral membranelles are formed very early in the oral primordium. (ii) Only five cirral anlagen streaks develop (six in most oxytrichids). (iii) Proter anlage I originates de novo, while it is generated by the parental undulating membranes in all other stichotrichine hypotrichs investigated. However, the anlage forms, as in other hypotrichs, frontal cirrus 1 and the undulating membranes. (iv) The opisthe oral primordium, which develops three anlagen streaks in most (all?) stichotrichine hypotrichs, produces only two streaks. However, the left streak is a primary primordium generating a third anlage when it splits transversely.

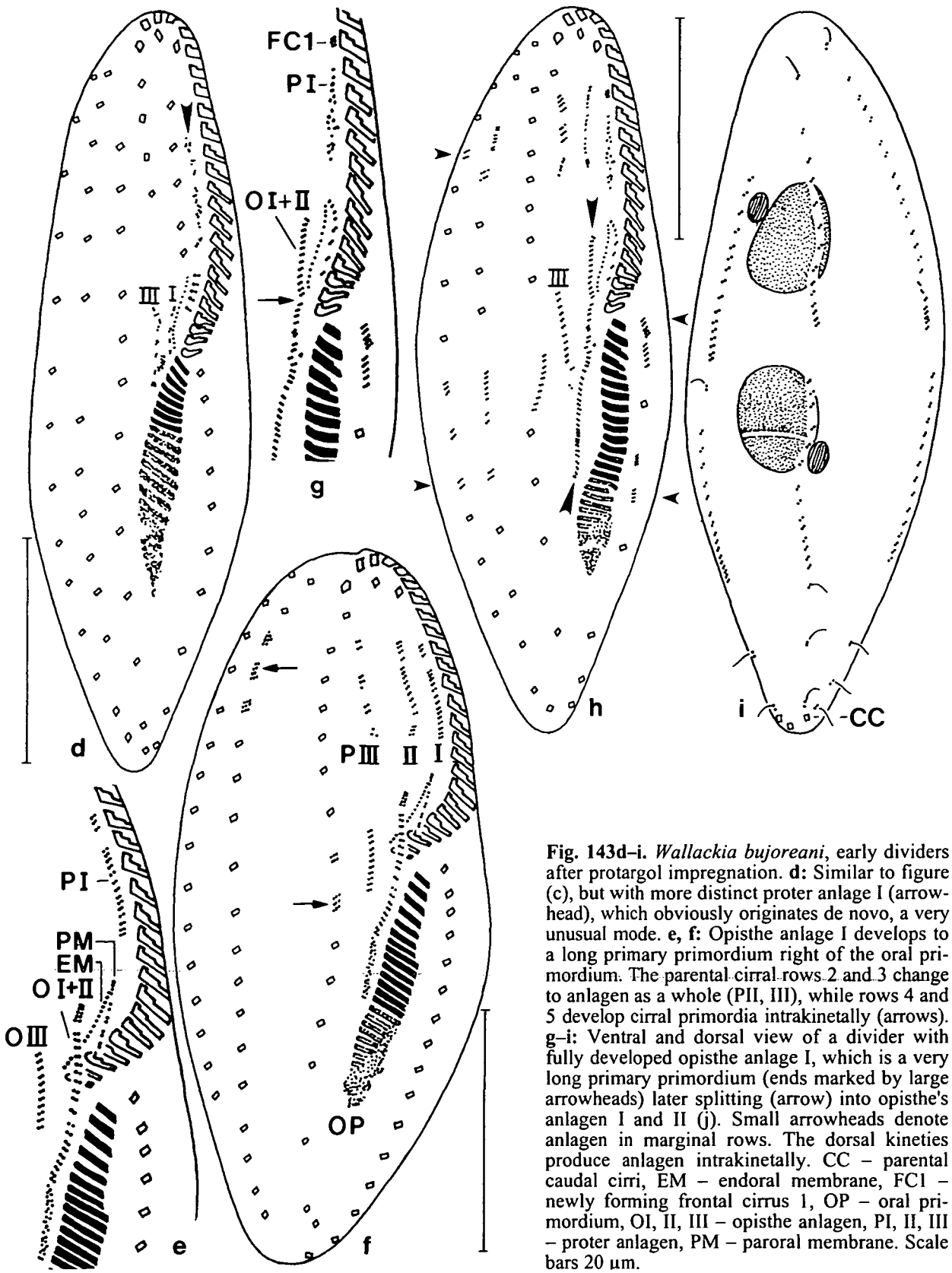

Fig. 143d–i. *Wallackia bujoreani*, early dividers after protargol impregnation. **d:** Similar to figure (c), but with more distinct proter anlage I (arrowhead), which obviously originates de novo, a very unusual mode. **e, f:** Opisthe anlage I develops to a long primary primordium right of the oral primordium. The parental cirral rows 2 and 3 change to anlagen as a whole (PII, III), while rows 4 and 5 develop cirral primordia intrakinetally (arrows). **g–i:** Ventral and dorsal view of a divider with fully developed opisthe anlage I, which is a very long primary primordium (ends marked by large arrowheads) later splitting (arrow) into opisthe's anlagen I and II (j). Small arrowheads denote anlagen in marginal rows. The dorsal kineties produce anlagen intrakinetally. CC – parental caudal cirri, EM – endoral membrane, FC1 – newly forming frontal cirrus 1, OP – oral primordium, OI, II, III – opisthe anlagen, PI, II, III – proter anlagen, PM – paroral membrane. Scale bars 20 µm.

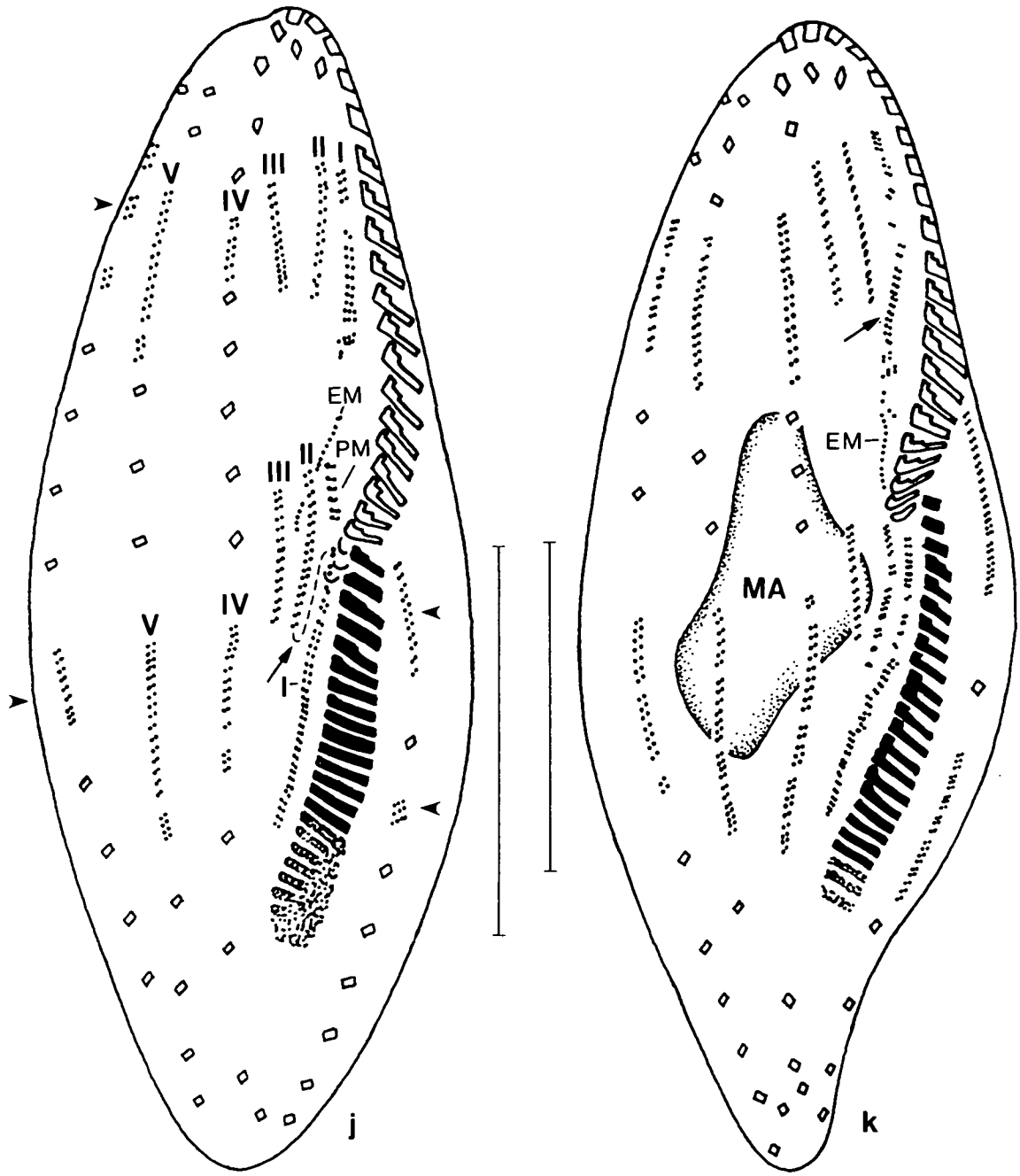

Fig. 143j, k. *Wallackia bujoreani*, ventral views of middle dividers after protargol impregnation. **j:** This specimen shows the origin of opisthe's anlage II by transverse splitting of anlage I (arrow marks dotted line connecting the fragments), which was an extraordinarily long primary primordium (Fig. 143h). The parental oral apparatus is still almost unchanged, proving that proter's anlage I originated de novo. Arrowheads mark anlagen in marginal rows. All anlagen (I–V) are now recognizable in proter and opisthe. In the proter, they were produced as follows: anlage I originated de novo and produced the first frontal cirrus and the paroral membrane; anlagen II and III originated from parental cirral rows 2 and 3, which changed to cirral primordia as a whole; anlagen IV and V originated intrakinetally from parental cirral rows 4 and 5. The opisthe anlagen originated differently: anlagen I, II and III were produced by the oral primordium, whereby anlage II was generated by a transverse split of a long primary primordium; anlagen IV and V originated intrakinetally from parental cirral rows 4 and 5. **k:** A typical middle divider with the macronuclear nodules fused to a globular mass. The parental undulating membranes are reorganizing, with the new, de novo-produced paroral in front (arrow). EM – endoral membrane, MA – fused macronuclear nodules, PM – paroral membrane, I, II, III, IV, V – proter and opisthe cirral anlagen. Scale bars 20 μm.

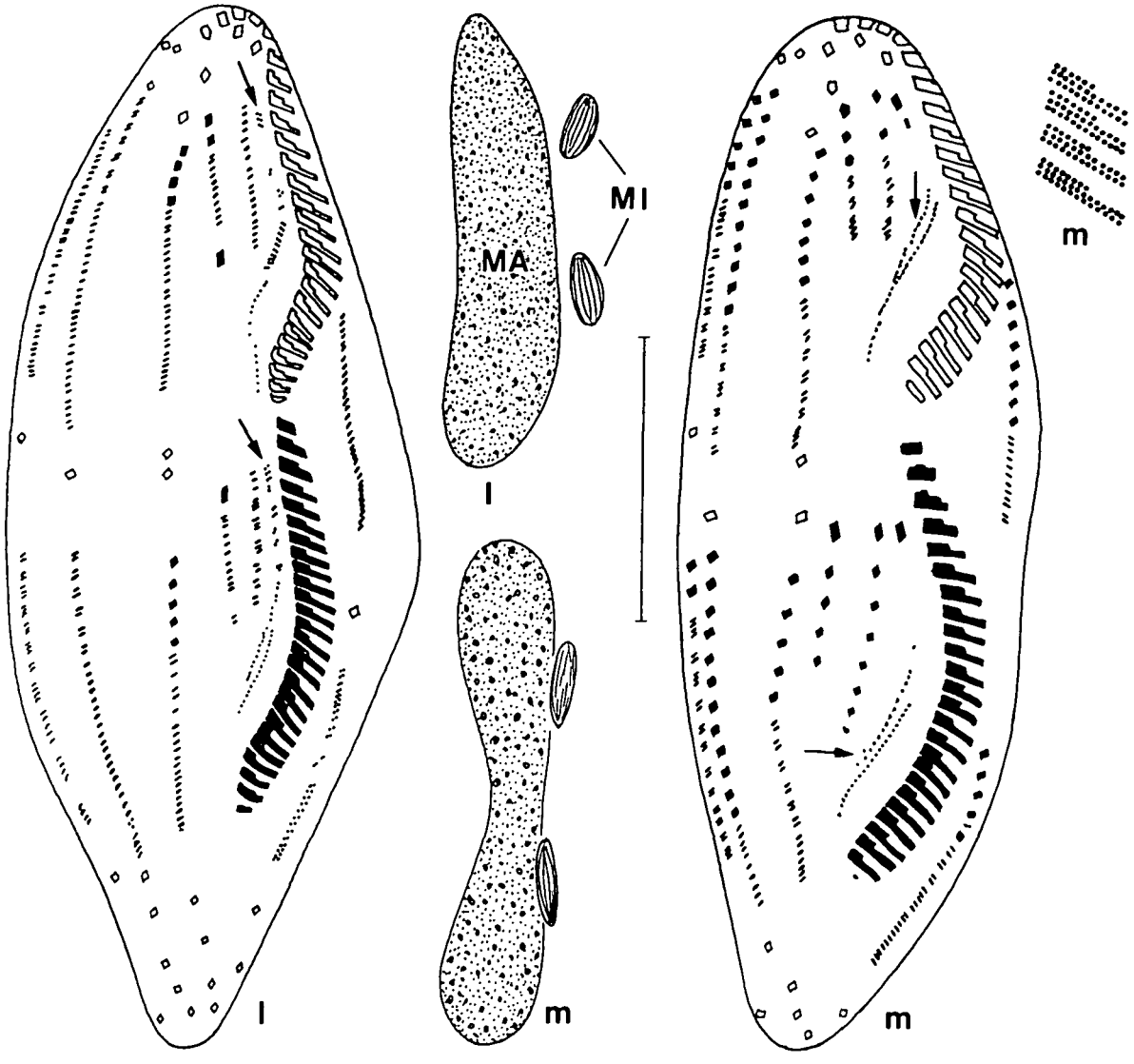

Fig. 143 l, m. *Wallackia bujoreani*, ventral views and nuclear apparatus (middle lane) of late dividers after protargol impregnation. **l:** All new adoral membranelles have been formed and cirri are now produced within the anlagen streaks. The undulating membranes are organizing and produce the first frontal cirrus in both filial products (arrows). The globular macronucleus mass elongates. **m:** Slightly later and very rapidly, the parental adoral zone performs an "internal" (without anlagen) reorganization, as evident by the changed fine structure of the membranelles (detail in right upper corner): row 4 disappeared and row 3 elongated. The new undulating membranes are now recognizable in both proter and opisthe; arrows denote the paroral, which is right of the endoral in this stage. MA – macronucleus, MI – micronuclei. Scale bar 20 µm.

This long primary primordium originates from basal bodies of the oral primordium and elongates to a conspicuous streak by proliferating basal bodies anteriorly and posteriorly. It produces opisthe's anlagen (cirral streaks) I and II, opisthe's undulating membranes, and opisthe's frontal cirrus 1.

These peculiarities show that *Wallackia* is a very distinct genus, although the interphase cirral pattern looks rather similar to that of *Kahliella* and *Orthoamphisiella*. However, *Kahliella* lacks caudal cirri and forms at least one of the ventral cirral rows neokinetally, that is, not

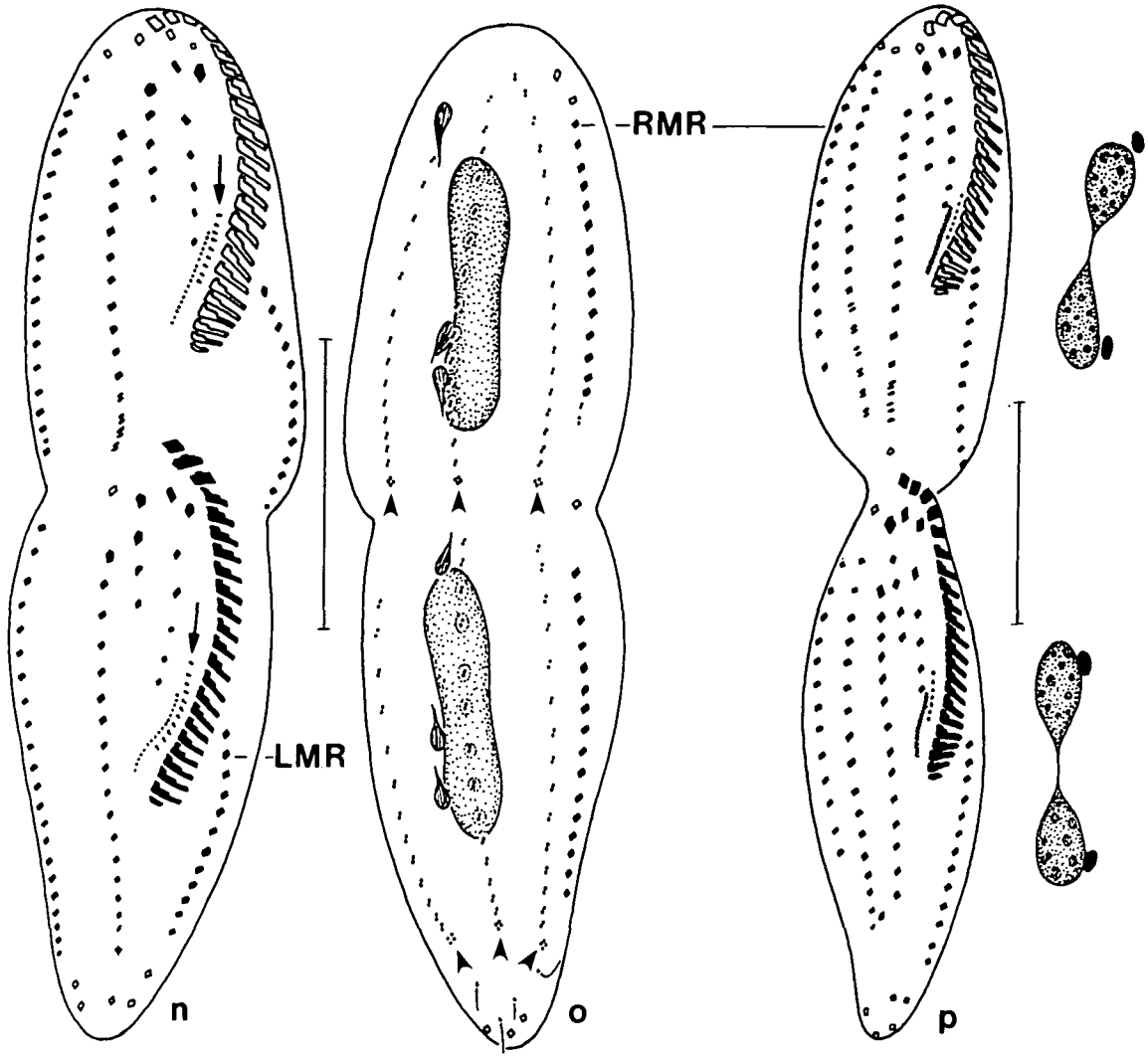

Fig. 143n–p. *Wallackia bujoreani*, ventral views of very late dividers after protargol impregnation. **n, o:** Cell division commences and formation of cirri within the anlagen is almost complete. Note that the paroral (arrows) migrated over the endoral. A caudal cirrus consisting of four cilia is formed at the end of each dorsal kinety (arrowheads). The first round of macronuclear and micronuclear division is complete. **p:** Cell elongation and shaping commence. Most cirri not involved in anlagen formation have been reduced and the second round of macronuclear division is almost complete. No distinct cirral migration is recognizable, indicating that transverse cirri are lacking; however, some migration occurs during final cell-shaping in post-dividers because cirral rows 4 and 5 extend to the posterior cell end in the interphase specimens (Fig. 143a, b). LMR – left marginal row, RMR – right marginal row. Scale bars 20 µm.

from a parental cirral row. *Orthoamphisiella* also lacks caudal cirri and produces the long ventral cirral row by a unique process, viz., from a single anlage in the mid of the row (EIGNER & FOISSNER 1991). We reinvestigated the slides of *Gonostomum franzi*, which EIGNER (1997) transferred to *Orthoamphisiella* and whose interphase cirral pattern is rather similar to that of *Wallackia*. This showed that BERGER & FOISSNER (1988b) described ontogenesis correctly. *Orthoamphisiella franzi* neither produces proter's anlage I de novo nor develops a long primary primordium in the opisthe. Accordingly, it does not belong to *Wallackia*.

The separation of *Wallackia* FOISSNER, 1976 from *Trachelochaeta* ŠRÁMEK-HUŠEK, 1954, whose ontogenesis is unknown because BERGER (1999) transferred *Trachelochaeta gonostomoida* HEMBERGER, 1985 to *Gonostomum* remains unclear. However, all differences mentioned by FOISSNER (1976) are still valid, and both type species are very likely representatives of distinct genera.

The above features make family classification of *Wallackia* difficult because it is unknown whether they are significant at genus or family level. The gross ontogenetic pattern of *Wallackia* matches the Orthoamphisiellidae, as defined by EIGNER (1997): "The Orthoamphisiellidae are unique by producing all cirral rows by within anlagen development, except those anlagen produced by the oral primordium".

Wallackia elegans nov. spec. (Fig. 144a–h, j–l; 381r; Table 126)

Diagnosis: Size about 60 × 17 µm in vivo. Lanceolate with narrowed posterior portion curved rightwards. Two closely spaced macronuclear nodules. On average 3 buccal cirri, 3 cirri in frontoventral row three, 6 cirri in frontoventral row four, 17 cirri in frontoventral row five, and 3 transverse cirri. Caudal cirri 1/3–1/2 of body length and thus very prominent. Adoral zone about 46% of body length, composed of 19 membranelles on average. Usually 10 paroral kinetids.

Type location: Mud and soil from road puddles in the Bambatsi Guest Farm, Namibia, 20°10'S 15°25'E (site 49 in figure 2 and chapter 2.1.2).

Etymology: The Latin adjective *elegans* (elegant) refers to the elegant appearance of the species.

Description of type population: Size 50–70 × 15–20 µm in vivo, length:width ratio usually 3–4:1 in vivo and after protargol impregnation (Table 126). Outline lanceolate to elongate elliptical with narrowed posterior portion usually curved rightwards; right margin thus often slightly sigmoidal and left convex; dorsoventrally flattened up to 2:1. Cells acontractile but flexible and fragile, narrowed end thus usually not recognizable in prepared specimens (Fig. 144c, d, j). Macronuclear nodules unusually arranged, that is, closely spaced with posterior nodule very near to left cell margin (Fig. 144a, d, h, k); individual nodules ellipsoidal to elongate ellipsoidal, contain numerous globular nucleoli. Micronuclei usually attached to macronuclear nodules, globular. Contractile vacuole without distinct collecting canals underneath buccal vertex at left cell margin. No cortical granules. Cytoplasm colourless, contains some yellowish, 1–3 µm-sized, highly refractive crystals mainly in posterior body portion. Feeds on bacteria digested in food vacuoles 3–5 µm across. Glides rather rapidly on microscope slide, occasionally resting for a few seconds.

Cirral pattern and number of cirri rather variable, that is, most variability coefficients > 10% (Table 126). Most cirri fine because composed of four cilia only (Fig. 144j). Marginal cirri about 8 µm long in vivo, arranged in two rows: right row begins at 10% and terminates at 78% of body length on average, left row terminates near rear end. Three inconspicuously enlarged frontal cirri arranged in typical *Gonostomum*-pattern, that is, very near to adoral zone

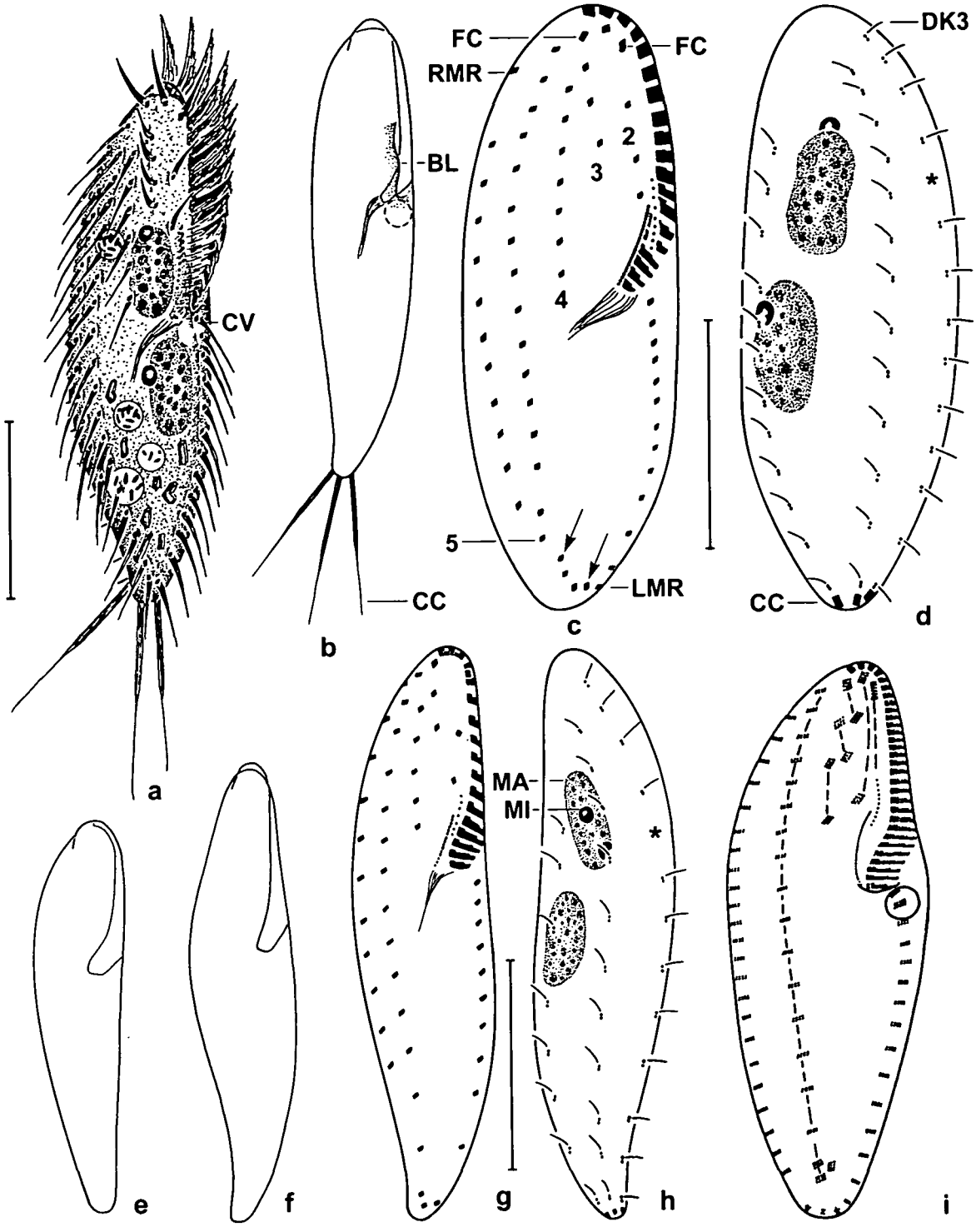

Fig. 144a–h. *Wallackia elegans*, Namibian site (49) specimens (a–e; type population) and Tenerife specimens (f–h) from life (a, b, e, f) and after protargol impregnation (c, d, g, h). **a, b:** Ventral views. **c, d, g, h:** Infraciliature of ventral and dorsal side and nuclear apparatus. Arrows mark transverse cirri. Asterisks denote gap in dorsal kinety 3. **e, f:** Shape variants. BL – buccal lip, CC – caudal cirri, CV – contractile vacuole, DK3 – dorsal kinety 3, FC – left and right frontal cirrus, LMR – last left marginal cirrus, MA – macronuclear nodule, MI – micronucleus, RMR – first right marginal cirrus, 2-5 – frontoventral rows (row 2 = row of buccal cirri). Scale bars 20 µm. **i:** *Gonostomum gonostomoida* (from HEMBERGER 1985).

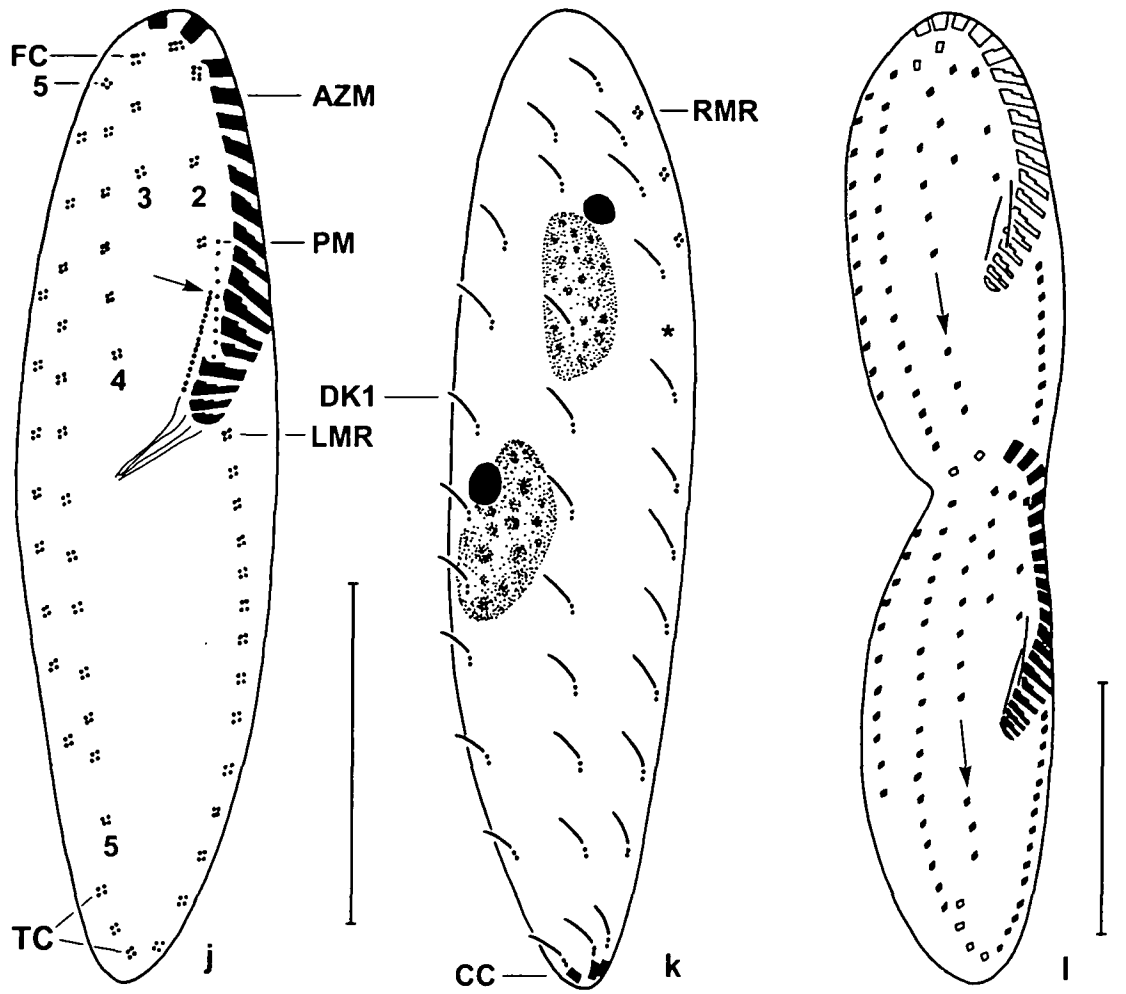

Fig. 144j–l. *Wallackia elegans*, type population after protargol impregnation. **j, k:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrow marks anterior end of endoral. Asterisk denotes break in dorsal bristle row 3. **l:** Ventral side of a late divider showing that the posterior portion of frontoventral row 4 migrates posteriad forming the transverse cirri (arrows). Parental structures shown by contour, newly formed shaded black. AZM – adoral zone of membranelles, CC – caudal cirri, DK1 – dorsal kinety 1, FC – right frontal cirrus, LMR – first cirrus of left marginal row, PM – paroral membrane, RMR – first cirrus of right marginal row, TC – transverse cirri, 2–5 – frontoventral rows. Scale bars 20 μm.

with right and middle cirrus about at same level and left cirrus slightly to distinctly shifted backwards (Fig. 144c). Invariably four frontoventral rows (numbered 2–5 in figures 1c and 1j, as proposed by BERGER & FOISSNER 1989a for *W. bujoreani*): row 2 (= buccal row) slightly longer than row 3, which terminates at 21% of body length on average; row 4 slightly shortened anteriorly, terminates at 38% of body length and is thus somewhat shorter than adoral zone (46% of body length); row 5 begins subapically, terminates at 91% of body length and is thus on average distinctly longer than right marginal row. Transverse cirri difficult to recognize in vivo and even protargol preparations because inconspicuously set off from posterior end of frontoventral row 5 (Fig. 144c, j); according to a few dividers, they originate from the posterior portion of frontoventral row 4 (Fig. 144 l).

Table 126. Morphometric data on *Wallackia elegans* from Namibian type location (upper line) and Tenerife, Canary Islands (lower line).

Characteristics[a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	53.0	53.0	4.4	1.0	8.3	44.0	62.0	21
	52.3	52.0	6.0	1.8	11.4	42.0	62.0	11
Body, width	16.0	16.0	1.8	0.4	11.0	14.0	19.0	21
	12.5	13.0	1.7	0.5	13.6	9.0	15.0	11
Body length:width, ratio	3.3	3.3	0.3	0.1	8.1	2.8	3.7	21
	4.3	4.1	0.7	0.2	16.1	3.3	6.0	11
Anterior body end to proximal end of adoral zone,	24.4	25.0	1.7	0.4	6.9	22.0	27.0	21
distance	21.1	21.0	2.1	0.6	9.8	18.0	26.0	11
Body length:length of adoral zone, ratio	2.2	2.1	0.2	0.1	10.1	1.8	2.6	21
	2.5	2.4	0.3	0.1	10.3	2.1	3.1	11
Anterior body end to paroral membrane, distance	14.4	14.0	1.8	0.4	12.3	11.0	18.0	21
	–	–	–	–	–	–	–	–
Paroral membrane, length	6.6	6.0	0.9	0.2	14.4	5.0	8.0	20
	–	–	–	–	–	–	–	–
Anterior body end to endoral membrane, distance	16.8	17.0	1.3	0.3	8.0	14.0	19.0	21
	–	–	–	–	–	–	–	–
Endoral membrane, length	7.6	8.0	0.9	0.2	11.5	6.0	9.0	21
	–	–	–	–	–	–	–	–
Anterior body end to posterior end of frontoventral	11.2	11.0	2.6	0.6	22.9	8.0	17.0	21
row 3, distance	7.7	7.0	2.1	0.6	27.8	5.0	12.0	11
Anterior body end to posterior end of frontoventral	20.5	21.0	3.1	0.7	15.1	14.0	25.0	21
row 4, distance	18.4	18.0	3.0	0.9	16.2	15.0	24.0	11
Anterior body end to posterior end of frontoventral	48.4	48.0	4.8	1.1	10.0	40.0	60.0	21
row 5, distance[b]	50.7	50.0	5.9	1.8	11.6	40.0	60.0	11
Anterior body end to right marginal row, distance	4.9	5.0	1.1	0.2	23.2	3.0	7.0	21
	–	–	–	–	–	–	–	–
Posterior body end to right marginal row, distance	11.6	10.0	5.8	1.3	50.3	4.0	26.0	21
	–	–	–	–	–	–	–	–
Anterior body end to first macronuclear nodule,	10.8	11.0	1.1	0.2	10.0	9.0	13.0	21
distance	–	–	–	–	–	–	–	–
Nuclear figure, length	22.6	23.0	2.0	0.4	8.9	18.0	26.0	21
	–	–	–	–	–	–	–	–
Macronuclear nodules, distance in between	2.6	2.5	0.9	0.2	36.1	1.0	4.0	21
	–	–	–	–	–	–	–	–
Anterior macronuclear nodule, length	10.4	10.0	1.0	0.2	9.4	9.0	13.0	21
	9.3	9.0	1.4	0.4	15.3	7.0	11.0	11
Anterior macronuclear nodule, width	4.4	4.0	0.7	0.1	15.3	3.0	6.0	21
	4.2	4.0	0.6	0.2	14.4	3.0	5.0	11
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
Anterior micronucleus, length	2.0	2.0	–	–	–	1.5	2.5	21
	2.1	2.0	–	–	–	2.0	2.2	11
Anterior micronucleus, width	1.7	1.5	–	–	–	1.5	2.0	21
	1.7	1.6	–	–	–	1.4	2.2	11
Micronuclei, number	2.0	2.0	0.3	0.1	15.8	1.0	3.0	21

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	2.1	2.0	–	–	–	2.0	3.0	11
Adoral membranelles, number	18.7	19.0	1.0	0.2	5.1	17.0	20.0	21
	16.9	16.0	1.1	0.3	6.7	16.0	19.0	11
Paroral membrane, number of cilia	9.5	9.5	1.1	0.2	11.1	8.0	11.0	20
	7.6	7.0	1.2	0.4	16.4	6.0	10.0	9
Frontal cirri, number [d]	3.0	3.0	–	–	–	2.0	4.0	21
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	6
Buccal cirri (= frontoventral row 2), number	2.8	3.0	0.9	0.2	34.2	2.0	5.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
Frontoventral row 3, number of cirri	2.9	3.0	0.9	0.2	31.9	2.0	5.0	21
	2.1	2.0	–	–	–	2.0	3.0	11
Frontoventral row 4, number of cirri	5.7	6.0	0.7	0.2	12.5	5.0	7.0	21
	5.5	5.0	0.8	0.2	15.0	5.0	7.0	11
Frontoventral row 5, number of cirri [b]	17.1	17.0	2.5	0.5	14.7	12.0	22.0	21
	16.5	16.0	2.0	0.6	12.3	14.0	21.0	11
Transverse cirri, number [c]	2.5	3.0	1.2	0.3	49.4	0.0	5.0	21
	–	–	–	–	–	–	–	–
Right marginal cirri, number	13.4	13.0	3.9	0.9	29.4	8.0	23.0	21
	11.2	11.0	1.4	0.4	12.5	9.0	14.0	11
Left marginal cirri, number	13.0	13.0	1.9	0.4	14.8	9.0	17.0	21
	10.9	11.0	1.2	0.4	11.2	9.0	13.0	11
Caudal cirri, number [e]	3.1	3.0	–	–	–	3.0	4.0	20
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
Dorsal kineties, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
Dorsal kinety 1, number of bristles	10.6	11.0	1.7	0.4	16.3	7.0	13.0	20
	–	–	–	–	–	–	–	–
Dorsal kinety 2, number of bristles	11.7	12.0	1.6	0.4	13.4	9.0	14.0	20
	–	–	–	–	–	–	–	–
Dorsal kinety 3, number of bristles	13.0	13.0	1.4	0.3	10.6	11.0	16.0	20
	–	–	–	–	–	–	–	–

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] In Tenerife specimens, transverse cirri are included.

[c] In the type population, cirri not in line with frontoventral row 5 and/or the marginal rows were counted as transverse cirri. In the population from Tenerife, these were included in frontoventral row 5.

[d] Of 21 specimens analyzed from the type population, two have two, and one has four frontal cirri.

[e] Of 20 specimens analyzed from the type population, two have four caudal cirri.

Dorsal bristles about 3 µm long in vivo, arranged in three rows (Fig. 144d, k; Table 126). Row 1 distinctly shortened, row 2 slightly shortened, and row 3 almost unshortened anteriorly; row 3 often with a slightly larger gap between fourth and fifth kinetid; each row

associated with a caudal cirrus. Caudal cirri highly conspicuous because 1/3–1/2 of body length, thicker than all other cirri, and Pasteur pipette-shaped with base about 0.5 µm across; closely spaced at rear body end, can whip very fast, left and right cirrus each about 20 µm, middle about 25 µm long in vivo.

Oral apparatus in *Gonostomum*-pattern (Fig. 144a–c, j; Table 126; BERGER 1999). Adoral zone occupies 38–54%, on average 46% of body length, composed of an average of 19 membranelles, commences near midline of anterior body end and extends straight along left body margin, performing abrupt right bend and slight clockwise rotation to plunge into buccal cavity near left body margin. Bases of largest membranelles about 3 µm wide in vivo. Proximal portion of adoral zone and buccal cavity almost entirely covered by the curved buccal lip bearing the paroral membrane, which consists of 9–11 widely spaced, about 5 µm long cilia. Buccal cavity flat and narrow, at right bordered by endoral slightly longer than paroral. Pharyngeal fibres clearly recognizable in vivo and protargol preparations, extend obliquely backwards.

Some dividers show that only five (not six as in most oxytrichids) fronto-ventral-transverse cirral anlagen are formed (including the anlage for the undulating membranes and the left frontal cirrus). The posterior cirri of anlage 4 migrate backwards forming the inconspicuous transverse cirri (Fig. 144 l).

Population from Tenerife: The Tenerife specimens match those from Namibia very well, both in general appearance and morphometric details (Fig. 144f–h; Table 126). The only difference worth mentioning concerns the transverse cirri, which are fewer in number (1 or 2) and thus hardly distinguishable from the marginal and caudal cirri. Furthermore, very slender specimens occur (length:width ratio 6:1; Table 126).

Occurrence and ecology: We discovered *Wallackia elegans* in soil from road puddles and thus cannot exclude that it is a limnetic species. However, the Tenerife[28] population, which occurred in an ordinary soil sample, indicates a preference for soil.

Generic classification and comparison with related species: We have known this distinct, *Gonostomum*-like species with conspicuous caudal cirri for many years. Now we have sufficient data to describe and classify it properly. According to the gonostomoid oral apparatus and the three dorsal kineties and caudal cirri, it could be assigned to *Gonostomum* STERKI, 1878 or *Wallackia* FOISSNER, 1976. However, according to the ventral cirral pattern, it unequivocally belongs to *Wallackia*. The pattern is, like in *W. schiffmanni* (type; Fig. 142g) and → *W. bujoreani* (Fig. 142a–f), composed of four frontoventral rows, including a row of buccal cirri. Furthermore, some dividing specimens show that only five fronto-ventral-transverse primordia are formed, namely one anlage for the undulating membranes and the left frontal cirrus, and four anlagen for frontoventral rows 2–5. And last but not least, *W. elegans* has, like the type species, prominent, Pasteur pipette-shaped caudal cirri (Fig. 144a, b), a feature only recognizable in live specimens. By contrast, *Gonostomum* has a single buccal cirrus and more or less distinctly scattered fronto-ventral-transverse cirri originating, as in typical oxytrichids, from six primordia. Furthermore, the caudal cirri are inconspicuous (for review, see BERGER 1999).

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[28] Canary Islands near beach of Candelaria, 28°N 17°W. Light grey, non-saline upper soil layer mixed with few roots and litter, pH 8.2. Sample kindly provided by Dr. Brigitte KRASSNIGG, Salzburg.

Wallackia elegans is easily distinguished from both congeners, *W. schiffmanni* FOISSNER, 1976 and → *W. bujoreani*, by the body shape (lanceolate with short tail curved to right vs. ellipsoidal), the relative length of the caudal cirri, and the lack of cortical granules. Furthermore, it differs from the limnetic *W. schiffmanni* by body length (50–70 µm vs. 85–100 µm) and the lower number of cirri in frontoventral rows two to four (2–5, 2–5, 5–7 vs. 5–7, 5–7, 13). FOISSNER (1976) described 4–6 bristle rows, whereas *W. elegans* and → *W. bujoreani* invariably have only three. However, a re-evaluation of the original notes showed that FOISSNER (1976) overinterpreted his data, which are entirely based on in vivo observations. → *Wallackia bujoreani* has conspicuous cortical granules and the fourth frontoventral row, which is composed of 10–14 cirri, terminates near the rear end (vs. 5–7 cirri and near buccal vertex in *W. elegans*).

Gonostomum gonostomoida (HEMBERGER, 1985) BERGER, 1999 has, like *Wallackia elegans*, a long frontoventral row left of the right marginal row (Fig. 144i). However, this species, which was discovered in an infusion of excrements from the terrestrial snail *Deroceras reticulatum*, is 110–200 µm long, has only one buccal cirrus, and forms six fronto-ventral-transverse cirral anlagen. Thus, it is a true *Gonostomum*.

In vivo, *Wallackia elegans* is characterized by the following combination of features: body 50–70 µm long; lanceolate with rear portion usually curved to right and bearing very long, prominent caudal cirri; many ventral cirri in several distinct rows.

Pseudouroleptus caudatus HEMBERGER, 1985

Improved diagnosis: Size about 230 × 50 µm in vivo. Slenderly lanceolate with posterior portion narrowed tail-like. 2 macronuclear nodules with 1 micronucleus each. Cortical granules in closely spaced rows, colourless, about 1.2 µm across. Amphisiellid median cirral row (ACR) extends to near body end and consists of about 56–60 cirri. On average 45–55 adoral membranelles, 55 cirri in right and near 50 in left marginal row, 1 cirrus left of ACR, 1 buccal and 1 postperistomial cirrus, 25–50 transverse cirri forming a shortened or unshortened row right of ACR, and 4 dorsal kineties.

Remarks: The diagnosis is based on HEMBERGER (1985) and the present investigations, which show that *P. caudatus* has cortical granules overlooked by HEMBERGER, in spite of their conspicuousness. However, HEMBERGER obviously did not study live specimens in detail, although he mentioned "cytoplasm slightly brownish", a feature likely caused by the dense cortical granulation! Recently, we found *P. caudatus* in Brazil. It has cortical granules, emphasizing that they were overlooked by HEMBERGER (1985).

We split the species in two subspecies mainly because of a distinct difference in the number of transverse cirri, which form a conspicuous, shortened or unshortened row right and along of the amphisiellid median cirral row, as first recognized by EIGNER & FOISSNER (1994). This is now a main feature of the genus.

Pseudouroleptus caudatus caudatus HEMBERGER, 1985 **nov. stat.** (Fig. 145a–g; Table 127)

Diagnosis: Transverse cirral row commences near level of buccal cirrus and extends to rear body end, composed of about 40–50 cirri.

Type location: Forest soil and Rio Tambopata in Peru (HEMBERGER 1985).

Description (of a population from a rice field soil in Zanzibar): Size 180–280 × 40–60 µm in vivo, usually near 230 × 50 µm, length:width ratio about 5:1 in vivo, while 4.3:1 on average in protargol preparations, where specimens are inflated because they are difficult to stabilize with the usual fixatives (Table 127). Elegant pisciform with tail-like posterior body portion, a conspicuous feature preserved even in most protargol-impregnated cells; invariably slightly twisted about main body axis, marginal rows thus never recognizable in full length if specimens are viewed ventrally (Fig. 145a, d–f); highly flexible and dorsoventrally flattened up to 2:1, acontractile. Nuclear apparatus in middle body third, left of midline. Macronuclear nodules distinctly separate, elongate ellipsoidal on average (3:1), contain many small, globular nucleoli. Micronuclei highly conspicuous in vivo and protargol preparations because compact and large, that is, about 10 × 7 µm in vivo (Fig. 145a, e). Contractile vacuole slightly above mid-body at left cell margin; we did not look for collecting canals. Cortex flexible, contains closely spaced rows of about 1.2 µm-sized granules leaving blank only cirral areas, provide cells with a brownish colour, although the individual granules are colourless, likely due to some light refraction (Fig. 145c); impregnate lightly with protargol. Cytoplasm colourless, packed with food vacuoles; fat globules; minute, protargol-affine granules; and various crystals up to 5 µm in size which make cells dark in posterior half, where they are concentrated (Fig. 145a, b). Feeds on coccal cyanobacteria, naked amoebae, flagellates, diatoms, and small and medium-sized testate amoebae (*Trinema lineare*, *T. enchelys*) and ciliates (*Plagiocampa* sp., *Metopus hasei*). Glides vividly on microscope slide and on and between soil particles showing great flexibility.

Cirral pattern and number of cirri of usual variability (Fig. 145a, d, e; Table 127). Cirri about 15 µm long in vivo, frontal cirri elongated to 20 µm, closely spaced within rows, distances between individual cirri increase slightly in posterior third of rows. Marginal rows follow body curvature and are thus distinctly spiralized, extend to posterior body end. Frontal cirri distinctly enlarged, first cirrus in body midline, third cirrus close to distalmost adoral membranelle, that is, far subapically at level of buccal cirrus. Invariable one enlarged frontoventral cirrus underneath frontal cirrus 3, that is, left of anterior end of amphisiellid median cirral row. Buccal cirrus slightly enlarged, right of anterior portion of undulating membranes (0–5 µm distant from anterior end). Postperistomial cirrus slightly enlarged, very near to buccal vertex. Amphisiellid median cirral row ("left ventral row") conspicuous because composed of an average of 60 cirri, commences at right body margin underneath distal end of adoral zone and extends obliquely to left body margin to end subterminally on average. Right of and parallel to amphisiellid median cirral row a series of about 50 transverse cirri (according to ontogenetic data, EIGNER & FOISSNER 1994) forming a ("right ventral") row commencing at the same level as the amphisiellid median cirral row, but extending to posterior body end. Dorsal infraciliature poorly impregnated in our specimens, consists of four kineties and three inconspicuous caudal cirri, according to HEMBERGER (1982, 1985).

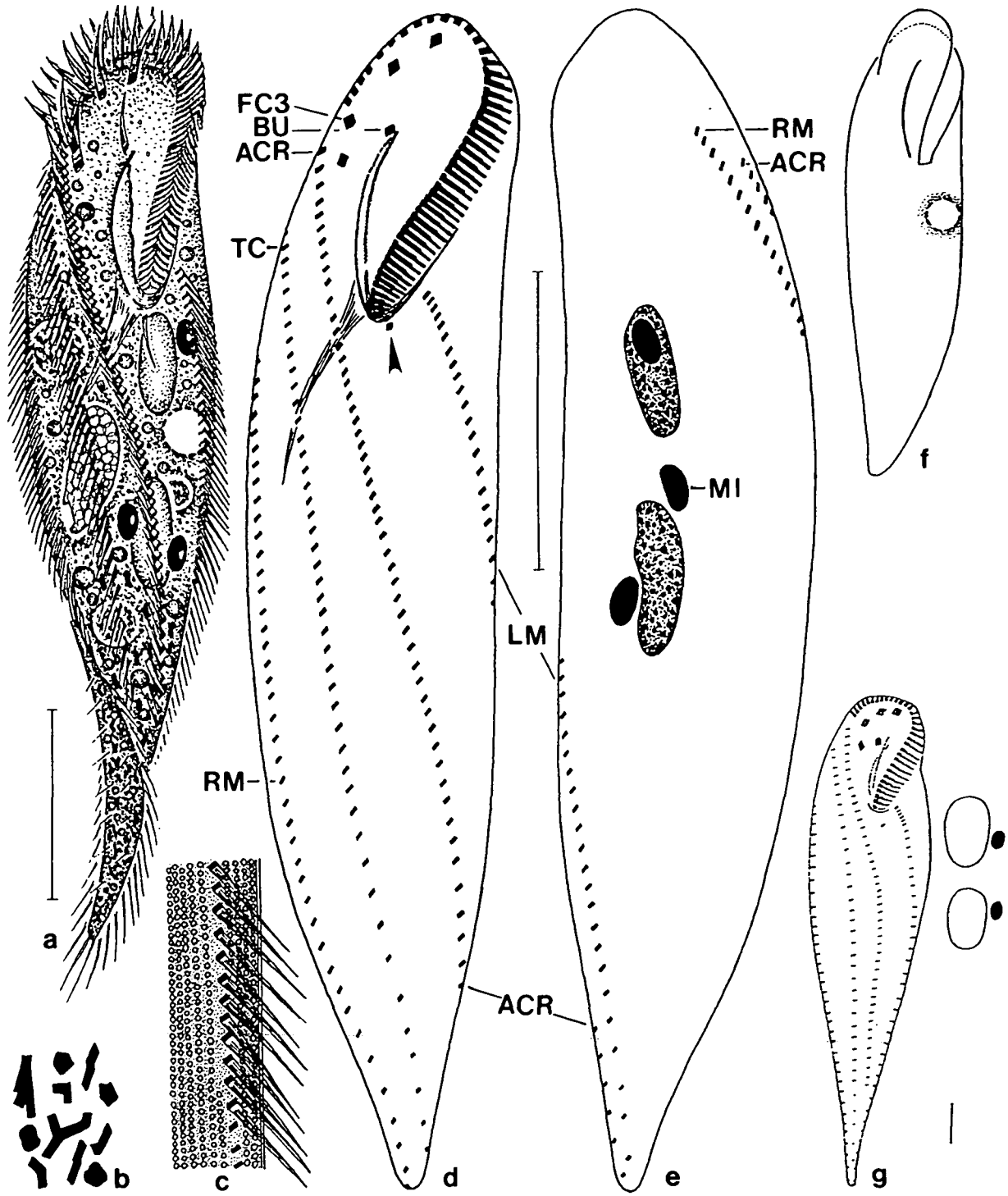

Fig. 145a–g. African (a–f) and South American (g) *Pseudouroleptus caudatus caudatus* from life (a–c, f) and after protargol impregnation (d, e, g). **a:** Ventral view of a representative specimen. Note the three compact, large micronuclei. **b:** Cytoplasmic crystals up to 5 µm in size. **c:** Surface view showing closely spaced rows of colourless cortical granules about 1.2 µm across. **d, e:** Infraciliature of ventral and dorsal side and nuclear apparatus. Dorsal bristle rows not shown because too indistinct in the preparation. Arrowhead marks postperistomial cirrus. **f:** Blunt shape variant. **g:** Holotype specimen (from HEMBERGER 1985). ACR – amphisiellid median cirral row, BU – buccal cirrus, FC3 – third frontal cirrus, LM – left marginal row, MI – micronucleus, RM – right marginal row, TC – transverse cirral row. Scale bars 50 µm (a, d, e) and 20 µm (g).

Adoral zone occupies 21–37%, on average 28% of body length, commences far subapically (18 µm on average), that is, at level of buccal cirrus (Fig. 145a, d; Table 127); composed of an average of 54 membranelles of ordinary fine structure, bases of largest membranelles 10 µm wide in vivo. Buccal cavity deep and of ordinary width, right half and last adoral membranelles covered by a very hyaline lip. Undulating membranes slightly curved and side by side, rarely intersecting optically in posterior third, paroral likely composed of dikinetids. Pharyngeal fibres distinct in vivo and protargol preparations, extend obliquely backwards.

Occurrence and ecology: HEMBERGER (1985) discovered *P. caudatus* in Peru, both in a forest soil and a river. We found it in a grey, sandy, circumneutral (pH 7.8), dry rice field soil collected by Mag. Hubert BLATTERER in the surroundings of the tourist office of the town of Zanzibar, East Africa (07°S 39°E). Obviously, this species occurs in both terrestrial and limnetic habitats. As yet, we have not found it in Laurasia.

Comparison with original description and related species: Our data match those of HEMBERGER (1985) fairly well, especially if the subspecies → *namibiensis* is included, except for the cortical granules discussed in the "remarks" to the species above. Specifically, body size and shape, the nuclear and cirral pattern, and main morphometrics are rather similar (Fig. 145g): body length 230/250 µm; number of adoral membranelles: 40–63, usually 53/33–50, usually 40; number of cirri in left ventral row (note that HEMBERGER confused right and left!): 59/55; number of cirri in right ventral row: 50/42.

In vivo, *Pseudouroleptus caudatus* is easily confused with *Hemiamphisiella granulifera* (FOISSNER, 1987c), which has a similar size, nuclear pattern, and cortical granulation, but lacks the long row of transverse cirri right of the amphisiellid median cirral row.

Pseudouroleptus caudatus namibiensis **nov. sspec.** (Fig. 146a–c; Table 127)

Diagnosis: Transverse cirral row commences near mid-body and extends to rear body end, composed of about 25 cirri.

Type location: Soil from margin of a small pond in the Aubschlucht, Namibia, 23°55'S 16°15'E (site 30 in figure 2 and chapter 2.1.2).

Etymology: Named after the country discovered.

Description: The new subspecies differs from → *P. caudatus caudatus* by the feature mentioned in the diagnosis. Thus, the description is restricted to the detailed morphometrics and figures and a few minor details, namely: (i) size 180–330 × 40–60 µm in vivo, that is, slightly larger than → *P. caudatus caudatus*; (ii) body never spiralized, a remarkable difference to → *P. caudatus caudatus* and other large soil hypotrichs; (iii) the large, conspicuous micronuclei are frequently ovate; (iv) cortical granule rows as distinct as in → *P. caudatus caudatus* and occasionally lightly impregnated with protargol; (v) as in → *P. caudatus caudatus*, the cytoplasm contains innumerable minute, protargol-affine granules making the analysis of the dorsal infraciliature difficult; (vi) buccal cirrus 5–9 µm, on average 6.3 µm distant from anterior end of paroral membrane; (vii) paroral and endoral frequently

intersect optically in posterior half; (viii) an early divider shows a long oral primordium near the amphisiellid median cirral row and seven cirral anlagen streaks in the opisthe; late dividers show the amphisiellid median cirral row to be composed of three smaller cirral rows, as suggested by EIGNER & FOISSNER (1994), based on the details given by HEMBERGER (1982); the right ventral row (= transverse cirral row) is ontogenetically inactive. These data match the more detailed observations by HEMBERGER (1982).

Occurrence and ecology: To date found only at type location, where it was rather abundant.

Table 127. Morphometric data on *Pseudouroleptus caudatus namibiensis* (PN) and *Pseudouroleptus caudatus caudatus* (PC).

Characteristics [a]	Subspecies	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	PN	214.3	208.0	32.2	7.4	15.0	167.0	295.0	19
	PC	201.8	200.0	33.3	10.5	16.5	150.0	255.0	10
Body, width	PN	45.6	45.0	3.9	0.9	8.5	40.0	55.0	19
	PC	47.0	47.5	5.7	1.8	12.1	39.0	55.0	10
Body length:width, ratio	PN	4.7	4.7	0.7	0.2	15.0	3.5	6.7	19
	PC	4.3	4.3	0.2	0.1	5.1	4.0	4.7	10
Anterior body end to proximal end of adoral zone, distance	PN	56.3	58.0	6.3	1.4	11.1	46.0	71.0	19
	PC	56.4	55.0	8.8	2.8	15.6	42.0	75.0	10
Body length: length of adoral zone, ratio	PN	3.8	3.7	0.6	0.1	15.7	2.7	6.5	19
	PC	3.6	3.6	0.2	0.1	6.3	3.2	3.9	10
Anterior body end to distal end of adoral zone, distance	PN	17.8	18.0	3.8	0.9	21.2	10.0	25.0	19
Anterior body end to postperistomial cirrus, distance	PN	60.6	58.0	9.6	2.2	15.8	51.0	90.0	19
Anterior body end to right marginal row, distance	PN	11.1	11.0	2.2	0.5	19.9	7.0	15.0	19
Anterior body end to left ventral cirral row, distance	PN	20.7	20.0	4.4	1.0	21.3	13.0	30.0	19
Posterior body end to left ventral cirral row, distance	PN	20.5	20.0	4.3	1.0	20.8	15.0	27.0	19
Anterior body end to right ventral (= transverse) cirral row, distance	PN	86.2	82.0	11.4	2.6	13.2	70.0	115.0	19
Anterior body end to buccal cirrus, distance	PN	22.6	22.0	3.1	0.7	13.8	18.0	30.0	19
Anterior body end to first macronuclear nodule, distance	PN	54.8	55.0	6.1	1.4	11.1	46.0	71.0	19
Nuclear figure, length	PN	61.8	59.0	8.5	2.0	14.0	48.0	80.0	19
Anterior macronuclear nodule, length	PN	22.1	22.0	2.4	0.6	10.9	18.0	27.0	19
	PC	25.1	26.0	3.0	0.9	11.8	20.0	30.0	10
Anterior macronuclear nodule, width	PN	8.6	8.0	1.5	0.4	17.9	6.0	12.0	19
	PC	8.5	8.0	1.4	0.5	16.9	7.0	11.0	10
Macronuclear nodules, number	PN	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
	PC	2.0	2.0	0.0	0.0	0.0	2.0	2.0	10
Micronuclei, length	PN	6.2	6.0	0.5	0.1	8.6	5.0	7.0	19
	PC	8.5	8.5	1.1	0.3	12.7	7.0	10.0	10

(continued)

Characteristics [a]	Subspecies	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Micronuclei, width	PN	4.3	4.5	–	–	–	3.5	5.0	19
	PC	5.2	5.0	–	–	–	5.0	6.0	10
Micronuclei, number	PN	2.4	2.0	0.7	0.2	28.6	1.0	4.0	19
	PC	3.0	3.0	0.7	0.2	22.2	2.0	4.0	10
Adoral membranelles, number	PN	43.9	45.0	4.7	1.1	10.8	33.0	51.0	19
	PC	53.2	54.0	6.5	2.0	12.1	40.0	63.0	10
Frontal cirri, number	PN	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
	PC	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10
Frontoventral cirri, number	PN	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
	PC	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10
Buccal cirri, number	PN	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
	PC	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10
Postperistomial cirri, number	PN	1.3	1.0	–	–	–	1.0	3.0	19
	PC	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10
Amphisiellid median cirral row (= left ventral row), number of cirri	PN	56.5	57.0	4.9	1.1	8.7	50.0	67.0	19
	PC	59.4	60.0	8.6	2.7	14.4	40.0	70.0	10
Right ventral (= transverse) cirral row, number of cirri	PN	25.5	26.0	2.9	0.7	11.2	20.0	31.0	19
	PC	50.1	50.0	6.7	2.1	13.2	35.0	60.0	10
Right marginal cirri, number	PN	55.4	55.0	4.8	1.1	8.6	47.0	70.0	19
	PC	55.1	55.0	7.5	2.4	13.7	43.0	70.0	10
Left marginal cirri, number	PN	51.5	50.0	5.3	1.2	10.2	44.0	61.0	19
	PC	46.6	47.5	5.5	1.7	11.8	35.0	53.0	10
Caudal cirri, number	PN	2.4	2.0	–	–	–	1.0	4.0	19
Dorsal kineties, number	PN	4.0	40	0.0	0.0	0.0	4.0	4.0	19

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Comparison with related species: *Pseudouroleptus caudatus namibiensis* differs from → *P. caudatus caudatus* by the distinctly shortened row of transverse cirri. The feature is stable and changes the overall cirral pattern rather distinctly. Thus, species rank would probably be more appropriate. However, the difference is simply based on a quantitative feature, suggesting subspecies rank, especially since the number of adoral membranelles is more similar to the South American than East African population of → *P. caudatus caudatus* (Table 127). Recently, we found *P. caudatus caudatus* in a Brazilean floodplain soil. It matches HEMBERGER's description, emphasizing that the shortened row of transverse cirri in *P. caudatus namibiensis* is a reliable difference.

Pseudouroleptus caudatus namibiensis is easily confused with *Hemiamphisiella wilberti* (FOISSNER, 1982), which has a similar body shape, size, as well as nuclear and cirral pattern (Fig. 146d, e). However, *H. wilberti* lacks cortical granules, as confirmed by a reinvestigation of the type slides and by the Namibian site (3) specimens. Likely, *H. wilberti* belongs to the genus *Pseudouroleptus*, but a transfer should await ontogenetic data.

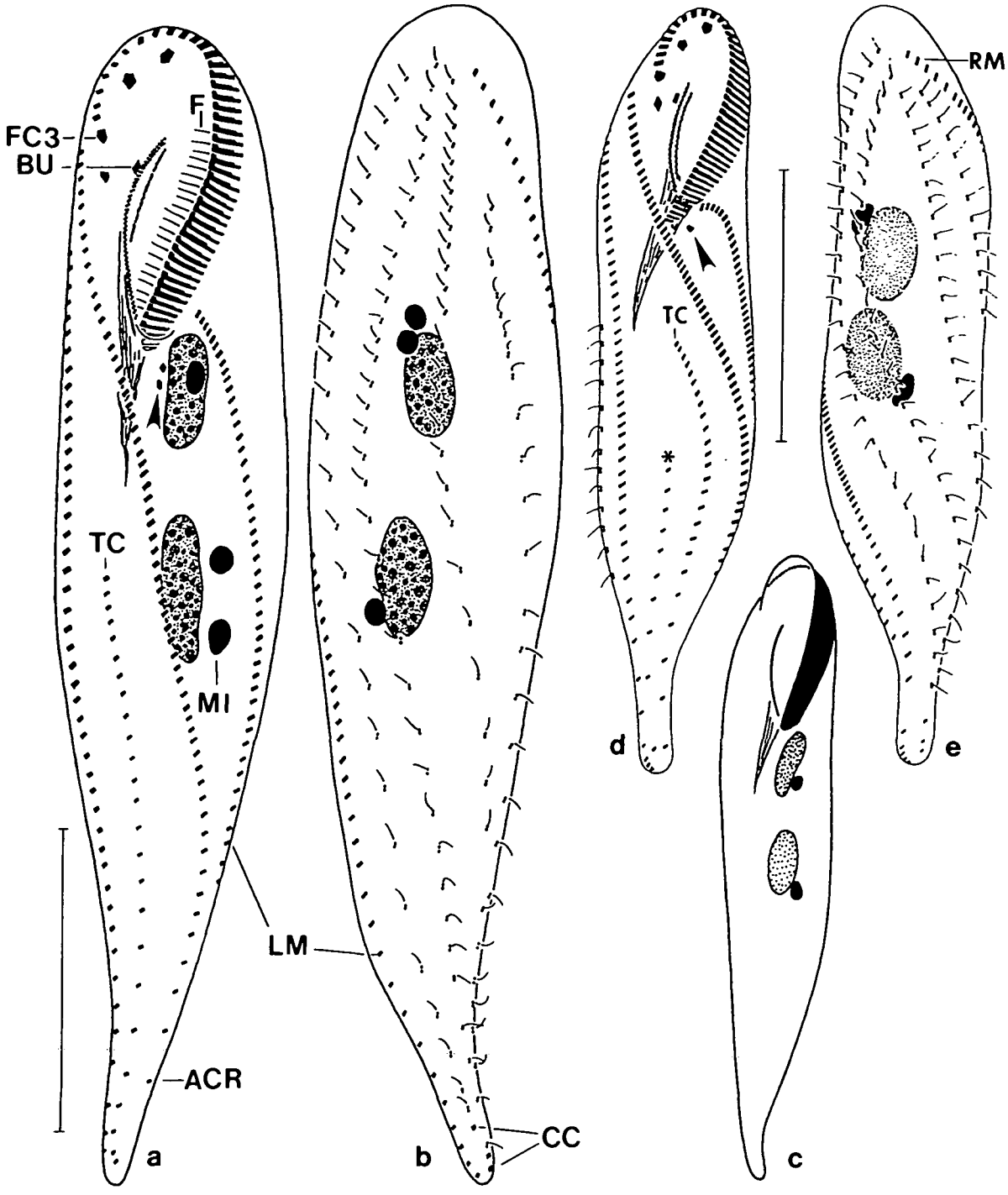

Fig. 146a–c. *Pseudouroleptus caudatus namibiensis* after protargol impregnation. **a, b:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrowhead marks postperistomial cirri. **c:** Shape variant.

Fig. 146d, e. *Hemiamphisiella wilberti*, infraciliature of ventral and dorsal side after protargol impregnation. Arrowhead marks postperistomial cirrus; asterisk denotes a short, supernumerary row present in only few specimens.

ACR – posterior end of amphisiellid median cirral row, BU – buccal cirrus, CC – caudal cirri associated with dorsal kineties 1 and 2, F – fibres extending from adoral membranelles into buccal cavity, FC3 – third frontal cirrus, LM – left marginal row, MI – micronucleus, RM – right marginal row, TC – long row of transverse cirri. Scale bars 50 μm.

Amphisiella namibiensis nov. spec. (Fig. 147a, b, h–l; 386a–g, 390f; Table 128)

Diagnosis: Size about 250 × 80 µm in vivo; elongate ellipsoidal. 2 macronuclear nodules and 2–6 ($\bar{x}$ = 4) micronuclei. Usually 2 long ventral rows extending to transverse cirri: right composed of 43, left of 40 cirri on average. On average 50 right marginal, 51 left marginal, 4 buccal, and 5 transverse cirri; 1–6 ($\bar{x}$ = 4) cirri between buccal row and anterior end of ventral rows. 3 dorsal kineties. Adoral zone about one third of body length, composed of 44 membranelles on average.

Type location: Highly saline soil from margin of Etosha Pan, Namibia, 19°S 15°50'E (site 54 in figures 2, 3 and chapter 2.1.2).

Etymology: Named after the country discovered.

Description: Size 140–300 × 40–100 µm in vivo, usually near 250 × 80 µm, length:width ratio about 3:1 in vivo, while 2.8–6.3:1, on average 4.3:1 in the preparations, where most specimens are rather distorted (Table 128); very flexible but acontractile. Overall shape elongate ellipsoidal, slightly narrowed posteriorly, both ends broadly rounded, dorsoventrally flattened up to 2:1 (Fig. 147a, b; 386a, 390f). Macronuclear nodules in middle third of cell, near or slightly left of midline, ellipsoidal, with numerous nucleoli 1–2 µm across. Micronuclei usually near or attached to macronuclear beads, globular. Contractile vacuole with two collecting canals extending anteriad and posteriad near mid-body at left cell margin. No specific cortical granules. Cytoplasm colourless, without crystalline inclusions, contains some colourless fat globules 1–5 µm across and about 10–40 µm-sized food vacuoles with residues of ciliates (e.g. *Drepanomonas revoluta*, *Gonostomum* sp.). Glides quickly to and fro on microscope slide.

Pattern and number of cirri of usual variability (Fig. 147h, j, k; 386a, d, e, 390f; Table 128), except for buccal cirri (2–5) and cirri left of ventral rows (1–6); in two out of 45 specimens a third ventral row occurs, and two specimens have some cirri between the anterior portion of the ventral rows. Marginal cirral rows more or less widely overlapping posteriorly, that is, left row extends to or above midline at posterior end of cell, while the right row commences dorsolaterally at level of anteriormost buccal cirrus and extends terminally to, or slightly above, midline; cirri usually composed of two kineties with six to seven cilia each, anteriormost cirri of both rows frequently slightly enlarged, that is, consisting of three to five kineties with five to seven cilia each. Frontal cirri about 25 µm long in vivo, right of midline, right cirrus close to distal end of adoral zone of membranelles; composed of 8–13 kineties with six to eight cilia each. Buccal cirri along mid-portion of paroral membrane, anteriormost cirrus invariably near level of posteriormost frontal cirrus, become slightly thinner from anterior to posterior; composed of four to seven kineties with six to nine cilia each. Postperistomial cirri lacking. Ventral cirri about 15 µm long in vivo, arranged in two (rarely three) rows commencing underneath distal end of adoral zone and extending slightly obliquely to transverse cirri; individual cirri usually composed of two kineties with six to seven cilia each, anteriormost cirri of both rows frequently slightly enlarged, that is, composed of three to five kineties with five to seven cilia each. One to six, usually four cirri between buccal row and anterior portion of ventral rows, usually arranged as shown in figures 147h, j, k, 386d and 390f, but several variations occur, for instance, cirri may be side by side ("midventral pattern"), or the left anterior cirrus is absent; cirri slightly enlarged, comprising five to six kineties with five to

eight cilia each. Transverse cirri about 25 µm long in vivo, inconspicuously projecting above posterior body margin, form slightly curved, oblique row at, or slightly left of, midline; usually composed of six to eight kineties with five to six cilia each. Fibrillar associates of cirri as shown in figures 147k, l and 386b–g; note lack of posterior fibre bundle in transverse cirri and anteriormost frontal cirrus as well as absence of anterior fibre bundle in buccal cirri.

Dorsal bristles about 3 µm long in vivo, arranged in three rows slightly shortened anteriorly and posteriorly (Fig. 147i). No caudal cirri.

Oral apparatus conspicuous because of the large, deep buccal cavity and curved paroral membrane resembling cyrtohymenid oxytrichids (Fig. 147a, h, j, k; 386d, 390f; Table 128). Adoral zone occupies about one third of body length, proximal third rather distinctly broadened and covered by a hyaline cortical process (lip); composed of an average of 44 membranelles, bases of largest membranelles about 20 µm wide. Structure of membranelles depends on zone region (Fig. 147j): those along buccal cavity composed of two long rows, one slightly shortened row, and a very short anterior row, which consists of only three basal bodies; the next 5–8 membranelles have the short anterior row composed of about 10 basal bodies; membranelles in distal third of zone composed of two long rows and one slightly shortened row of basal bodies, to which, except for last membranelle, a fairly short row is attached in mid-portion. Fibrillar system of adoral membranelles also depends on zone region (Fig. 147k): membranelles of region (a) with short fibre bundle directed to frontal field and bent dorsally; membranelles of region (b) with short fibre bundle directed to frontal field and curved dorsally and to the left, likely touching fibre bundle from neighbouring membranelle; membranelles of region (c) with very long submembranellar fibre bundle originating from left half of membranelle and extending to proximal end of zone; fibrillar associates of region (d) like those of region (c), but with fine, straight fibre extending between individual membranelles into buccal cavity; membranelles of region (e) also have intermembranellar fibres, but all other associates are lacking or inconspicuous.

Buccal cavity deep and wide, with conspicuous accumulation of argyrophilic granules right of adoral zone and in posterior half of right wall (Fig. 147h, j, k; 386a–d, f). Paroral composed of closely spaced, about 15 µm long cilia, straight in posterior half, strongly bent leftwards anteriorly, where it follows curvature of buccal cavity, optically crosses endoral in mid-buccal area. Endoral membrane posteriorly slightly longer than paroral, so strongly curved that ends almost touch adoral zone of membranelles, anterior half traverses bottom of buccal cavity. Both membranes associated with 10–20 µm long fibre bundles, those of paroral line right wall of buccal cavity, those of endoral line bottom. Pharyngeal fibres surprisingly inconspicuous, extend obliquely backwards.

Occurrence and ecology: To date found only at various sites of the Etosha National Park (Table 4). The large, blunt body indicates that it may be a limnetic species active mainly during floods. Very recently found in a forest soil of Austria!

Generic classification and comparison with similar species: The species described resembles *Amphisiella* GOURRET & ROESER, 1888 and *Lamtostyla* BUITKAMP, 1977a as defined by PETZ & FOISSNER (1996), except for the second ventral row. Although this is a conspicuous feature, separation at genus level must await ontogenetic data. Probably, *Amphisiella namibiensis*, *Pseudouroleptus buitkampi* (Fig. 147g; FOISSNER 1982), and *P. terrestris* (Fig. 147f; HEMBERGER 1985) form a distinct genus.

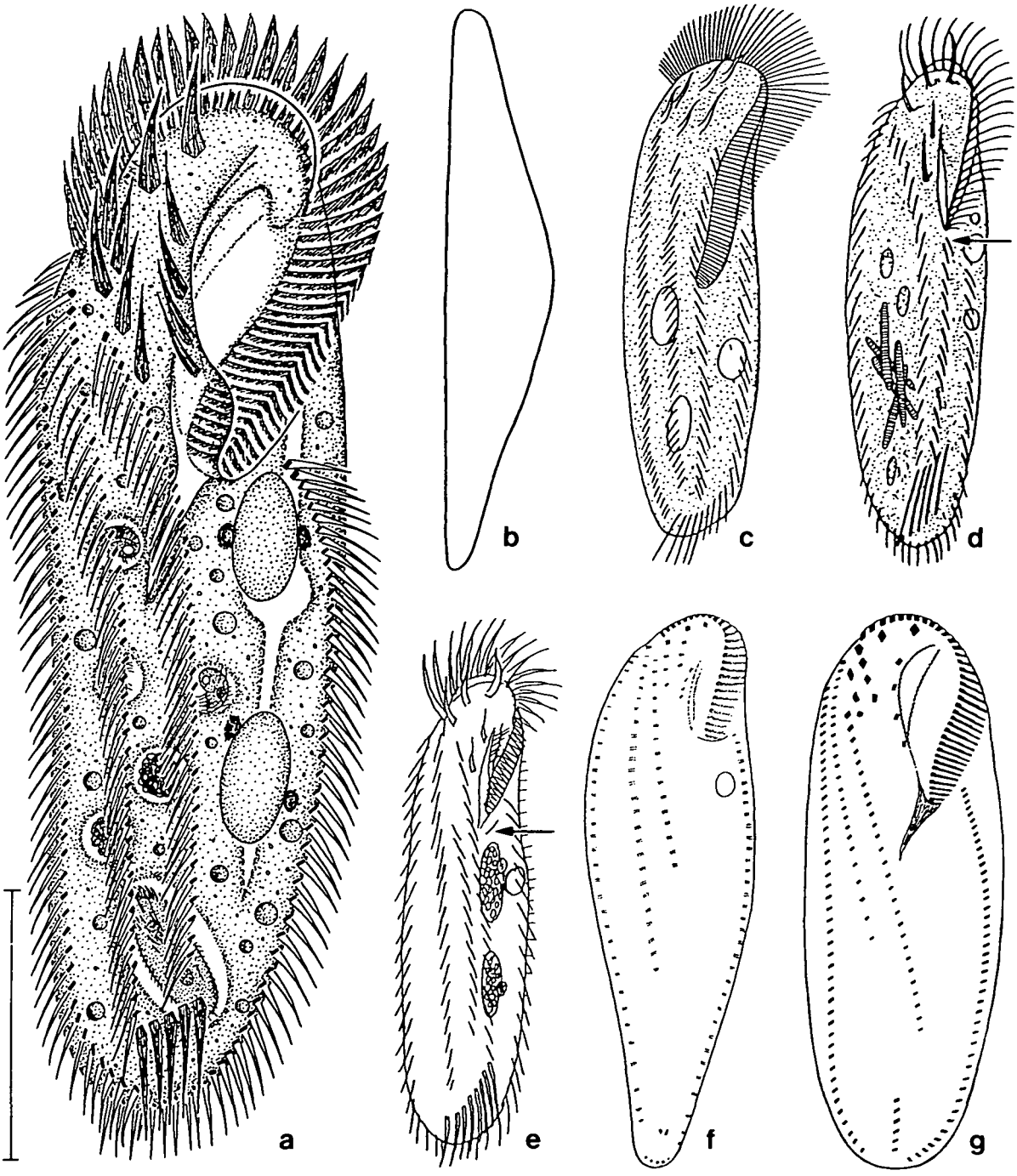

Fig. 147a–g. *Amphisiella namibiensis* (a, b) and similar species (c–g) from life (a–e) and after protargol impregnation (f, g). **a, b:** Ventral and lateral view of a representative specimen with food vacuoles containing ciliates. Scale bar 60 µm. **c:** *Holosticha wrzesniowskii* (length about 250 µm) differs from *A. namibiensis* in the marine habitat and the very long adoral zone of membranelles (from MERESCHKOWSKY 1878). **d:** *Apoamphisiella hymenophora* (length 170–200 µm) has a postperistomial cirrus (arrow; from STOKES 1886a). **e:** *Paraurostyla fossicola* (length 200–220 µm) has a postperistomial cirrus (arrow) and three ventral rows (from KAHL 1932). **f:** *Pseudouroleptus terrestris* (length about 190 µm) has an inconspicuous buccal field, distinctly shortened ventral rows, and only two transverse cirri (from HEMBERGER 1985). **g:** *Pseudouroleptus buitkampi* (length 135–180 µm) differs from *A. namibiensis* in that the transverse cirri are longitudinally arranged and the nuclear apparatus consists of four macronuclear nodules (from FOISSNER 1982).

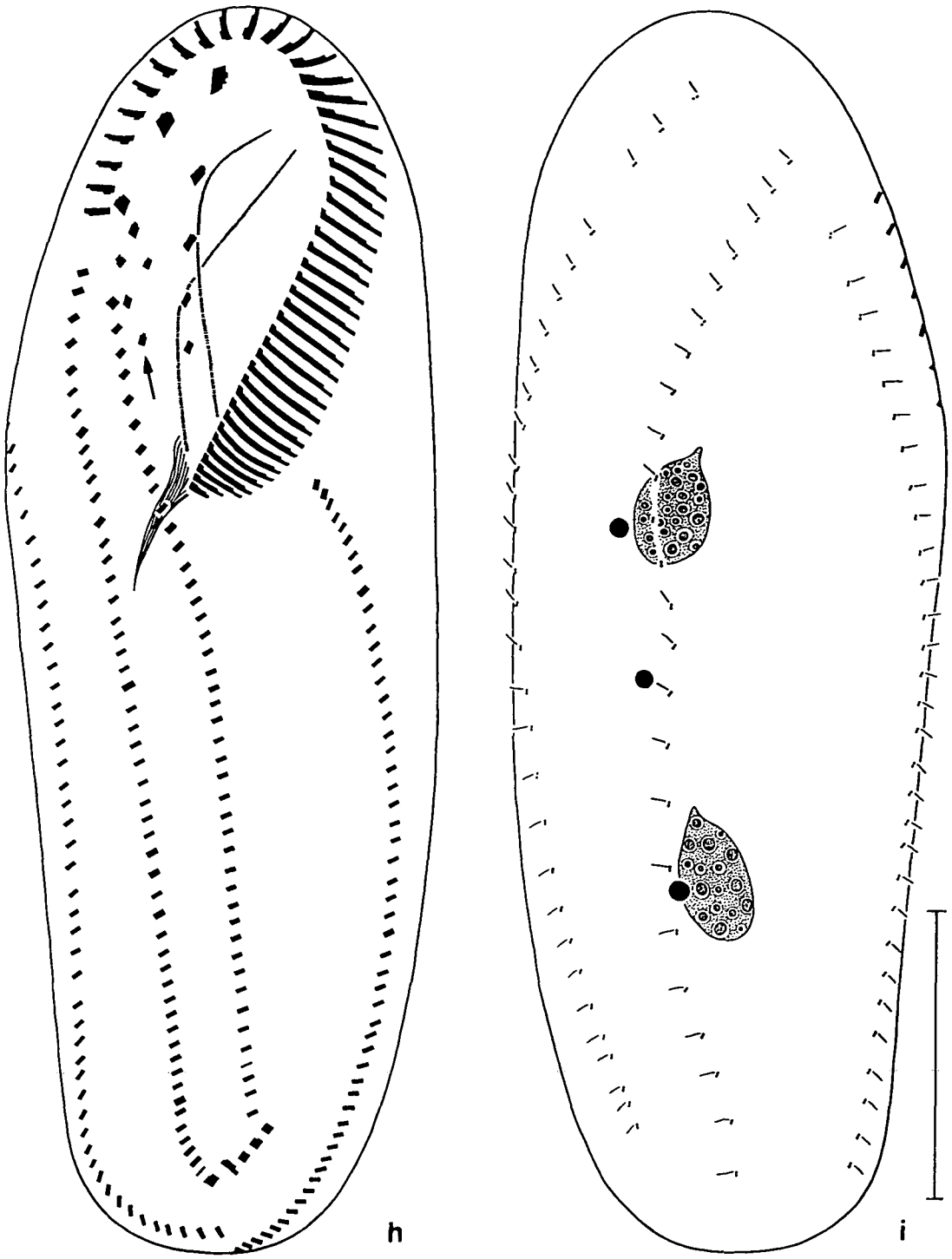

Fig. 147h, i. *Amphisiella namibiensis*, infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen after protargol impregnation. The two ventral rows extend to the transverse cirri, which form an oblique row. The five cirri between the buccal row and the anterior portion of the ventral rows are arranged in two rows side by side (arrow). The marginal rows slightly overlap posteriorly. Note the large buccal area and the strongly curved undulating membranes. Scale bar 60 μm.

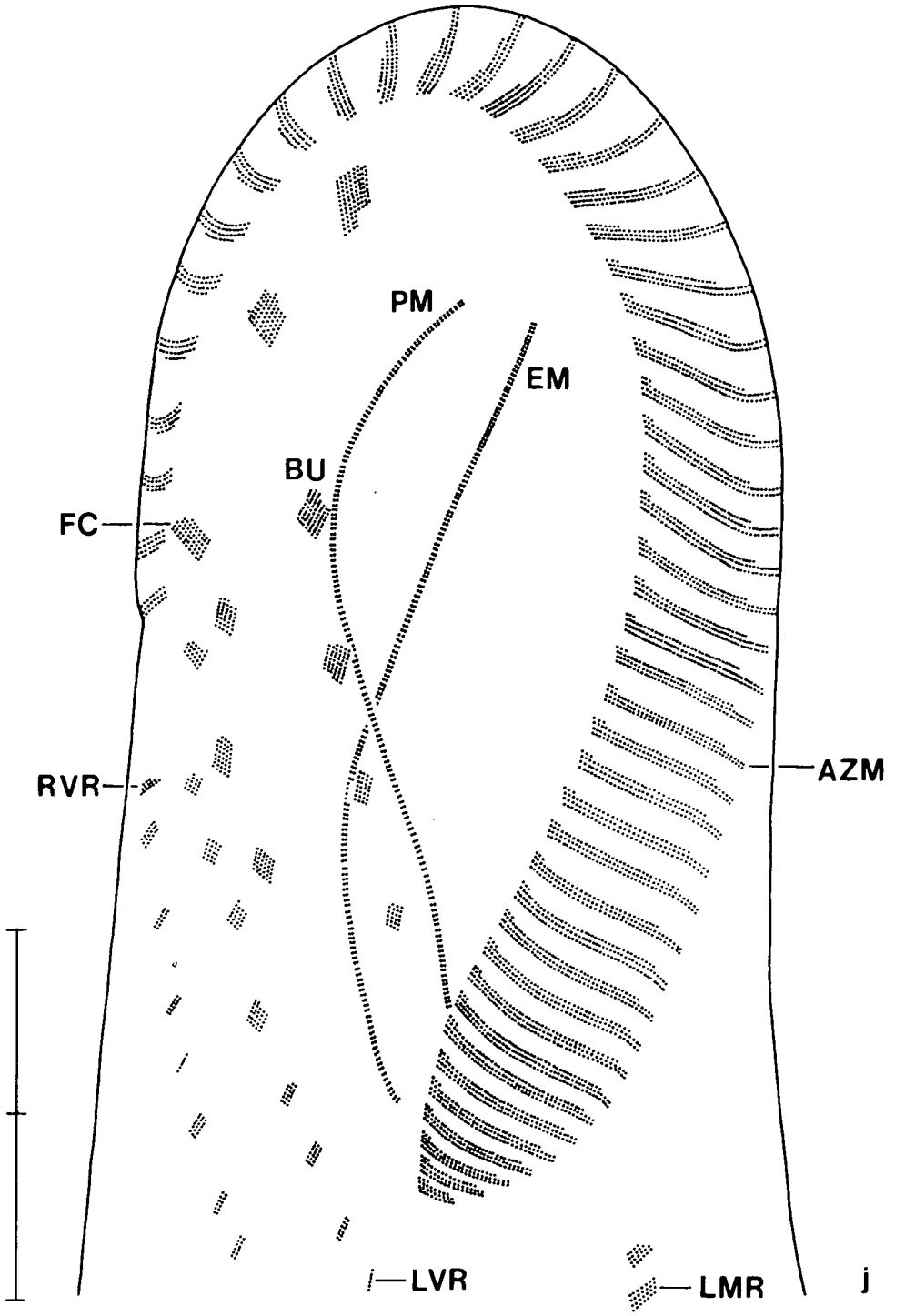

Fig. 147j. *Amphisiella namibiensis*, somatic and oral infraciliature of anterior ventral third after protargol impregnation. The oral apparatus is conspicuous because of the large and deep buccal cavity and the distinctly curved undulating membranes resembling cyrtohymenid oxytrichids. Note that the frontal cirri are left of midline and the structure of the adoral membranelles depends on the zone region. AZM – adoral zone of membranelles, BU – buccal cirri, EM – endoral membrane, FC – right frontal cirrus, LMR – left marginal row, LVR – left ventral row, PM – paroral membrane, RVR – right ventral row. Scale bar division 20 µm.

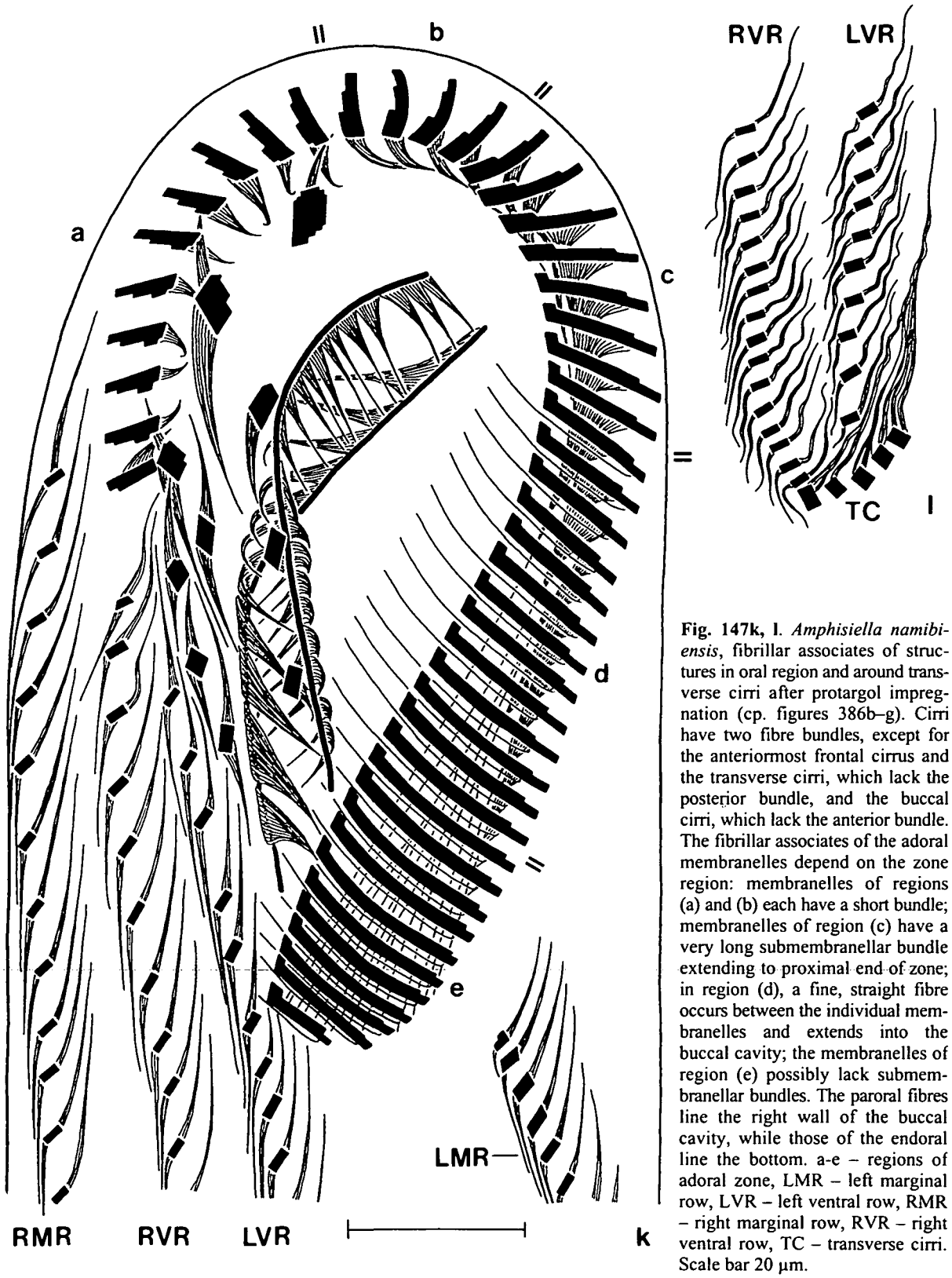

Fig. 147k, l. *Amphisiella namibiensis*, fibrillar associates of structures in oral region and around transverse cirri after protargol impregnation (cp. figures 386b–g). Cirri have two fibre bundles, except for the anteriormost frontal cirrus and the transverse cirri, which lack the posterior bundle, and the buccal cirri, which lack the anterior bundle. The fibrillar associates of the adoral membranelles depend on the zone region: membranelles of regions (a) and (b) each have a short bundle; membranelles of region (c) have a very long submembranellar bundle extending to proximal end of zone; in region (d), a fine, straight fibre occurs between the individual membranelles and extends into the buccal cavity; the membranelles of region (e) possibly lack submembranellar bundles. The paroral fibres line the right wall of the buccal cavity, while those of the endoral line the bottom. a-e – regions of adoral zone, LMR – left marginal row, LVR – left ventral row, RMR – right marginal row, RVR – right ventral row, TC – transverse cirri. Scale bar 20 μm.

Table 128. Morphometric data on *Amphisiella namibiensis*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	238.9	234.0	47.8	12.4	20.0	143.0	320.0	15
	189.8[b]	190.0	20.7	4.7	10.9	152.0	220.0	19
Body, width	57.3	53.0	12.3	3.2	21.5	41.0	84.0	15
	65.9[b]	67.0	10.3	2.4	15.6	50.0	90.0	19
Body length:width, ratio	4.3	4.2	1.0	0.3	23.7	2.8	6.3	15
	2.9[b]	2.8	0.4	0.1	15.1	2.3	4.3	19
Anterior body end to right (distal) end of adoral zone, distance	31.5	33.0	7.5	1.9	23.6	19.0	44.0	15
	24.1[b]	25.0	5.5	1.3	22.8	15.0	35.0	19
Anterior body end to proximal end of adoral zone, distance	72.5	69.0	12.3	3.2	17.0	59.0	103.0	15
	62.8[b]	62.0	5.8	1.3	9.2	50.0	70.0	19
Anterior body end to proximal end of adoral zone:body length, ratio in %	30.9	30.1	4.4	1.1	14.3	25.1	42.0	15
Anterior body end to rear end of left ventral row, distance	207.3	200.0	44.2	11.4	21.3	125.0	294.0	15
Anterior body end to rear end of right ventral row, distance	220.4	215.0	47.3	12.2	21.5	134.0	326.0	15
Anterior body end to front end of left ventral row, distance	53.2	48.0	17.8	4.6	33.4	32.0	93.0	15
Anterior body end to front end of right ventral row, distance	50.5	45.0	16.5	4.3	32.6	24.0	85.0	15
Anterior macronuclear nodule, length	27.7	28.0	3.1	0.5	11.1	24.0	35.0	15
Anterior macronuclear nodule, width	13.2	14.0	1.9	0.5	14.4	10.0	16.0	15
Micronuclei, diameter	4.1	4.0	–	–	–	4.0	5.0	15
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15
Micronuclei, number	3.6	4.0	1.1	0.3	29.3	2.0	6.0	15
Adoral membranelles, number	43.6	44.0	2.6	0.7	5.9	39.0	48.0	15
Right marginal cirri, number	50.2	51.0	4.9	1.3	9.7	42.0	61.0	15
Left marginal cirri, number	50.9	50.0	4.4	1.9	8.6	44.0	58.0	15
Right ventral row, number of cirri	43.1	42.0	3.3	0.9	7.7	38.0	50.0	15
Left ventral row, number of cirri	39.6	40.0	3.5	0.9	8.9	33.0	46.0	15
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
Cirri left of ventral rows, number	4.1	4.0	1.3	0.4	32.8	1.0	6.0	15
Buccal cirri, number	3.7	4.0	0.7	0.2	18.8	2.0	5.0	15
Transverse cirri, number	5.0	5.0	0.4	0.1	7.6	4.0	6.0	15
Dorsal kineties, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
Middle dorsal kinety, number of kinetids	29.5	29.0	2.2	0.6	7.6	27.0	34.0	15

[a] Data based, if not otherwise stated, on protargol-impregnated (WILBERT's method), mounted, and selected specimens (those deformed by the preparation were excluded) from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Cells impregnated with protargol according to FOISSNER (1991), where they are less distorted.

At species level, *Amphisiella namibiensis* resembles, due to the long ventral rows, *Pseudouroleptus buitkampi* (FOISSNER, 1982) BERGER & FOISSNER, 1987 (four macronuclear nodules, transverse cirri in vertical row; Fig. 147g), *P. terrestris* HEMBERGER, 1985 (buccal field inconspicuous, only two to three transverse cirri, ventral rows distinctly shortened; Fig. 147f), *Apoamphisiella tihanyiensis* (GELLÉRT & TAMAS, 1958) FOISSNER, 1997d (with

postperistomial cirrus and caudal cirri), *Apoamphisiella hymenophora* (STOKES, 1886a) BERGER, 1999 (with caudal and postperistomial cirri; Fig. 147d; redescription see GRIMES & L'HERNAULT 1978), *Parentocirrus hortualis* VOSS, 1997 (many macronuclear nodules, caudal cirri present), *Holosticha wrzesniowskii* (MERESCHKOWSKY, 1878) KAHL, 1932 (marine, adoral zone of membranelles about 50% of body length; Fig. 147c), and *Parauro-styla fossicola* (KAHL, 1932) BORROR, 1972a (no cirri between buccal row and ventral rows, a third ventral row commences at level of buccal vertex, postperistomial cirri present; Fig. 147e).

Amphisiella binucleata (HEMBERGER, 1985) FOISSNER, 1988

Improved diagnosis: Size about 160–300 x 30–50 µm, usually > 200 µm long in vivo. Slenderly to very slenderly lanceolate. 2 macronuclear nodules and 3 dorsal kineties. Cortical granules colourless, inconspicuous and about 1 µm across or in conspicuous clusters composed of small (about 0.5 µm) and large (up to 3 µm across) globules around bases of cirri and dorsal bristles. Amphisiellid median cirral row (ACR) extends beyond mid-body, composed of 22–67 cirri. On average 24–32 adoral membranelles, 42–81 cirri in right marginal row, 3 cirri left of ACR, 1 buccal cirrus, and 2–3 transverse cirri very near to posterior body end.

Remarks: The diagnosis is based on HEMBERGER (1985), BERGER & FOISSNER (1989a), and the present investigations. We split the species into two subspecies because of distinct differences in the cortical granules, some main morphometrics, and body shape.

Amphisiella binucleata binucleata (HEMBERGER, 1985) FOISSNER, 1988a **nov. stat.**

Diagnosis: Posterior body end bluntly pointed. Cortical granules inconspicuous, about 1 µm across. On average 24–25 adoral membranelles, 42–60 cirri in right marginal row, and 22–36 cirri in amphisiellid median cirral row.

Type location: Not given in original description, likely a forest soil near Bonn, Germany.

Remarks: Diagnosis according to HEMBERGER (1985) and BERGER & FOISSNER (1989a).

Amphisiella binucleata multicirrata **nov. sspec.** (Fig. 148a–i; Tables 129, 130, 131)

Diagnosis: Posterior body portion narrowed tail-like. Cortical granules conspicuous, form clusters composed of small (about 0.5 µm) and large (up to 3 µm across) globules around bases of cirri and dorsal bristles. On average 32 adoral membranelles, 81 cirri in right marginal row, and 67 cirri in amphisiellid median cirral row.

Type location: Soil from *Aloe dichotoma* forest near the Gariganus Guest Farm, Namibia, 26°30'S 18°25'E (site 5 in figure 2 and chapter 2.1.2).

Etymology: Composite of *multi* (many) and *cirri* (compound ciliary organelles of hypotrich ciliates), referring to the high number of cirri and adoral membranelles characterizing this subspecies.

Description: Size 180–300 × 35–65 µm in vivo, usually about 230 × 50 µm; length: width ratio about 4.5–5.5:1, in protargol preparations stouter, that is, about 4:1 on average because very soft and thus more or less inflated due to the preparation procedures (Fig. 148a–c; Table 129); dorsoventrally only slightly flattened. Elegant pisciform with tail-like posterior body portion, a conspicuous feature preserved even in most protargol-impregnated cells, which are lanceolate or clavate; invariably rather distinctly twisted about main body axis, marginal rows thus never recognizable in full length if specimens are viewed ventrally; very flexible but acontractile. Macronuclear nodules usually in middle third of cell, ellipsoidal (2.2:1) to elongate ellipsoidal (3:1), on average 2.6:1; nucleoli numerous and minute. Micronuclei near or attached to macronuclear nodules, ellipsoidal to broadly ellipsoidal, conspicuous because about 6–7 × 4–5 µm in vivo; in some specimens inflated to up to 10 µm-sized globules. Contractile vacuole slightly above mid-body at left cell margin, likely with collecting canals. Cortical granules as described in *A. multinucleata*, that is, found only around bases of cirri and dorsal bristles, colourless and globular, occasionally impregnate with protargol showing a minute, heavily argyrophilic inclusion (Fig. 148f); granules around cirri 0.8–1 µm across, clusters around dorsal bristles composed of small (about 0.5–1 µm) and large (up to 3 µm) granules. Cytoplasm colourless, contains many lipid droplets up to 10 µm across, especially in tail region, which is thus dark at low (≤ ×100) magnification. Voracious predator ingesting bacterial rods, coccal green algae, naked amoebae, heterotrophic flagellates (*Polytomella*), and medium-sized ciliates, such as *Sathrophilus muscorum*, *Colpoda maupasi*, and *C. cucullus*. Prey is ingested whole and rotates for some minutes in the food vacuoles. Movement conspicuous because slow and serpentine, showing great flexibility between soil particles; however, can also swim rather rapidly by rotation about main body axis.

Cirral pattern and number of cirri rather variable, as indicated by the high variability coefficients (Fig. 148a, b; Table 129). Frontal and transverse cirri about 20 µm, other cirri 12–15 µm long in vivo and closely spaced within rows, distances between individual cirri increase only in posterior portion of marginal rows. Marginal rows follow body curvature and thus usually distinctly spiralized, extend to near posterior body end, which bears two to four transverse cirri. Frontal cirri distinctly enlarged, form concave row with third cirrus close to distalmost adoral membranelle. Usually three slightly enlarged cirri left of anterior end of amphisiellid median cirral row. Buccal cirrus slightly enlarged, near summit of curve formed by undulating membranes. Amphisiellid median cirral row conspicuous because composed of 67 cirri occupying 82% of body length on average, commences right of distal end of adoral zone and extends obliquely to subterminal left body margin.

Dorsal bristles about 4 µm long in vivo, arranged in three rows leaving broad blank stripe in midline; rows 1 and 2 extend near left body margin and are slightly shortened anteriorly and posteriorly; row 3 extends along right body margin, anteriorly more distinctly shortened than rows 1 and 2 (Fig. 148c).

Adoral zone occupies only 15–23%, on average 19% of body length, of usual shape and structure, except for proximal half, which is widened spoon-like (Fig. 148e); composed of an

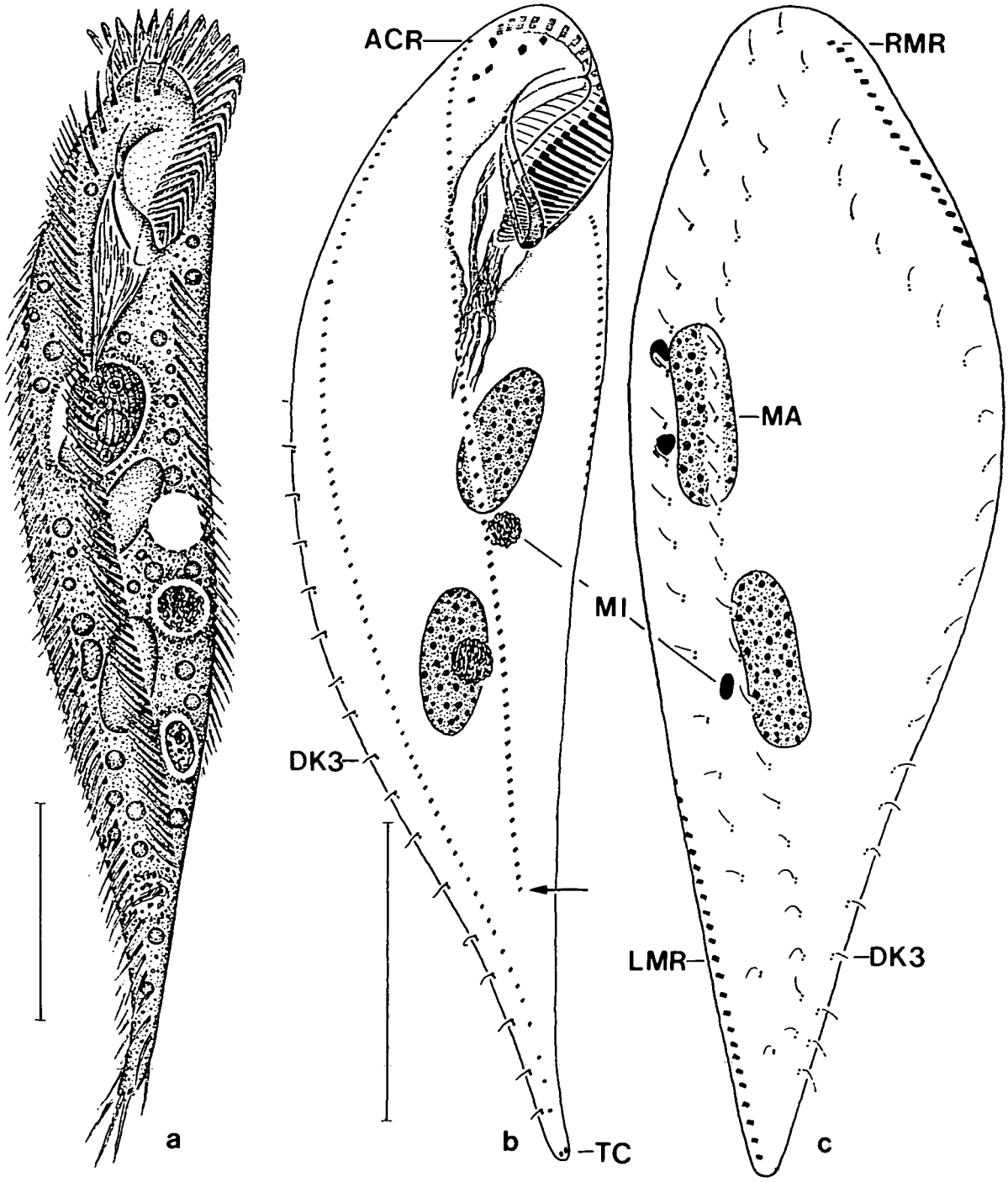

Fig. 148a–c. *Amphisiella binucleata multicirrata* from Namibian site (5) in vivo (a) and after protargol impregnation (b, c). **a:** Ventral view of a representative specimen. This new subspecies is usually longer than 200 µm and very flexible. It differs from the nominal subspecies mainly by the tail-like posterior body portion and the higher number of adoral membranelles (25 vs. 32 on average), a rather constant and thus important feature in hypotrich taxonomy. **b, c:** Infraciliature of ventral and dorsal side of two different specimens because the holotype specimen (b) is too opaque to see the dorsal side clearly. For details on the conspicuous oral apparatus, see figure 148d. Note that the specimens are rather strongly inflated due to the preparation procedures. The holotype specimen (b) has inflated micronuclei. Arrow marks end of the long amphisiellid median cirral row. ACR – amphisiellid median cirral row, DK3 – dorsal kinety 3, MA – macronuclear nodule, MI – micronuclei, LMR – left marginal row, RMR – right marginal row, TC – transverse cirri. Scale bars 50 µm.

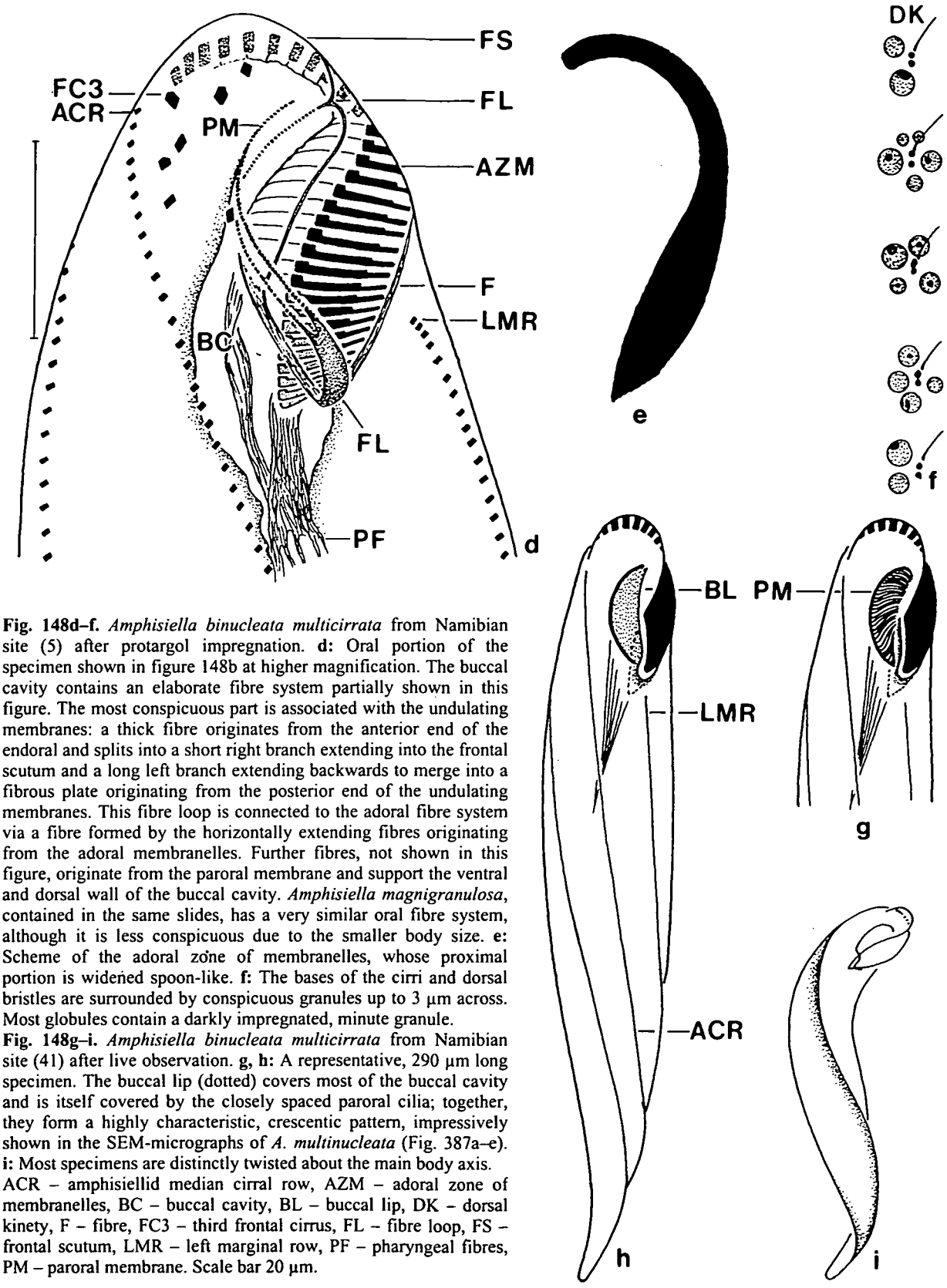

Fig. 148d–f. *Amphisiella binucleata multicirrata* from Namibian site (5) after protargol impregnation. **d:** Oral portion of the specimen shown in figure 148b at higher magnification. The buccal cavity contains an elaborate fibre system partially shown in this figure. The most conspicuous part is associated with the undulating membranes: a thick fibre originates from the anterior end of the endoral and splits into a short right branch extending into the frontal scutum and a long left branch extending backwards to merge into a fibrous plate originating from the posterior end of the undulating membranes. This fibre loop is connected to the adoral fibre system via a fibre formed by the horizontally extending fibres originating from the adoral membranelles. Further fibres, not shown in this figure, originate from the paroral membrane and support the ventral and dorsal wall of the buccal cavity. *Amphisiella magnigranulosa*, contained in the same slides, has a very similar oral fibre system, although it is less conspicuous due to the smaller body size. **e:** Scheme of the adoral zone of membranelles, whose proximal portion is widened spoon-like. **f:** The bases of the cirri and dorsal bristles are surrounded by conspicuous granules up to 3 µm across. Most globules contain a darkly impregnated, minute granule.

Fig. 148g–i. *Amphisiella binucleata multicirrata* from Namibian site (41) after live observation. **g, h:** A representative, 290 µm long specimen. The buccal lip (dotted) covers most of the buccal cavity and is itself covered by the closely spaced paroral cilia; together, they form a highly characteristic, crescentic pattern, impressively shown in the SEM-micrographs of *A. multinucleata* (Fig. 387a–e). **i:** Most specimens are distinctly twisted about the main body axis.

ACR – amphisiellid median cirral row, AZM – adoral zone of membranelles, BC – buccal cavity, BL – buccal lip, DK – dorsal kinety, F – fibre, FC3 – third frontal cirrus, FL – fibre loop, FS – frontal scutum, LMR – left marginal row, PF – pharyngeal fibres, PM – paroral membrane. Scale bar 20 µm.

Table 129. Morphometric data on *Amphisiella binucleata multicirrata* from Namibian sites 5 (upper line; type location) and 41 (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	213.1	207.0	31.7	8.2	14.9	150.0	265.0	15
	234.2	232.0	29.1	7.5	12.4	186.0	290.0	15
Body, width	51.5	52.0	8.7	2.2	16.8	36.0	63.0	15
	61.4	60.0	9.8	2.5	15.9	48.0	80.0	15
Body length:width, ratio	4.2	4.2	0.9	0.2	21.2	2.9	6.0	15
	3.9	3.8	0.4	0.1	10.0	2.9	4.6	15
Anterior body end to end of adoral zone, distance	40.3	40.0	4.7	1.2	11.7	33.0	48.0	15
	49.4	51.0	5.2	1.3	10.5	40.0	56.0	15
Body length:length of adoral zone, ratio	5.3	5.4	0.6	0.2	11.9	4.4	6.5	15
	4.8	4.5	0.5	0.1	10.9	4.0	5.6	15
Anterior body end to amphisiellid median cirral row, distance	8.3	7.0	3.3	0.9	40.0	5.0	15.0	15
	10.7	10.0	2.7	0.7	25.0	7.0	17.0	15
Anterior body end to last cirrus of amphisiellid median cirral row, distance	175.5	180.0	28.5	7.4	16.3	121.0	240.0	15
	218.3	219.0	29.2	7.5	13.4	173.0	280.0	15
Anterior body end to right marginal row, distance	7.9	9.0	3.6	0.9	44.8	0.0	14.0	15
	8.9	9.0	3.4	0.9	38.3	0.0	14.0	15
Anterior body end to paroral membrane, distance	9.6	11.0	2.9	0.7	29.9	5.0	15.0	15
	9.1	9.0	1.9	0.5	21.0	5.0	12.0	15
Anterior body end to first macronuclear nodule, distance	70.1	70.0	15.8	4.1	22.5	39.0	97.0	15
	67.3	70.0	9.8	2.5	14.5	52.0	84.0	15
Nuclear figure, length	65.7	63.0	11.7	3.0	17.7	52.0	90.0	15
	81.1	78.0	12.9	3.3	15.9	63.0	110.0	15
Macronuclear nodules, distance in between	15.3	13.0	8.9	2.3	58.1	0.0	30.0	15
	30.3	28.0	9.7	2.5	32.1	17.0	52.0	15
Macronuclear nodules, length	26.5	26.0	2.5	0.6	9.2	22.0	30.0	15
	25.9	26.0	3.8	1.0	14.6	20.0	33.0	15
Macronuclear nodules, width	10.3	10.0	0.7	0.2	6.9	9.0	12.0	15
	10.4	10.0	1.9	0.5	18.5	8.0	16.0	15
Macronuclear nodules, number	2.3	2.0	–	–	–	2.0	4.0	15
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15
Micronuclei, length [b]	4.8	5.0	0.7	0.2	13.8	4.0	6.0	13
	4.8	5.0	0.6	0.2	12.8	4.0	6.0	15
Micronuclei, width [b]	3.0	3.0	–	–	–	3.0	4.0	13
	3.0	3.0	0.2	0.1	7.6	2.5	3.5	15
Micronuclei, number	1.9	2.0	1.9	0.5	103.0	0.0	5.0	15
	4.8	4.0	3.6	0.9	74.4	1.0	15.0	15
Adoral membranelles, number	32.1	32.0	1.9	0.5	6.1	28.0	36.0	15
	39.9	41.0	3.5	0.9	8.8	34.0	45.0	15
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
Amphisiellid median cirral row, number of cirri	66.7	65.0	8.5	2.2	12.7	50.0	84.0	15
	80.7	77.0	10.3	2.7	12.8	63.0	99.0	15
Cirri left of amphisiellid median cirral row, number	3.4	3.0	0.9	0.2	26.8	3.0	6.0	15
	3.3	3.0	1.0	0.3	31.6	3.0	7.0	15
Buccal cirri, number	1.1	1.0	–	–	–	1.0	2.0	15

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Transverse cirri, number	2.6	2.0	0.8	0.2	31.9	2.0	4.0	15
	3.5	3.0	–	–	–	3.0	4.0	15
Right marginal cirri, number	80.5	82.0	9.8	2.5	12.2	65.0	98.0	15
	91.3	88.0	12.0	3.1	13.1	72.0	112.0	15
Left marginal cirri, number	73.7	75.0	8.8	2.3	12.0	60.0	89.0	15
	77.9	76.0	14.2	3.7	18.2	50.0	108.0	15
Dorsal kineties, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Inflated micronuclei, as shown in figure 148b, excluded.

average of 32 membranelles, bases of largest membranelles 10–12 µm wide in vivo. Buccal cavity deep and large as in *Cyrtohymena*, bears complicated fibre system described in explanation to figure 148d. Furthermore, the large buccal lip and the up to 20 µm long paroral cilia form a conspicuous, crescentic pattern, as shown in figures 148g, h and the SEM-micrographs of *Amphisiella multinucleata* (Fig. 387b–e). Undulating membranes distinctly curved, close together, optically intersecting near mid of buccal cavity. Pharyngeal fibres very prominent in vivo and protargol preparations, because mixed with the about 40 µm (!) long endoral cilia.

Occurrence and ecology: To date found at type location, where it was rare, and at Namibian site (41), where it was rather abundant. Although being large, the species is well-adapted to the soil environment by the slender shape and soft body. *Amphisiella binucleata multicirrata* is a voracious predator often containing several individuals of *Colpoda maupasi*.

Comparison with related species: Previous (FOISSNER 1982, 1988a) and the present investigations discovered a group of closely related amphisiellids differing mainly in the five features compiled in table 131. The Namibian site (5) population is obviously most closely related to → *A. multinucleata*, differing from that species mainly by having only two macronuclear nodules.

In 1985, HEMBERGER described *Uroleptoides binucleata* from a soil in Germany. FOISSNER (1988a) transferred it to *Amphisiella*. This species obviously belongs to the group characterized above. HEMBERGER (1985) used protargol impregnation (Table 130), but studied live specimens only very superficially, if at all. Thus, it is unknown whether *A. binucleata* has cortical granules, which effectively makes the species indeterminable, because, as shown above, the group contains species with and without cortical granules. However, BERGER & FOISSNER (1989a) identified a German population with rather inconspicuous cortical granules and which otherwise matched the HEMBERGER population rather well as *A. binucleata* (Table 130). Although this identification cannot be proven or disproven, the amended description of BERGER & FOISSNER (1989a) should be accepted because it is the most parsimonious solution of the problem.

Table 130. Comparison of main morphometrics in *Amphisiella binucleata* s.l. populations and *A. magnigranulosa*.

Characteristics [a]	*Amphisiella binucleata* s.l.			*Amphisiella magnigranulosa* FOISSNER, 1988a
	HEMBERGER (1985)	BERGER & FOISSNER (1989a)	Namibia	
Body, length	220–260	126–168 (141)	150–265 (213)	84–123 (104)
Adoral membranelles, number	24–28 (25)	22–28 (24)	28–36 (32)	21–25 (23)
Dorsal kineties, number	3	3	3	2–3 (3)
Right marginal cirri, number	60	38–46 (42)	65–98 (81)	35–54 (41)
Amphisiellid median row, number of cirri	33–40	20–24 (22)	50–84 (67)	12–19 (16)
Macronuclear nodules, number	2	2	2	2

[a] All data from protargol-impregnated specimens. Extreme values and, where available, means are given in parentheses.

Table 131. Features distinguishing a group of closely related *Amphisiella* species. Data from BERGER & FOISSNER (1989a), BUITKAMP & WILBERT (1974), FOISSNER (1982, 1988a), and the present investigations.

Species	Macronuclear nodules			Cortical granules		Dorsal kineties		ACR [a]		Body size (µm)	
	2	4	many	present	absent	2	3	above	beyond	< 200	> 200
A. acuta			+		+		+	+		+	
A. multinucleata			+	+			+		+		+
A. binucleata binucleata [b]	+			+			+		+		+
A. binucleata multicirrata [b]	+			+			+		+		+
A. longiseries		+		+			+		+	+	
A. magnigranulosa	+			+			+	+		+	
A. raptans			+	?		?			+		+
A. australis [c]	+				+		+	+		+	
A. procera	+				+	+		+		+	
A. elegans		+			+	+		+		+	

[a] Amphisiellid median cirral row ending above or near mid-body vs. distinctly beyond mid-body.

[b] For distinguishing these subspecies, see the present monograph.

[c] Now in genus *Lamtostyla*, according to ontogenetic data. Possibly, all other species of this list also belong to *Lamtostyla*.

The Namibian site (5) population differs more distinctly from *A. binucleata binucleata* than the population studied by BERGER & FOISSNER (1989a). Thus, we classify it as a subspecies, differing from the German populations mainly by the non-overlapping numbers of adoral membranelles and cirri in the amphisiellid median cirral row. Considering the tailed body,

even species status would be appropriate. However, this soft-bodied group of hypotrichs has a profound variability, and thus it is more honest to classify the Namibian population as a subspecies at the present state of knowledge. This is emphasized by the population from site (41), which was analyzed long after the paragraphs above were written. These specimens, which are well preserved, are even larger than those from site 5 (Table 129), but the cortical granules are inconspicuous, like those of *A. binucleata binucleata*, that is, pale (with a minute compact centre, however) and only 0.4–0.8 µm across.

Amphisiella binucleata multicirrata occurred together with *A. magnigranulosa* FOISSNER, 1988a at both sites. Although the extreme individuals of both species were difficult to separate in vivo, most could be easily distinguished, especially in the protargol slides, by the different length of the amphisiellid median cirral row and the tail-like, respectively, comparatively widely rounded posterior body end (Table 130). Indeed, most specimens were highly similar to those figured in the original description (FOISSNER 1988a). The oral fibre system is very similar in both species.

Amphisiella procera nov. spec. (Fig. 149a–g; Table 132)

Diagnosis: Size about 170 × 18 µm in vivo, that is, almost vermiform with posterior fifth narrowed tail-like. 2 macronuclear nodules. Amphisiellid median cirral row (ACR) ends above mid-body, composed of an average of 15 cirri. On average 20 adoral membranelles, 55 cirri in left and 57 in right marginal row, 3 cirri left of anterior end of ACR, 1 buccal cirrus, 4 transverse cirri, and 2 dorsal kineties which extend along right body margin in posterior body portion.

Type location: Rare in a soil sample under *Aloe dichotoma* (Quivertree) in Namibia, 26°25'S 18°20'E (site 7 in figure 2 and chapter 2.1.2).

Etymology: The Latin adjective *procerus* (elongate) refers to the slender body shape.

Description: Size 130–210 × 15–25 µm in vivo, length:width ratio about 9:1 in vivo and 6.1:1 on average in protargol preparations. Outline almost vermiform with posterior fifth narrowed tail-like in vivo; tail very fragile and thus rarely preserved in protargol preparations (Fig. 149a, b, e, f; Table 132); trunk dorsoventrally flattened up to 1.5:1. Extremely flexible but acontractile, often coiled about main body axis by half a turn. Usually two macronuclear nodules slightly left of midline; individual nodules elongate ellipsoidal, often dumb-bell-shaped or of irregular outline, with many medium-sized and small nucleoli. Micronuclei difficult to recognize in vivo and protargol preparations, attached to macronuclear nodules, conspicuously small (Fig. 149a, c, d, f; Table 132). Contractile vacuole with two collecting canals slightly above mid-body at left cell margin. Cortical granules lacking. Cytoplasm colourless with many lipid droplets 1–3 µm across. Feeds on sporulating bacteria digested in vacuoles about 7 µm across. Moves slowly and rather clumsily.

Cirral pattern rather constant, number of cirri of usual variability (Fig. 149a–f; Table 132). All cirri about 8 µm long in vivo, fine because usually composed of two or four cilia only (Fig. 149g). Marginal rows end slightly to distinctly subterminally, right row extends onto dorsolateral surface anteriorly. Frontal cirri slightly to distinctly enlarged, right cirrus, as is

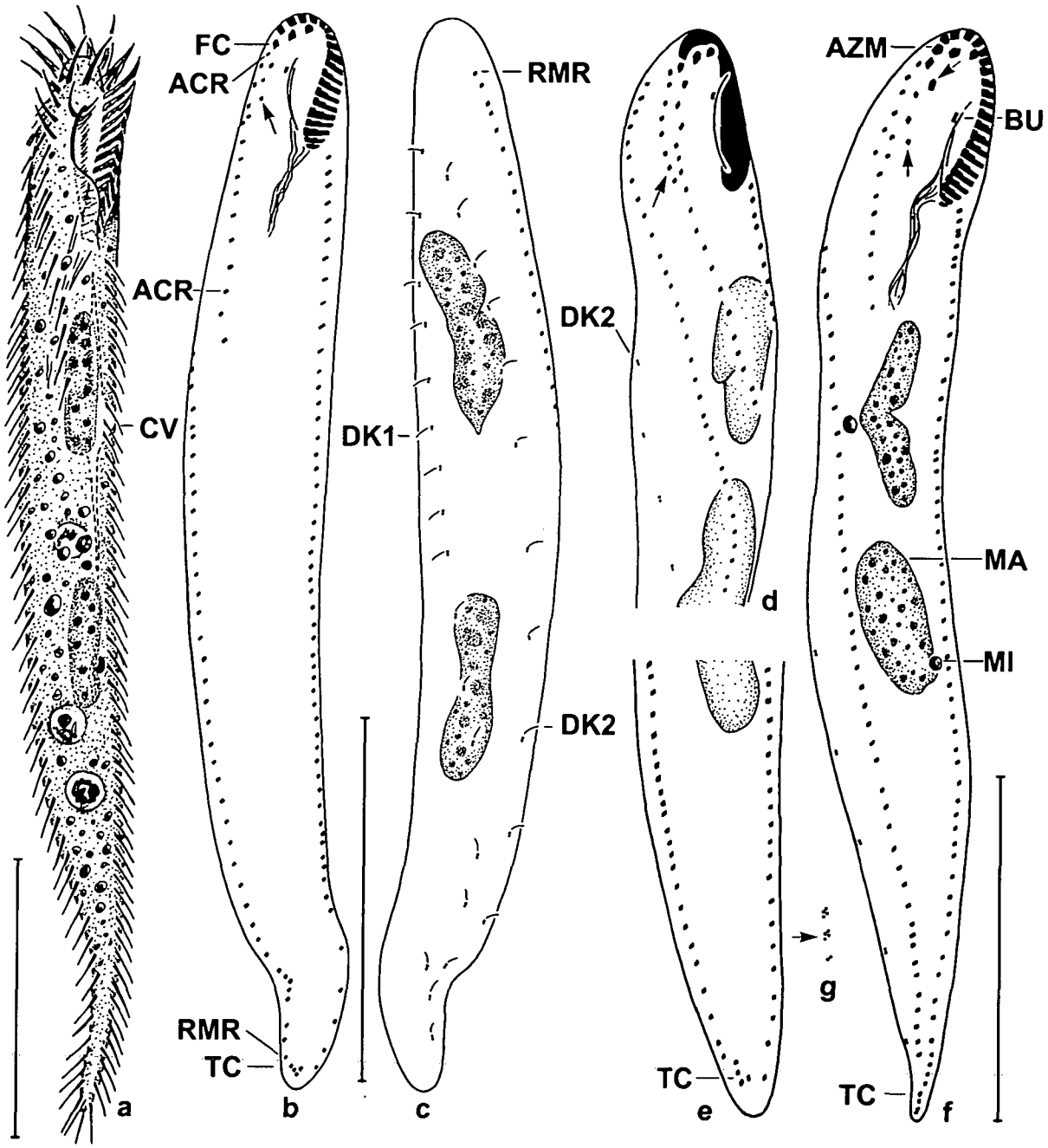

Fig. 149a–g. *Amphisiella procera*, type population from life (a) and after protargol impregnation (b–e, g), and specimen from Namibian site (9) after protargol impregnation (f). **a:** Ventral view of a representative specimen. **b, c:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrow marks three cirri left of anterior end of amphisiellid median cirral row. **d:** Ventral infraciliature of a specimen with a long amphisiellid median cirral row, which is composed of two slightly overlapping segments (arrow). **e:** Posterior portion showing inconspicuous transverse cirri, which are easily misinterpreted as marginal cirri. **f:** Infraciliature of ventral side and nuclear apparatus of a specimen with four cirri (arrows) left of the anterior end of the amphisiellid median cirral row. **g:** Most cirri are composed of four (arrow) or two cilia only. ACR – amphisiellid median cirral row, AZM – adoral zone of membranelles, BU – buccal cirrus, CV – contractile vacuole with collecting canals, DK1, 2 – dorsal kineties, FC – right frontal cirrus, MA – posterior macronuclear nodule, MI – micronucleus, RMR – right marginal row, TC – transverse cirri. Scale bars 50 µm.

usual, at distal end of adoral zone. Buccal cirrus slightly behind anterior end of undulating membranes. Type population usually with three, specimens from Namibian site (9) usually with four cirri left of anterior end of amphisiellid median cirral row (ACR; Fig. 149b, d, f); anteriormost cirrus of ACR often slightly enlarged. Amphisiellid median cirral row begins close to right frontal cirrus and terminates at 30% of body length on average, composed of two segments of unequal length, often slightly overlapping at level of buccal vertex (Fig. 149d, f). Transverse cirri inconspicuous both in vivo and after protargol impregnation because of same size as marginal cirri and often close to marginal rows.

Dorsal bristles about 3 µm long in vivo, arranged in two sparsely ciliated rows. Both rows commence subapically left of body midline and course obliquely backwards ending at right posterior margin of cell. Caudal cirri absent (Fig. 149c).

Adoral zone of membranelles occupies only 11–18%, on average 15% of body length, of usual shape and structure. Buccal cavity deep and moderately wide; anterior portion of right cavity margin thickened, posterior forms prominent lip covering proximal portion of adoral zone. Exact structure and arrangement of undulating membranes not clearly recognizable; paroral and endoral slightly to distinctly curved, almost parallel to each other, paroral cilia about 5 µm long in vivo. Pharyngeal fibres clearly recognizable in vivo and after protargol impregnation, of ordinary length and structure, extend obliquely backwards (Fig. 149a, b, d, f).

Table 132. Morphometric data on *Amphisiella procera* from Namibian sites 7 (type location; upper line) and 9 (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	129.3	126.0	16.7	4.3	13.0	112.0	172.0	15
	138.9	145.0	25.3	9.5	18.2	96.0	172.0	7
Body, width	21.6	21.5	3.1	0.9	14.4	16.0	26.0	12
	21.4	20.0	3.6	1.4	17.0	17.0	28.0	7
Body length:width, ratio	6.1	5.7	1.0	0.3	16.4	5.0	7.7	11
	6.6	6.5	1.3	0.5	19.8	4.8	8.5	7
Anterior body end to proximal end of adoral zone, distance	20.1	20.0	1.5	0.4	7.6	17.0	22.0	16
	22.3	22.0	3.3	1.2	14.8	18.0	28.0	7
Body length:length of adoral zone of membranelles, ratio	6.5	6.4	0.9	0.2	14.0	5.4	8.6	15
	6.3	6.1	1.3	0.5	20.1	4.8	8.7	7
Anterior body end to last cirrus of amphisiellid median cirral row, distance	39.4	40.0	5.0	1.2	12.6	30.0	49.0	16
	44.4	41.0	10.2	3.9	23.0	33.0	60.0	7
Body length:length of amphisiellid median cirral row, ratio	3.3	3.3	0.2	0.1	6.8	3.0	3.7	15
	3.2	3.1	0.5	0.2	16.0	2.4	3.8	7
Anterior body end to buccal cirrus, distance	7.4	8.0	1.1	0.3	14.7	6.0	9.0	16
	11.0	10.0	1.8	0.7	16.6	9.0	14.0	7
Anterior body end to anterior end of right marginal row, distance	6.5	6.0	1.3	0.3	20.3	5.0	9.0	16
	4.9	5.0	1.8	0.7	36.5	2.0	7.0	7
Anterior macronuclear nodule, length	24.3	24.0	4.1	1.1	16.9	14.0	29.0	15
	24.9	26.0	2.5	0.9	10.0	20.0	27.0	7
Anterior macronuclear nodule, width	7.4	6.5	1.7	0.4	23.0	6.0	10.0	16
	7.0	7.0	1.2	0.4	16.5	6.0	9.0	7

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Macronuclear nodules, number [b]	2.2	2.0	–	–	–	2.0	4.0	16
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	7
Anterior micronucleus, length	2.6	2.5	–	–	–	2.4	3.0	6
	2.7	2.0	–	–	–	2.0	4.0	3
Anterior micronucleus, width	2.5	2.5	–	–	–	1.6	3.0	6
	2.7	2.0	–	–	–	2.0	4.0	3
Micronuclei, number	1.7	2.0	0.8	0.3	44.1	1.0	3.0	7
	1.3	1.0	–	–	–	1.0	2.0	3
Adoral membranelles, number	20.2	20.0	1.7	0.4	8.6	17.0	23.0	15
	20.3	20.0	1.6	0.6	7.9	18.0	23.0	7
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	14
	3.1	3.0	–	–	–	3.0	4.0	7
Amphisiellid median cirral row, number of cirri	14.9	15.0	1.5	0.4	10.1	12.0	17.0	15
	15.9	15.0	4.4	1.7	27.8	11.0	23.0	7
Cirri left of amphisiellid median cirral row, number	3.2	3.0	–	–	–	3.0	4.0	13
	3.3	4.0	1.2	0.5	36.3	1.0	4.0	6
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	16
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	7
Transverse cirri, number	4.2	4.0	0.8	0.2	18.8	3.0	6.0	10
	3.5	4.0	1.9	0.8	53.5	0.0	5.0	6
Right marginal cirri, number	56.8	55.0	6.6	1.8	11.7	48.0	75.0	14
	58.9	53.0	13.4	5.1	22.7	48.0	87.0	7
Left marginal cirri, number	54.6	53.5	6.3	1.8	11.6	47.0	72.0	12
	54.9	51.0	11.8	4.5	21.6	43.0	80.0	7
Dorsal kineties, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	12
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	7

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Of 16 specimens analyzed, one had three nodules and one four.

Occurrence and ecology: To date found only at Namibian sites (7; type location) and (9). Abundance was very low in both cultures. With its slender body, *Amphisiella procera* is well-adapted to live in terrestrial habitats.

Generic assignment and comparison with related species: This species belongs either to → *Amphisiella* GOURRET & ROESER, 1888 or *Lamtostyla* BUITKAMP, 1977a because it has (i) a ventral row likely originating from two rightmost anlagen (Fig. 149d, f), (ii) more than one cirrus left of the anterior end of the amphisiellid median cirral row, (iii) transverse cirri, and (iv) lacks caudal cirri (EIGNER & FOISSNER 1994). In the absence of ontogenetic data, which separate → *Amphisiella* and *Lamtostyla* (PETZ & FOISSNER 1996), we assign it to → *Amphisiella* as defined by EIGNER & FOISSNER (1994). *Amphisiella procera* is most similar to → *A. binucleata* (HEMBERGER, 1985) FOISSNER, 1988a (redescribed by BERGER & FOISSNER 1989a). It differs from that species in the location of the buccal cirrus

(near anterior end of paroral vs. near posterior end or middle portion), cortical granules (absent vs. present), number of dorsal kineties (2 vs. 3), and the length of the ventral cirral row (1/3 of body length vs. ≥ 2/3). Further similar, but comparatively very distinct species are *A. magnigranulosa* FOISSNER, 1988a (with conspicuous cortical granules) and *Lamtostyla australis* (BLATTERER & FOISSNER, 1988), a rather small (length 90–160 µm), elongate ellipsoidal species with three dorsal kineties (BLATTERER & FOISSNER 1988, FOISSNER 1988a, VOSS 1992; detailed comparison, see Table 131). In vivo, *Amphisiella procera* is identified by the following combination of features: very slender body with distinct tail, two macronuclear nodules, very inconspicuous transverse cirri, lack of cortical granules and postperistomial ventral cirri.

Amphisiella elegans nov. spec. (Fig. 150a–d; Tables 133, 134)

Diagnosis: Size about 170 × 35 µm in vivo; narrowly lanceolate and slightly sigmoidal. Usually 4 macronuclear nodules forming 2 pairs left of midline. Amphisiellid median cirral row (ACR) ends above mid-body, composed of about 12 cirri. On average 23 adoral membranelles, about 48 cirri each in right and left marginal row, 3 cirri left of ACR, 1 buccal cirrus, 4 transverse cirri, and 2 dorsal kineties extending along right body margin in posterior body portion.

Type location: Soil from Wadi Ram about 10 km east of Al Aqaba, Jordan, 29°30'N 35°E.

Etymology: The Latin adjective *elegans* (elegant) refers to the elegant appearance of the species.

Description: This species is highly variable, even in features which are usually constant in hypotrichs. Thus, we separated specimens with four, respectively, six or more macronuclear nodules in the morphometry (Table 133). However, no clear-cut relationships emerged because, for instance, specimens with four or six macronuclear nodules may have three dorsal kineties, but all specimens with three kineties have six or more beads. Furthermore, some observations on other populations show that the Jordanian specimens do not exhaust the whole range of variability (see below).

Amphisiella elegans is, like several congeners, difficult to preserve. Only if the fixative is amended with osmium tetroxide, do they stabilize; however, the specimens from Namibian site (47) even disintegrated in osmium amended STIEVE solution.

Size 140–200 × 25–45 µm in vivo, usually about 170 × 35 µm, length:width ratio highly variable also in protargol preparations, that is, 3.4–7.6:1, on average 5:1; dorsoventrally flattened up to 2:1. Outline slender and often slightly sigmoidal with posterior end more narrowly rounded than anterior; body very flexible but acontractile, often twisted about main axis by half a turn (Fig. 150a; Table 133). Nuclear apparatus in middle third of cell left of midline. Number and arrangement of macronuclear nodules highly variable, usually a pair of nodules each above and below mid-body; in specimens with six or eight nodules, they form a strand, with one half of the nodules usually still separated from the other by a slightly increased distance. Of 56 specimens analyzed, 13 have more than the usual four macronuclear

nodules, an unusual high percentage (23%) for this kind of hypotrich. Individual nodules ellipsoidal on average and often connected by a strand of lighter impregnated material; nucleoli small and numerous. Micronuclei near or attached to macronuclear nodules, about 4 × 3 µm in vivo, number highly variable, especially in specimens with more than four macronuclear nodules (Table 133). Contractile vacuole with two collecting canals slightly above mid-body at left cell margin. Cortical granules lacking. Cytoplasm colourless, contains many lipid droplets 1–4 µm across, mainly in posterior half of cell. Feeds on small ciliates (*Pseudocohnilembus* sp., *Colpoda aspera*, swarmers of *Vorticella astyliformis*) and naked amoebae digested in vacuoles up to 30 µm across. Glides slowly and, although being very flexible, rather clumsily, possibly due to the twisted body, on microscope slide and soil particles.

Cirral pattern rather constant, while cirral number unusually variable, especially in specimens with six or more macronuclear nodules (Fig. 150a, b; Table 133). Most cirri 8–10 µm long in vivo and rather fine, especially in posterior portion of marginal rows and in median cirral row. Right marginal row extends onto dorsal side in anterior body quarter and ends far subterminally, that is, at or above level of transverse cirri. Left marginal row extends onto dorsal side in posterior body fifth to end terminally in body midline; last cirri easily misinterpreted as caudal cirri. Frontal cirri slightly enlarged, right cirrus, as is usual, at distal end of adoral zone. Buccal cirrus near summit of curve formed by paroral membrane. On average three cirri left of anterior half of amphisiellid median cirral row, which commences close to the right frontal cirrus and on average terminates at 31% of body length right of cell's midline; occasionally a distinct break in anterior third of row, showing that it is composed of at least two segments, as is typical for the group (EIGNER & FOISSNER 1994). Transverse cirri subterminally inserted, about 12 µm long in vivo, inconspicuous because fine, likely consisting of only four cilia each.

Dorsal bristles about 3 µm long in vivo, arranged in two ordinary rows or in three rows with left row very sparsely ciliated, indicating that it is a remnant of a previous generation (Fig. 150c, d). Both rows commence subapically left of or in body midline and course obliquely backwards ending at right posterior margin of cell, an unusual and highly constant pattern found also in several congeners, for instance, → *Amphisiella procera*. Caudal cirri lacking.

Adoral zone occupies only 16–23%, on average 19% of body length, of usual shape and structure, composed of an average of 23 membranelles; frontal scutum possibly unusually thick because often faintly impregnated. Buccal cavity moderately deep and wide, posterior cavity margin projects angularly partially covering adoral zone. Paroral and endoral membrane both rather distinctly curved and optically intersecting in mid-portion, likely composed of dikinetids. Paroral cilia about 7 µm long and very closely spaced forming compact, sail-like structure in vivo. Endoral cilia at least 15 µm long, beat into the pharynx, form conspicuous bundle with pharyngeal fibres extending obliquely backwards (Fig. 150a, b).

Observations on other populations: We found this or very similar species also in African soil samples (see occurrence section). Unfortunately, they did not withstand the preparation procedures, as explained above, and thus we have data only from live observations. The specimens from Namibian site (51) are only 120–130 µm long, very slender (about 7:1 in vivo), and have minute (≤ 0.2 µm), colourless cortical granules around the bases of the cirri and dorsal bristles. Furthermore, they possess some lithosomes about 3 µm across. The specimens from the highly saline sample of Saudi Arabia are very similar to those from Jordan,

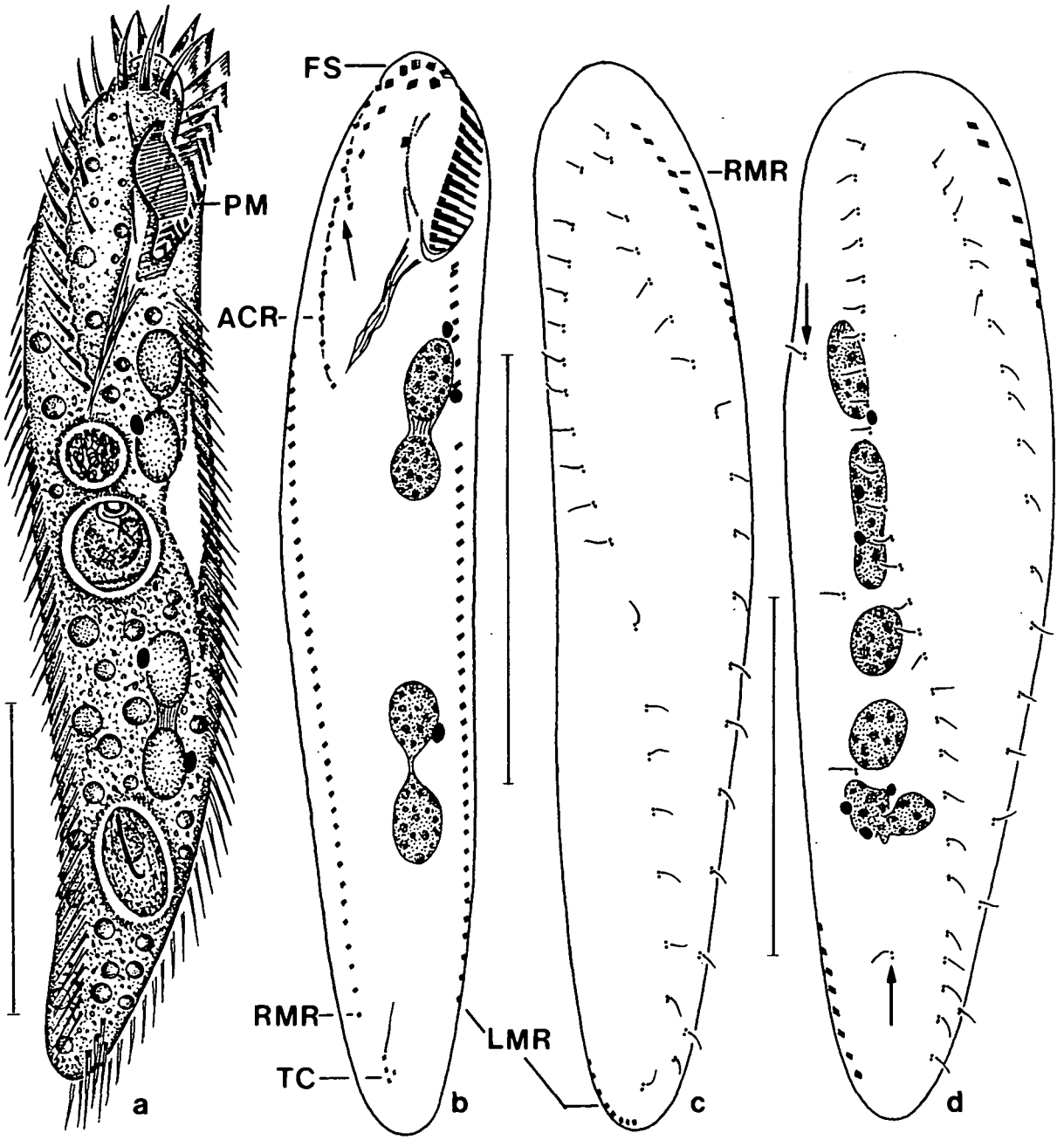

Fig. 150a–d. *Amphisiella elegans* from life (a) and after protargol impregnation (b–d). **a:** Ventral view of a representative, slightly twisted specimen. Note the sail-like paroral membrane composed of very closely spaced, 7 µm long cilia. **b, c:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrow marks break in the amphisiellid median cirral row, whose cirri are connected by lines. **d:** About 13% of the specimens have five, six, or eight macronuclear nodules and a third, loosely ciliated dorsal kinety (arrows). ACR – amphisiellid median cirral row, FS – frontal scutum, LMR – left marginal row, PM – paroral membrane, RMR – right marginal row, TC – transverse cirri. Scale bars 50 µm.

but have three buccal cirri, indicating that they might be a slender variant of *A. quadrinucleata* (Table 134). Considering the high variability of the Jordanian *A. elegans*, it seems reasonable to assign these populations to this species.

Table 133. Morphometric data on *Amphisiella elegans*. Upper line: specimens with four macronuclear nodules; middle line: specimens with five to eight, usually six macronuclear nodules; lower line: all specimens combined.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	155.0	150.0	18.8	5.0	12.1	126.0	190.0	14
	153.3	154.0	11.1	3.9	7.3	140.0	170.0	8
	154.4	150.0	16.1	3.4	10.5	126.0	190.0	22
Body, width	29.6	29.0	5.2	1.4	17.7	25.0	45.0	14
	35.4	35.0	5.6	2.0	15.9	26.0	43.0	8
	31.7	30.0	6.0	1.3	18.8	25.0	45.0	22
Body length:width, ratio	5.3	5.0	0.9	0.2	16.9	3.4	7.6	14
	4.5	4.0	0.8	0.3	18.8	3.6	6.0	8
	5.0	5.0	1.0	0.2	19.1	3.4	7.6	22
Anterior body end to proximal end of adoral zone of membranelles, distance	28.0	28.0	1.7	0.5	6.1	25.0	31.0	14
	32.9	33.0	2.9	1.0	8.8	29.0	37.0	8
	29.8	29.0	3.2	0.7	10.8	25.0	37.0	22
Body length:length of adoral zone of membranelles, ratio	5.5	6.0	0.6	0.2	10.3	4.6	6.3	14
	4.7	5.0	0.5	0.2	10.0	4.2	5.5	8
	5.2	5.0	0.7	0.1	12.5	4.2	6.3	22
Anterior body end to last cirrus of amphisiellid median cirral row, distance	47.6	47.0	9.5	2.5	20.0	34.0	73.0	14
	49.5	49.0	8.1	2.9	16.3	39.0	62.0	8
	48.3	47.0	8.9	1.9	18.3	34.0	73.0	22
Body length:length of amphisiellid median cirral row, ratio	3.3	3.0	0.5	0.1	14.1	2.3	4.0	14
	3.1	3.0	0.5	0.2	16.9	2.3	3.7	8
	3.2	3.0	0.5	0.1	14.9	2.3	4.0	22
Anterior body end to buccal cirrus, distance	10.7	11.0	0.9	0.2	8.5	10.0	13.0	14
	14.6	15.0	2.5	0.9	16.7	11.0	19.0	8
	12.1	11.0	2.5	0.5	20.6	10.0	19.0	22
Anterior body end to anterior end of right marginal row, distance	8.0	7.0	3.0	0.8	38.0	4.0	14.0	14
	11.4	11.0	4.3	1.5	37.9	5.0	18.0	8
	9.2	9.0	3.8	0.8	41.5	4.0	18.0	22
Anterior macronuclear nodule, length	12.3	13.0	1.5	0.4	12.5	10.0	15.0	14
	13.3	14.0	2.7	0.9	20.1	9.0	17.0	8
	12.6	13.0	2.0	0.4	15.9	9.0	17.0	22
Anterior macronuclear nodule, width	7.5	8.0	–	–	–	7.0	8.0	14
	6.8	7.0	1.2	0.4	17.3	5.0	9.0	8
	7.2	7.0	0.9	0.2	12.0	5.0	9.0	22
Macronuclear nodules, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	14
	6.2	6.0	0.8	0.3	13.4	5.0	8.0	8
	4.9	4.0	1.2	0.3	25.0	4.0	8.0	22
Nuclear figure, length	72.5	70.0	9.3	2.5	12.8	60.0	86.0	14
	76.4	80.0	8.4	3.0	10.9	62.0	85.0	8
	73.9	73.0	8.9	1.9	12.1	60.0	86.0	22

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Macronuclear groups, distance in between	23.9	21.0	6.1	1.6	25.5	15.0	35.0	14
	9.0	8.0	2.9	1.0	32.5	6.0	14.0	8
	18.5	20.0	8.9	1.9	48.3	6.0	35.0	22
Anterior micronucleus, length	2.4	2.5	–	–	–	2.0	3.0	14
	2.5	2.5	–	–	–	2.0	3.0	8
	2.4	3.0	–	–	–	2.0	3.0	22
Anterior micronucleus, width	2.0	2.0	–	–	–	1.5	2.0	14
	1.8	2.0	–	–	–	1.5	2.0	8
	1.9	2.0	–	–	–	1.5	2.0	22
Micronuclei, number	2.7	3.0	1.0	0.3	36.6	0.0	4.0	14
	7.5	7.0	5.0	1.8	66.1	2.0	18.0	8
	4.5	3.0	3.8	0.8	85.1	0.0	18.0	22
Adoral membranelles, number	21.7	23.0	2.0	0.5	9.3	18.0	24.0	14
	25.4	26.0	2.5	0.9	9.6	22.0	29.0	8
	23.1	23.0	2.8	0.6	12.1	18.0	29.0	22
Frontal cirri, number	2.6	3.0	0.8	0.2	29.4	1.0	3.0	14
	2.8	3.0	–	–	–	2.0	3.0	8
	2.6	3.0	0.7	0.1	25.0	1.0	3.0	22
Amphisiellid median cirral row, number of cirri	12.8	13.0	2.7	0.7	20.9	7.0	16.0	14
	11.1	12.0	5.6	2.0	50.3	4.0	20.0	8
	12.2	13.0	3.9	0.8	32.3	4.0	20.0	22
Cirri left of amphisiellid median cirral row, number	3.5	3.0	1.1	0.3	31.2	2.0	6.0	14
	2.6	2.0	1.7	0.6	64.2	0.0	5.0	8
	3.2	3.0	1.4	0.3	43.0	0.0	6.0	22
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	14
	0.8	1.0	–	–	–	0.0	1.0	8
	0.9	1.0	–	–	–	0.0	1.0	22
Transverse cirri, number	3.9	4.0	1.2	0.3	31.9	0.0	5.0	14
	3.4	4.0	1.4	0.5	41.7	1.0	5.0	8
	3.7	4.0	1.3	0.3	35.0	0.0	5.0	22
Right marginal cirri, number	47.7	46.0	5.2	1.4	10.8	43.0	63.0	14
	41.5	42.0	11.8	4.2	28.5	24.0	56.0	8
	45.5	46.0	8.5	1.8	18.7	24.0	63.0	22
Left marginal cirri, number	48.6	50.0	5.1	1.4	10.4	38.0	57.0	14
	45.9	49.0	7.8	2.7	16.9	31.0	55.0	8
	47.6	49.0	6.1	1.3	12.9	31.0	57.0	22
Dorsal kineties, number	2.3	2.0	–	–	–	2.0	3.0	14
	3.0	3.0	–	–	–	3.0	3.0	8
	2.5	3.0	–	–	–	2.0	3.0	22

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and selected (for well-preserved cells, see introduction to description) specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Occurrence and ecology: The sample from type location, kindly provided by Mag. Hubert BLATTERER (Linz), contained red sand mixed with litter from shrubs (possibly

Chenopodiaceae) and grasses, pH 6.7, salinity < 2‰. While *A. elegans* was rare at type location, an abundant population developed in brownish soil mixed with plant litter and rabbit (?) droppings from the same area. Furthermore, we found *A. elegans* in a highly saline (21‰) soil sample collected in Saudi Arabia near the village of Alqasab. Finally, we observed some specimens at Namibian sites (47) and (51), that is, in bark from *Combretum imberbe* and *Colophospermum mopane*. Thus, *Amphisiella elegans* is euryhaline and has a broad ecological range. In spite of this, we did not find it in about 1000 other samples from terrestrial habitats collected world-wide.

Generic assignment and comparison with related species: For generic assignment, see → *Amphisiella procera*. Generally, *Amphisiella elegans* differs from the quadrinucleate species compiled in table 134 and those mentioned below by the large (length ~ 150 µm vs. ≤ 100 µm after protargol impregnation), slender body (5:1 vs. ≤ 3:1), except of → *A. longiseries*, which has thrice the number of cirri in the amphisiellid median cirral row. Thus, it is easily identified in vivo. Other quadrinucleate soil hypotrichs belong to different genera: → *Terricirra matsusakai* BERGER & FOISSNER, 1989a (oral apparatus differently organized, green cortical granules; Fig. 388f, g); *Hemisincirra quadrinucleata* HEMBERGER, 1985 and → *H. namibiensis* (ventral cirral row not longer than adoral zone); → *Parakahliella halophila* (four dorsal kineties with caudal cirri, no transverse cirri); *Paraurostyla buitkampi* FOISSNER, 1982 (Fig. 147g) and *Fragmocirrus espeletiae* FOISSNER, 2000b (ventral cirral rows extend to near transverse cirri, ≥ three buccal cirri and dorsal kineties; rather broad, massive species; Fig. 136x). Further, care must be taken not to confuse *A. elegans* with binucleate congeners and *Lamtostyla* species, especially *L. australis* (BLATTERER & FOISSNER, 1988).

Table 134. Distinguishing features between *Amphisiella elegans* and other quadrinucleate soil hypotrichs.

Characteristics [a]	*Amphisiella*				*Hemiamphisiella quadrinucleata*
	elegans	→ *longiseries*	*quadrinucleata*	*vitiphila*	
Body, length	154	160–179	86	89	68
Body length:width, ratio	5	3.9–4.7	1.8	2.4	2.7
Body length:length of amphisiellid cirral row, ratio	3.2	5.5–5.9	2.6	2.4	1.5
Macronuclear nodules, number	4	4	4	4	4
Macronuclear nodules in distinct groups	yes	no	no	no	no
Adoral membranelles, number	23	24–26	17	21	22
Amphisiellid median cirral row, number of cirri	12	39–48	15	13	15
Buccal cirri, number	1	1	3	1	1
Right marginal cirri, number	46	56–75	36	33	25
Dorsal kineties, number	2–3	3	2	3	4
Cortical granules	no	yes	no	no	yes

[a] Arithmetic means from protargol-impregnated specimens. Measurements in µm. Data from FOISSNER (1984, 1987c) and BERGER & FOISSNER (1989a). For authors and combining authors, see BERGER (2001).

Amphisiella longiseries nov. spec. (Fig. 151a–g; Tables 135, 136)

Diagnosis: Size about 190 × 30 µm in vivo; very slenderly lanceolate. 4 macronuclear nodules. Cortical granules colourless, 0.5–1.5 µm across, in clusters around cirri and dorsal bristles. Amphisiellid median cirral row (ACR) extends beyond mid-body, composed of about 39 cirri. On average 24 adoral membranelles, about 56 cirri each in right and left marginal row, 3 cirri left of ACR, 1 buccal cirrus, 4 transverse cirri very near to posterior body end, and 3 dorsal kineties.

Type location: Sieved litter from bank of Bukaos River, about 80 km north of the town of Keetmanshoop, Namibia, 25°40'S 18°10'E (site 4 in figure 2 and chapter 2.1.2).

Etymology: Composite of the Latin words *longus* (long) and *series* (row), referring to the long amphisiellid median cirral row.

Description: Two populations were studied. However, since they are from rather distant locations, namely Namibia (Fig. 151a–e) and Israel (Fig. 151f, g), data are kept separate and the diagnosis and description contain only observations from the type population. The Israeli specimens, which were not studied in vivo, are highly similar to the Namibian type population, both in morphometry and the rare property that the cortical granules impregnate with protargol (Fig. 151f, g; Table 135).

Size 160–230 × 25–40 µm in vivo, usually about 190 × 30 µm; length:width ratio in vivo about 5–7:1, in protargol preparations 3.2–8.1, on average 4.7:1, that is, slightly stouter than in vivo because more or less distinctly inflated by the preparation procedures (Table 135). Outline slenderly pisciform with anterior end slightly more broadly rounded than posterior; rear portion often almost tail-like and curved rightwards, a feature preserved even in most protargol-impregnated specimens; body very flexible but acontractile, often slightly to distinctly twisted about main axis (Fig. 151a, d). Macronuclear nodules serially in middle third of cell slightly left of midline, individual nodules ellipsoidal and with small to medium-sized nucleoli. Usually one micronucleus attached to anterior and to posterior macronuclear nodule, posterior micronucleus sometimes between third and fourth nodule; individual micronuclei ellipsoidal, occasionally pyriform, conspicuous because about 5–6 × 3 µm in vivo. Contractile vacuole with lacunar collecting canals slightly above mid-body. Cortical granules as in → *Amphisiella magnigranulosa*, → *A. multinucleata*, and → *A. binucleata multicirrata*, that is, found only around bases of cirri and dorsal bristles, colourless and globular, those around bristle rows 1 and 3 usually impregnate with protargol (Fig. 151d, e), while granules of row 2 rarely impregnate, possibly due to a preparation artifact because they impregnate in the Israeli specimens (Fig. 151g). Granules around cirri about 0.5 µm across, clusters around dorsal bristles composed of small (0.5 µm) and large (up to 1.5 µm) granules (Fig. 151b, c). Cytoplasm colourless, contains many lipid droplets up to 5 µm across mainly in posterior body portion, and some food vacuoles with small ciliates (*Colpoda maupasi*) and filamentous bacteria. Movement without peculiarities, that is, swims and glides rather rapidly on microscope slide and debris showing great flexibility.

Cirral pattern and number of cirri of usual variability (Fig. 151a, d, f; Table 135). Cirri short compared to size of cell, that is, 8–10 µm long in vivo, usually composed of two rows with four cilia each, closely spaced within rows, distances between individual cirri increase slightly

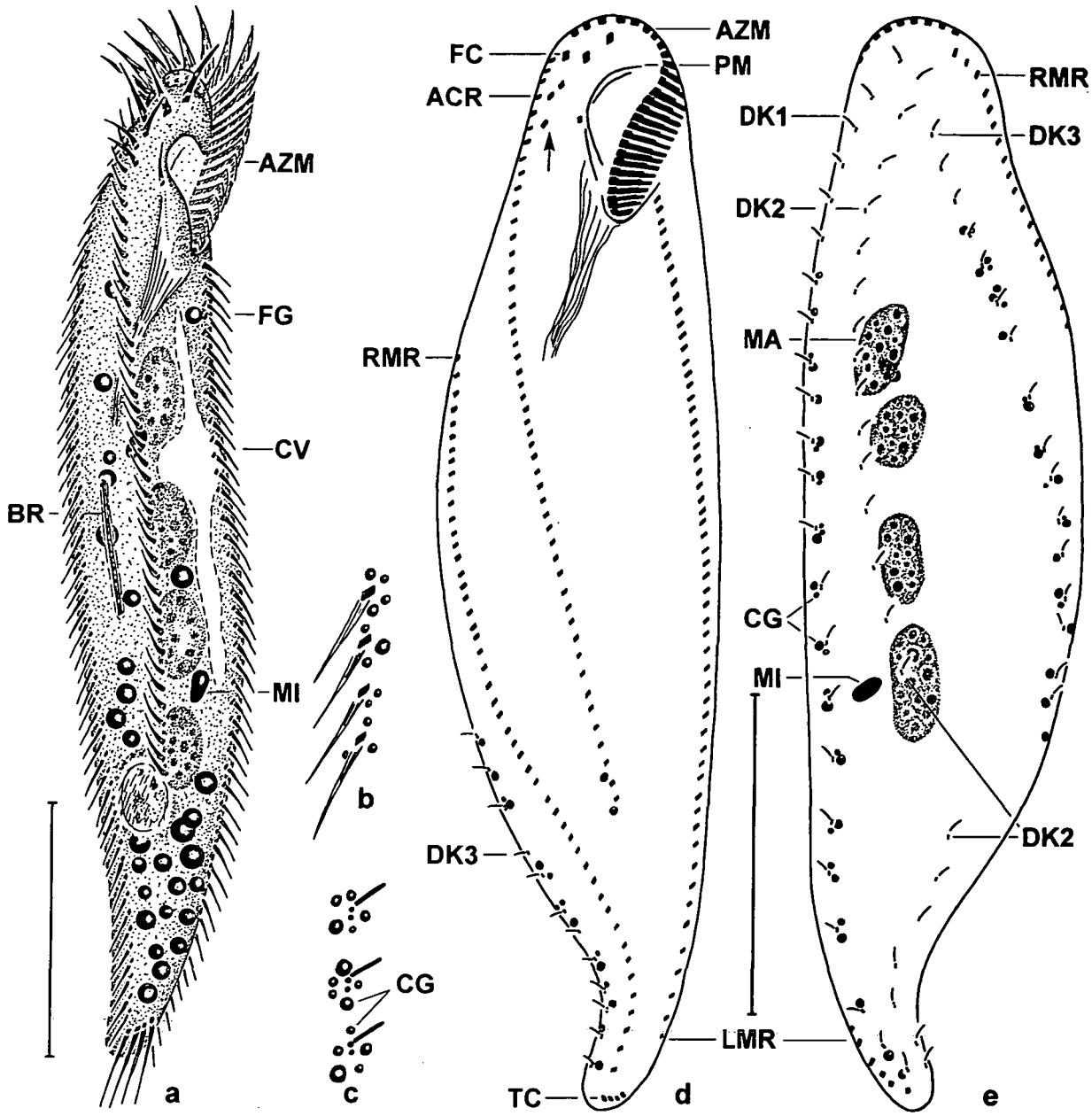

Fig. 151a–e. *Amphisiella longiseries*, type population from life (a–c) and after protargol impregnation (d, e). a: Ventral view of a representative specimen having ingested a long bacterial rod and a small ciliate. Note the short adoral zone of membranelles and the deep buccal cavity. b, c: The cortical granules around cirri and dorsal bristles are colourless and 0.5–1.5 μm across, as in several other species of the group. d, e: Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen, which is rather strongly inflated due to the preparation procedures. Arrow marks three cirri left of amphisiellid median cirral row. Note that the cortical granules are not impregnated in bristle kinety 2, which has a short break in this specimen. ACR – amphisiellid median cirral row, AZM – adoral zone of membranelles, BR – bacterial rod, CG – cortical granules, CV – contractile vacuole, DK1-3 – dorsal kineties, FC – right frontal cirrus, FG – fat globule, LMR – left marginal row, MA – macronuclear nodule, MI – micronucleus, PM – paroral membrane, RMR – right marginal row, TC – transverse cirri. Scale bars 50 μm.

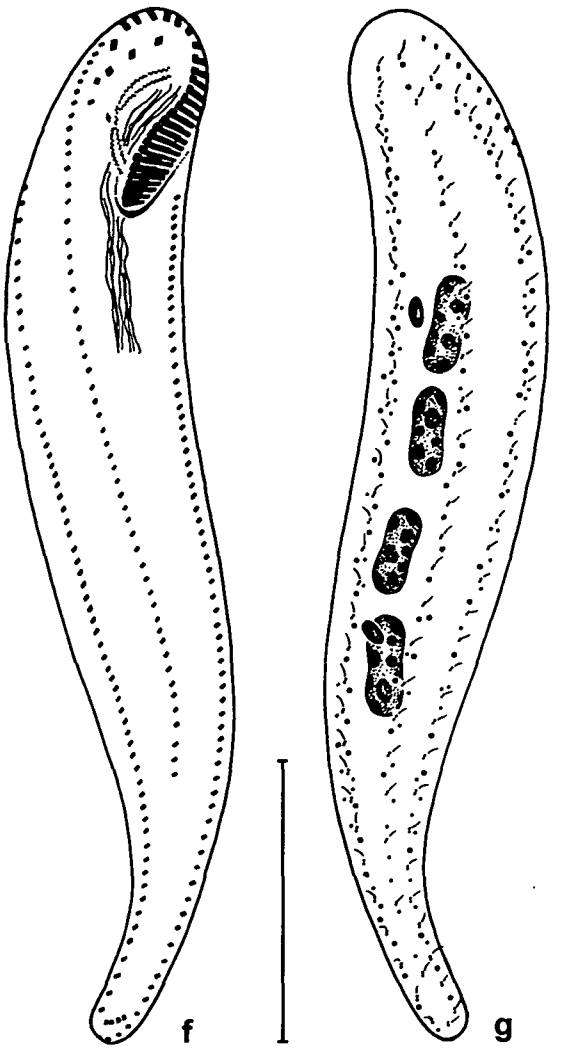

Fig. 151f, g. *Amphisiella longiseries*, infraciliature of ventral and dorsal side and nuclear apparatus of an Israeli specimen after protargol impregnation. In this population, the cortical granules of all dorsal kineties impregnate. Scale bar 50 µm.

in posterior portion of marginal rows. Right marginal row extends onto dorsolateral surface anteriorly, terminates slightly ahead of right transverse cirrus; left row ends at about same level or even at top of body. Frontal cirri distinctly enlarged and longer than marginal and ventral cirri, form concave row. Usually three cirri left of anterior end of amphisiellid median cirral row, anterior cirrus behind right frontal cirrus, middle and posterior cirrus slightly rightwards. Buccal cirrus at summit of curve formed by undulating membranes. Amphisiellid median cirral row conspicuous because terminating at 70% of body length on average, commences right of distal end of adoral zone and extends obliquely to midline in posterior body portion. Transverse cirri terminal and thus distinctly projecting, bases not larger than those of marginal cirri. Dorsal bristles about 3 µm long in vivo, arranged in three bipolar rows. Caudal cirri absent.

Adoral zone occupies 14–22%, on average 17% of body length, of usual shape and structure, except for proximal half, which is slightly spoon-like widened (Fig. 151d); composed of an average of 24 membranelles, bases of largest membranelles about 7 µm wide in vivo. Buccal cavity deep, as in *Cyrtohymena*, right margin forms curved lip covering proximal adoral membranelles and bearing paroral membrane composed of about 10 µm long, closely spaced cilia. Undulating membranes distinctly curved, optically intersecting near mid of buccal cavity. Pharyngeal fibres prominent in vivo and protargol preparations.

Occurrence and ecology: To date found at type location and in the Golan Heights, Israel (Fig. 151f, g), where it occurred in the upper layer of a moist, dark moder soil of an uncultivated grassland dominated by *Poa* sp. (collected on February 14, 1985 by Dr. Johannes AUGUSTIN, Salzburg). *Amphisiella longiseries*, which is well-adapted to soil life by the slender shape, was rare at both sites.

Comparison with related species: This species belongs to the *Amphisiella* group whose median cirral row extends beyond mid-body (Table 131). Furthermore, most (all?) taxa of this group have clusters of cortical granules around the cirri and dorsal bristles. However, they

Table 135. Morphometric data on *Amphisiella longiseries* from Namibian site 4 (type population; upper line) and Israel (lower line).

Characteristics[a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	179.2	174.0	21.3	5.9	11.9	152.0	224.0	13
	160.0	162.4	15.8	5.6	9.7	140.0	182.0	8
Body, width	40.3	38.0	9.3	2.6	23.0	24.0	60.0	13
	43.0	42.0	7.7	2.7	18.0	35.0	56.0	8
Body length:width, ratio	4.7	4.5	1.3	0.4	28.4	3.2	8.1	13
	3.9	4.2	0.9	0.3	22.6	2.5	5.2	8
Anterior body end to proximal end of adoral zone of membranelles, distance	30.4	31.0	2.1	0.6	6.9	27.0	33.0	13
	29.4	28.5	1.7	0.6	5.7	28.0	32.0	8
Body length:length of adoral zone, ratio	5.9	6.1	0.9	0.3	14.9	4.6	7.2	13
	5.5	5.4	0.7	0.2	12.0	4.4	6.5	8
Anterior body end to amphisiellid median cirral row, distance	7.3	7.5	1.9	0.5	25.7	5.0	10.0	12
	not analyzed							
Anterior body end to last cirrus of amphisiellid median cirral row, distance	123.9	123.0	13.0	3.6	10.5	106.0	152.0	13
	109.5	107.5	8.9	3.1	8.1	100.0	124.0	8
Body length:length of amphisiellid median cirral row, ratio	1.4	1.4	0.1	0.0	6.3	1.4	1.6	13
	1.5	1.5	0.2	0.1	10.1	1.3	1.8	8
Anterior body end to right marginal row, distance	6.9	6.5	1.9	0.5	27.2	4.0	10.0	12
	not analyzed							
Anterior body end to paroral membrane, distance	7.5	7.0	1.5	0.4	20.2	6.0	10.0	13
	not analyzed							
Anterior body end to first macronuclear nodule, distance	49.8	48.0	8.9	2.5	17.9	38.0	66.0	13
	not analyzed							
Nuclear figure, length	65.0	64.0	5.6	1.7	8.7	54.0	75.0	11
	not analyzed							
Anterior macronuclear nodule, length	16.5	16.0	1.7	0.5	10.1	14.0	19.0	13
	15.4	16.0	2.3	0.8	15.1	11.0	18.0	8
Anterior macronuclear nodule, width	7.8	8.0	0.7	0.2	8.8	7.0	9.0	13
	7.1	7.0	–	–	–	7.0	8.0	8
Macronuclear nodules, number[b]	4.0	4.0	0.0	0.0	0.0	4.0	4.0	13
	4.0	4.0	0.0	0.0	0.0	4.0	4.0	7
Anterior micronucleus, length	4.2	4.0	0.9	0.3	22.5	3.0	6.0	12
	4.1	4.0	0.9	0.3	21.7	3.0	5.6	8
Anterior micronucleus, width	2.7	2.5	–	–	–	2.5	3.0	12
	2.9	3.0	–	–	–	2.5	3.0	8
Micronuclei, number	1.9	2.0	–	–	–	1.0	2.0	12
	1.9	2.0	–	–	–	1.0	2.0	8
Adoral membranelles, number	24.0	23.0	2.0	0.5	8.2	22.0	27.0	13
	26.3	26.0	0.9	0.3	3.4	25.0	28.0	8
Frontal cirri, number[c]	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	8
Amphisiellid median cirral row, number of cirri	39.0	40.0	6.4	1.8	16.3	24.0	50.0	13
	47.6	46.5	3.9	1.4	8.2	43.0	54.0	8
Cirri left of anterior end of amphisiellid median cirral row, number[d]	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	8
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	8
Transverse cirri, number	3.8	4.0	0.8	0.2	19.7	2.0	5.0	11
	4.2	4.0	–	–	–	4.0	5.0	8
Right marginal cirri, number	55.8	55.0	5.8	1.7	10.3	49.0	69.0	12
	75.1	75.5	8.5	3.0	11.3	60.0	86.0	8
Left marginal cirri, number	55.8	56.0	3.8	1.1	6.9	49.0	62.0	12
	61.5	62.5	5.7	2.0	9.2	52.0	68.0	8
Dorsal kineties, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	12
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	8

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. As the species is very fragile, some drops of osmium tetroxide (2%) were added to STIEVE's fluid used for fixation. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Rarely occur specimens with six nodules in type population.

[c] Rarely occur specimens with only one frontal cirrus in type population.

[d] Rarely occur specimens with four cirri in type population.

Table 136. Comparison of main morphometrics in *Amphisiella* species with the amphisiellid median cirral row distinctly extending beyond mid-body.

Characteristics [a]	Species				
	binucleata binucleata [b]	*binucleata multicirrata* [c]	*longiseries* [d]	*raptans* [e]	*multinucleata* [f]
Body, length [µm]	220–260 126–168 (141)	150–265 (213)	152–224 (179) 140–182 (162)	300–500	188–296 (259)
Adoral membranelles, number	24–28 (25) 22–28 (24)	28–36 (32)	22–27 (24) 25–28 (26)	33	27–33 (30)
Right marginal cirri, number	60 38–46 (42)	65–98 (81)	49–69 (56) 60–86 (75)	80	85–103 (95)
Amphisiellid median cirral row, number of cirri	33–40 20–24 (22)	50–84 (67)	24–50 (39) 43–54 (48)	76	43–73 (61)
Macronuclear nodules, number	2 2	2	4 4	8	34–38 (36)

[a] All data from protargol-impregnated specimens. Extreme values and, where available, means are given in parentheses.

[b] From HEMBERGER (1985; upper line) and BERGER & FOISSNER (1989a; lower line).

[c] From table 129.

[d] Type population (upper line) and Israel population (lower line) from table 135.

[e] From BUITKAMP & WILBERT (1974).

[f] From table 137.

can be easily distinguished by the number of macronuclear nodules: two in *A. binucleata*, four in *A. longiseries*, eight in *A. raptans* (Fig. 152h), and 34–38 in *A. multinucleata*. Some further, admittedly less conspicuous differences are compiled in Table 136.

Amphisiella longiseries occurred together with *A. magnigranulosa* FOISSNER, 1988a. Both could be easily distinguished by the length of the amphisiellid median cirral row (ending underneath vs. above mid-body) and the number of macronuclear nodules (four vs. two).

Amphisiella multinucleata nov. spec. (Fig. 152a–g, i–m; 387a–e; Table 137)

Diagnosis: Size about 250–300 × 30–40 µm in vivo. Very slender and narrowed posteriorly. Cortical granules colourless, form clusters composed of small (about 0.5 µm) and large (up to 3 µm across) globules around cirri and dorsal bristles. Amphisiellid median cirral row (ACR) extends beyond mid-body, composed of an average of 53–61 cirri. On average 35–48 macronuclear nodules, 30 adoral membranelles, about 90 cirri each in right and left marginal row, 4 cirri left of ACR, 1 buccal cirrus, 3 transverse cirri, and 3 dorsal kineties.

Type location: Mud and soil from road puddles in the Bambatsi Guest Farm, Namibia, 20°10'S 15°25'E (site 49 in figure 2 and chapter 2.1.2).

Etymology: The Latin adjective *multinucleata* (having many nuclei) refers to the numerous macronuclear nodules.

Remarks: In eight protargol slides from the type locality, we found only six specimens, including one reorganizer. Furthermore, the impregnation was of mediocre quality because the fixative had to be amended with osmium tetroxide for better preservation of this fragile organism. Thus, we could not clarify all details necessary for a perfect description and generic classification. However, we later found three further populations, whereby the one from Kenya matches the type material very well in almost all features, so that conspecificity is beyond reasonable doubt (Fig. 152i–m; Table 137). The Namibian site (52; Table 137) and Venezuelan (Fig. 387a–e) specimens also agree with the type population in the main features, such as cirral pattern, oral apparatus including number of adoral membranelles, nuclear figure, and cortical granulation. However, they are about one third smaller and thus the number of cirri is lower in the amphisiellid median cirral row and the marginal rows. Possibly, these populations form a distinct subspecies. Hence, the data are kept separate, while the Kenyan observations, reported below, are included in the diagnosis.

Description of type population: Size 250–350 × 30–50 µm in vivo, length:width ratio about 7.7:1 both in vivo and after protargol impregnation (Table 137). Outline very elongate cuneate with anterior end more broadly rounded than posterior; body very flexible and slightly to distinctly spiralized about main axis (Fig. 152a, e, f). Macronuclear nodules in second to fifth sixth of cell, globular, ellipsoidal to elongate ellipsoidal, or even slightly dumb-bell-shaped, on average ellipsoidal (2:1); nucleoli numerous and minute. Micronuclei about 4 µm across in vivo. Contractile vacuole with conspicuous collecting canals, distinctly above mid-body at left cell margin. Cortical granules around cirri and dorsal bristles, colourless and globular, occasionally some impregnate with protargol; granules around cirri usually about 0.8 µm across, those around cirri of amphisiellid median row sometimes larger;

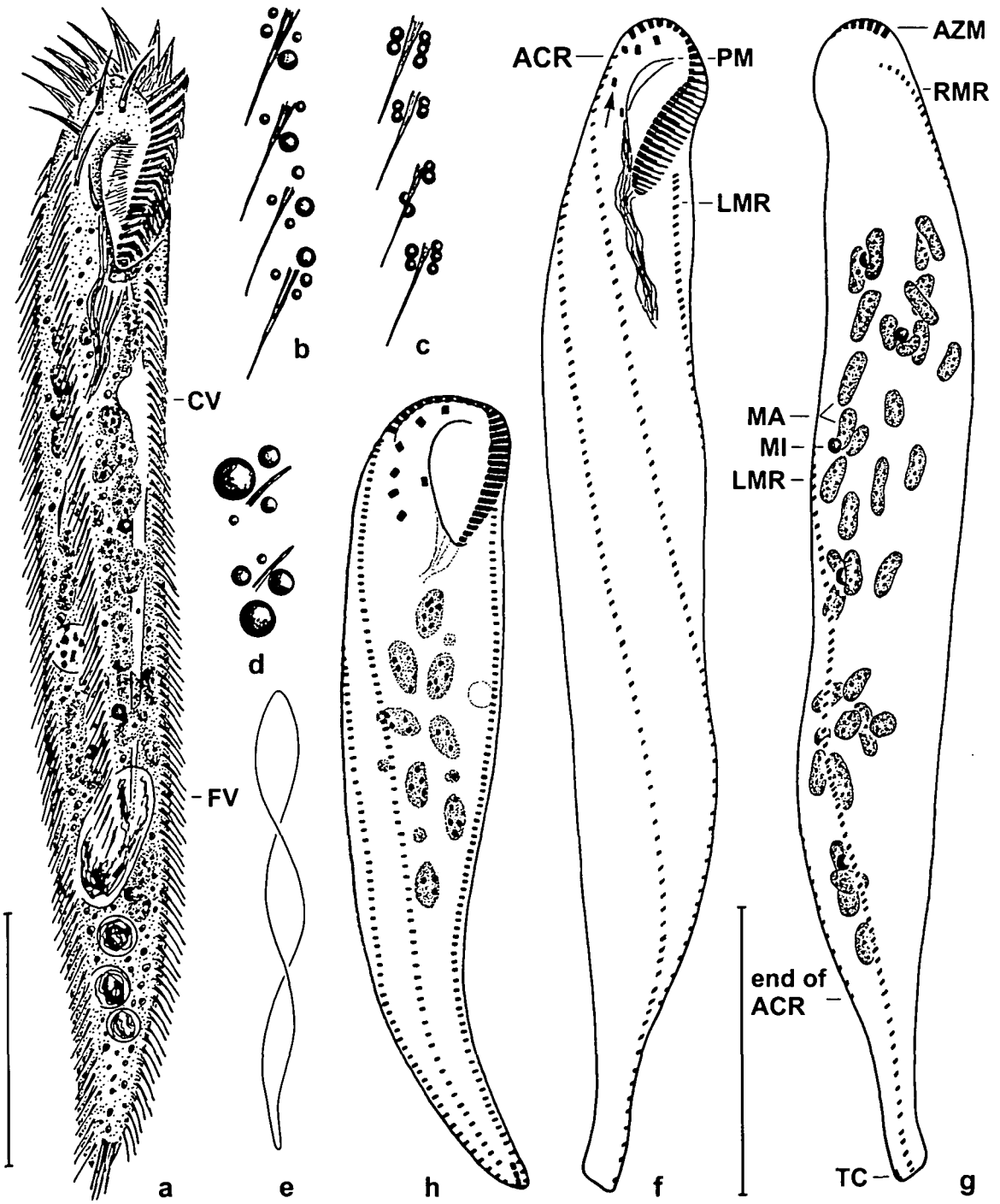

Fig. 152a–g. *Amphisiella multinucleata* from life (a–e) and after protargol impregnation (f, g). **a:** Ventral view of a representative specimen. **b–d:** Cortical granules around cirri (b, c) and dorsal bristles (d), granules 0.5–3 µm across. **e:** Strongly spiralized specimen. **f, g:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrow denotes a single cirrus left of the anterior end of the amphisiellid cirral row. Dorsal bristle rows impregnated incompletely and are thus not shown. ACR – amphisiellid median cirral row, AZM – adoral zone of membranelles, CV – contractile vacuole, FV – large food vacuole with a ciliate, LMR – left marginal row, MA – macronuclear nodules, MI – one of several micronuclei, PM – paroral membrane, RMR – right marginal row, TC – transverse cirri. Scale bars 70 µm.

Fig. 152h. *Amphisiella raptans*, ventral view after protargol impregnation (WILBERT's method), length 330 µm (from BUITKAMP & WILBERT 1974).

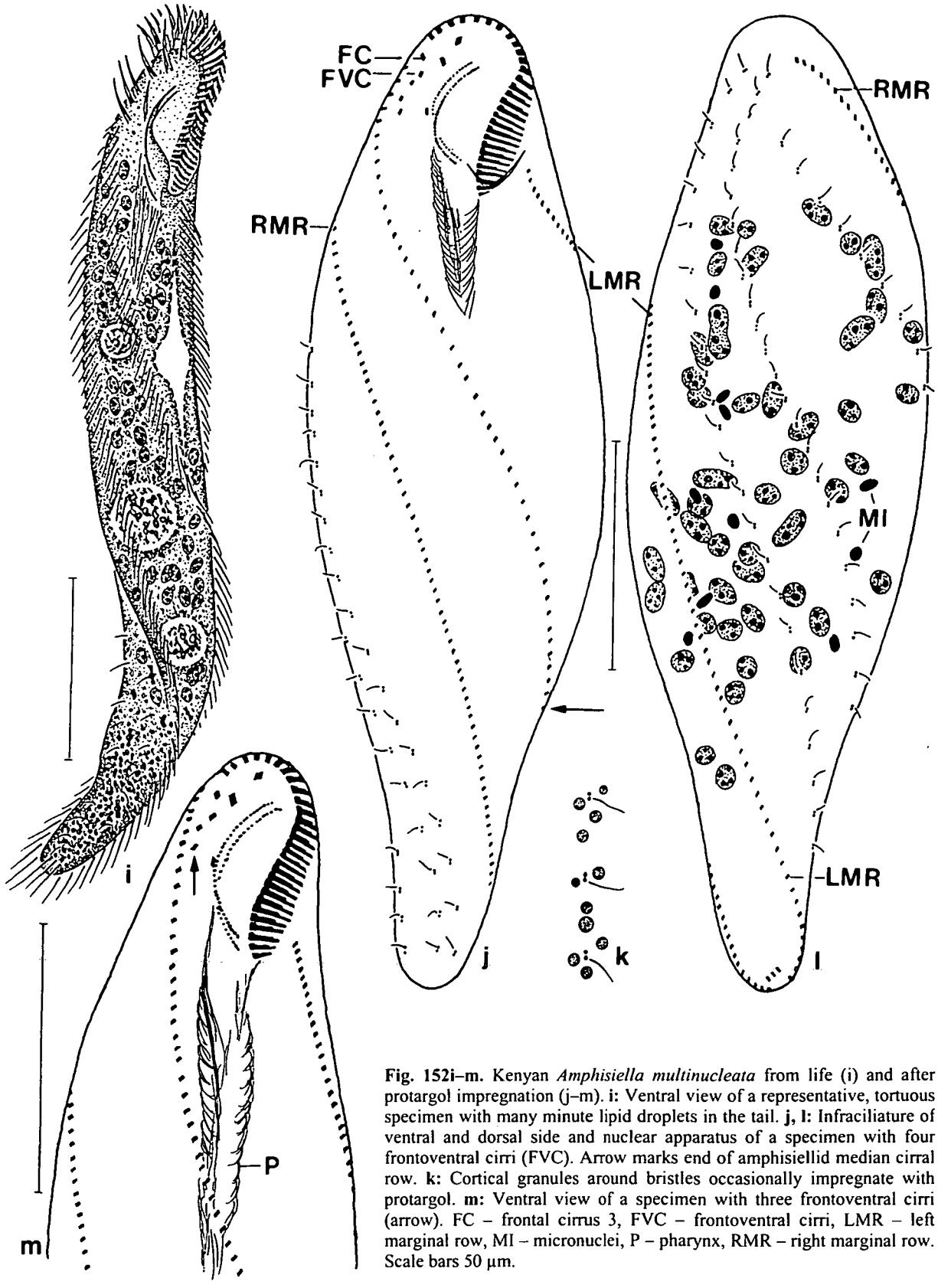

Fig. 152i–m. Kenyan *Amphisiella multinucleata* from life (i) and after protargol impregnation (j–m). **i:** Ventral view of a representative, tortuous specimen with many minute lipid droplets in the tail. **j, l:** Infraciliature of ventral and dorsal side and nuclear apparatus of a specimen with four frontoventral cirri (FVC). Arrow marks end of amphisiellid median cirral row. **k:** Cortical granules around bristles occasionally impregnate with protargol. **m:** Ventral view of a specimen with three frontoventral cirri (arrow). FC – frontal cirrus 3, FVC – frontoventral cirri, LMR – left marginal row, MI – micronuclei, P – pharynx, RMR – right marginal row. Scale bars 50 µm.

clusters around dorsal bristles composed of small (about 0.5 µm) and large (up to 3 µm) granules (Fig. 152b–d). Cytoplasm colourless, contains many fat globules 1–3 µm in diameter. Voracious predator ingesting ciliates and flagellates (*Polytomella*) digested in food vacuoles up to 50 µm across. Movement conspicuous because very slow and serpentine, showing great flexibility between soil particles.

Cirral and dorsal bristle pattern could not be recognized in every detail (but see Kenyan population). Marginal cirri about 10 µm long in vivo, that is, short compared to size of cell, arranged in two rows unshortened posteriorly, right row extends onto dorsal surface anteriorly. Frontal cirri about 15 µm long in vivo and distinctly enlarged, right one, as is usual, at distal end of adoral zone. Buccal cirrus close to summit of paroral membrane. Number of cirri left of anterior portion of amphisiellid median cirral row difficult to recognize due to reasons mentioned above: one specimen unequivocally with only one cirrus, three specimens very likely with two cirri, and one likely with three. Amphisiellid median cirral row begins close to distal end of adoral zone and terminates at 71% of body length on average, composed of about 61 cirri. Transverse cirri terminal, only 15 µm long and thus inconspicuous in vivo; prominent fibres extend from transverse cirri anteriad. Dorsal bristles 3–4 µm long in vivo, likely arranged in three rows. Caudal cirri lacking (Fig. 152a, f, g).

Adoral zone occupies only 13–18%, on average 15% of body length, of usual shape and structure, except for proximal half, which widens spoon-like (Fig. 152a, f; Table 137); composed of an average of 30 membranelles, bases of largest membranelles about 12 µm wide in vivo. Buccal cavity deep and large, as in *Cyrtohymena*, right posterior margin forms inconspicuous lip covering only few proximal adoral membranelles (but see new observations on a Venezuelan population described below). Undulating membranes distinctly curved and optically intersecting near mid, roughly as in *Cyrtohymena*. Pharyngeal fibres very prominent in vivo and protargol preparations, extend obliquely backwards, likely mixed with long endoral cilia.

Observations on a Kenyan population (Fig. 152i–m; Table 137): As described in the occurrence section, *Amphisiella multinucleata* was found also in a soil sample from Kenya. The data match well, suggesting conspecificity. Some supplementary observations and a more detailed morphometric analysis define the species more exactly: (i) cells distinctly broadened in the protargol slides because some in vivo measurements show that they are as slender as those from Namibia, viz., 260 × 30 µm, 230 × 32 µm, 230 × 30 µm; (ii) morphometrics independent of the preparation procedures match very well, for instance, the number of adoral membranelles and marginal cirri; (iii) cortical granules, although rather large, easily overlooked because very hyaline, but occasionally impregnate with protargol; (iv) all in vivo observations match well; (v) cirri conspicuously short, viz., 8 µm, as in the Namibian specimens, except the transverse cirri, which are 20 µm long; (vi) there are three to six, usually four cirri right of the amphisiellid median cirral row and two to five, on average three transverse cirri in a short, oblique row; (vii) buccal field deep and almost semicircular; (viii) there are three bipolar dorsal kineties without caudal cirri.

Observations on a Namibian site (52) population (Table 137): Size 140–210 × 20–35 µm in vivo and thus about one third smaller than type and Kenyan specimens; length:width ratio around 7:1 both in vivo and after protargol impregnation. Micronuclei ellipsoidal. Cytoplasm with many fat globules 1–10 µm across and 10 µm-sized food vacuoles containing heterotrophic flagellates. Cortical granulation as in type population.

Table 137. Morphometric data on *Amphisiella multinucleata*.

Characteristics[a]	Pop[b]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	N49	259.4	281	43.7	19.5	16.8	188.0	296.0	5
	N52	173.1	168.0	19.3	4.2	11.2	138.0	204.0	21
	KEN	207.8	210.0	20.5	5.7	9.9	172.0	240.0	13
Body, width	N49	34.0	32.0	6.3	2.8	18.6	28.0	44.0	5
	N52	26.7	26.0	3.3	0.7	12.5	20.0	34.0	21
	KEN	64.3	63.0	5.1	1.4	7.9	56.0	73.0	13
Body length:width, ratio	N49	7.7	7.8	1.0	0.4	12.4	6.7	8.9	5
	N52	6.5	6.7	0.7	0.2	10.5	5.4	7.8	21
	KEN	3.2	3.3	0.3	0.1	9.5	2.8	3.8	13
Anterior body end to end of adoral zone, distance	N49	38.0	39.0	3.9	1.8	10.4	34.0	43.0	5
	N52	33.1	32.0	2.3	0.5	6.8	30.0	38.0	21
	KEN	38.8	39.0	3.6	1.0	9.4	30.0	43.0	13
Body length:length of adoral zone, ratio	N49	6.8	7.1	0.8	0.4	11.9	5.5	7.6	5
	N52	5.2	5.3	0.4	0.1	7.5	4.3	5.9	21
	KEN	5.4	5.4	0.7	0.2	12.8	3.9	6.5	13
Anterior body end to last cirrus of amphisiellid median cirral row, distance	N49	183.6	165.0	36.9	16.5	20.1	152.0	237.0	5
	N52	90.0	87.0	15.6	3.5	17.3	64.0	124.0	20
	KEN	153.5	145.0	16.0	4.4	10.4	135.0	180.0	13
Body length:length of amphisiellid cirral row, ratio	N49	1.4	1.4	0.3	0.1	21.7	1.2	2.0	5
	N52	1.9	1.9	0.2	0.0	9.6	1.5	2.4	20
	KEN	1.4	1.4	0.1	0.1	6.9	1.2	1.5	13
Anterior body end to buccal cirrus, distance	N49	17.2	17.0	3.2	1.4	18.6	13.0	22.0	5
	N52	15.8	16.0	1.1	0.3	6.7	14.0	18.0	12
Anteriormost macronuclear nodule, length	N49	11.4	12.0	2.4	1.1	21.1	8.0	14.0	5
	N52	7.5	8.0	2.5	0.5	32.9	4.0	13.0	21
	KEN	9.3	9.0	1.9	0.5	20.5	5.6	13.0	13
Anteriormost macronuclear nodule, width	N49	5.2	6.0	1.1	0.5	21.1	4.0	6.0	5
	N52	3.9	4.0	0.6	0.1	16.0	3.0	5.0	21
	KEN	4.6	4.2	–	–	–	4.0	5.6	13
Macronuclear nodules, number	N49	35.6	35.0	1.8	0.8	5.1	34.0	38.0	5
	N52	26.0	26.0	4.0	1.0	15.3	17.0	32.0	17
	KEN	47.5	50.0	7.5	2.1	15.7	32.0	60.0	13
Anterior micronucleus, length	N49	3.8	3.0	1.1	0.5	28.8	3.0	5.0	5
	N52	4.0	4.0	0.7	0.2	17.8	3.0	5.0	15
	KEN	5.0	5.6	0.8	0.2	16.4	3.0	5.0	13
Anterior micronucleus, width	N49	2.7	2.5	–	–	–	2.5	3.0	5
	N52	1.8	2.0	–	–	–	1.5	2.0	15
	KEN	2.7	2.8	–	–	–	2.2	3.0	13
Micronuclei, number	N49	6.6	7.0	–	–	–	6.0	7.0	5
	N52	2.9	3.0	1.5	0.4	50.9	1.0	6.0	14
	KEN	8.9	8.0	3.9	1.1	44.0	5.0	20.0	13
Adoral membranelles, number	N49	30.0	30.0	2.2	1.0	7.5	27.0	33.0	5
	N52	28.4	28.0	2.4	0.6	8.4	25.0	33.0	15
	KEN	29.3	29.0	1.2	0.3	4.0	28.0	32.0	13
Frontal cirri, number	N49	3.0	3.0	0.0	0.0	0.0	3.0	3.0	5
	N52	3.0	3.0	0.0	0.0	0.0	3.0	3.0	6

(continued)

Characteristics[a]	Pop[b]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	KEN	.0	3.0	0.0	0.0	0.0	3.0	3.0	13
Amphisiellid median cirral row, number of cirri	N49	61.2	63.0	11.9	5.3	19.5	43.0	73.0	5
	N52	34.2	35.0	5.5	1.5	16.2	22.0	43.0	13
	KEN	52.5	53.0	4.4	1.2	8.4	46.0	61.0	13
Cirri left of amphisiellid median cirral row, number	KEN	3.9	4.0	1.0	0.3	24.5	3.0	6.0	13
Buccal cirri, number	N49	1.0	1.0	0.0	0.0	0.0	1.0	1.0	5
	N52	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13
	KEN	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13
Right marginal cirri, number	N49	95.3	96.5	7.5	3.8	7.9	85.0	103.0	4
	N52	72.0	73.5	14.2	3.1	16.2	51.0	90.0	14
	KEN	90.5	90.0	12.1	3.3	13.3	73.0	106.0	13
Left marginal cirri, number	N49	88.5	90.5	5.9	3.0	6.7	80.0	93.0	4
	N52	68.6	67.5	8.3	2.2	12.1	56.0	85.0	14
	KEN	80.3	79.0	10.1	2.8	12.6	67.0	102.0	13
Transverse cirri, number	KEN	3.4	3.0	0.9	0.2	25.7	2.0	5.0	13
Dorsal kineties, number	KEN	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13

[a] Data based on mounted and protargol-impregnated (FOISSNER's protocol) specimens from non-flooded Petri dish cultures. The Kenyan specimens were randomly selected, while all five specimens available from the type population and all usable specimens from Namibian site (52) were analyzed. Data from type population inexact because of mediocre preparations (see text). Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] N49 – type population from Namibian site (49), N52 – Namibian site (52) population, KEN – Kenyan population.

Almost invariably four transverse cirri. Three dorsal kineties easily recognizable in vivo due to the cortical granule clusters around the individual bristles. Paroral cilia up to 10 µm long and very closely spaced forming a conspicuous, almost semicircular, plate-like membrane.

Observations on the oral apparatus of a Venezuelan population (Fig. 387a–e): The South American specimens resemble the Namibian site (52) population in most morphometrics, that is, cells are about one third smaller than those of the type population. The SEM micrographs show a peculiarity not previously documented, namely, a large plate, likely the buccal lip, covering the semicircular, *Cyrtohymena*-like buccal field (Fig. 387b–e; arrowheads). Obviously, this structure is very hyaline because it was not recognized in vivo. Furthermore, it is masked by the paroral membrane, whose tightly spaced, up to 10 µm long cilia form a velum of similar size and shape. Further details, see figure explanations.

Occurrence and ecology: In Africa as yet found at type location (Namibian site 49), where it was very rare, in dung balls formed by a large *Scarabaeus* (Namibian site 52) with moderate abundance, and in Kenya (red soil under shrubs and trees in the Escarpment Mountains near the village of Limuru, surroundings of Nairobi, pH 6.6), where it was numerous. The Venezuelan population occurred in mosses from a rain forest near the village of Pavoni, south of Puerto Ayacucho, 05°40'N 67°38'W.

Generic classification and comparison with related species: This large species is classified in *Amphisiella* GOURRET & ROESER, 1888 because it lacks caudal cirri and has more than one cirrus left of the amphisiellid median cirral row (EIGNER & FOISSNER 1994, PETZ & FOISSNER 1996). *Amphisiellides* FOISSNER, 1988a, *Paramphisiella* FOISSNER, 1988a, and *Hemiamphisiella* FOISSNER, 1988a have caudal cirri.

Amphisiella multinucleata is obviously most closely related to *A. raptans* BUITKAMP & WILBERT, 1974 (Fig. 152h). This 300–500 µm long species from a Canadian prairie soil has only eight macronuclear nodules (vs. more than 26 on average in *A. multinucleata*) and lacks cortical granules. However, such granules might have been overlooked by BUITKAMP & WILBERT (1974), who did not study live specimens in detail. If further investigations show that *A. raptans* has cortical granules, *A. multinucleata* should probably be ranked as a subspecies with smaller size and distinctly more macronuclear nodules. As concerns the cortical granules, their pattern and size highly resembles that of → *A. magnigranulosa*, which, however, has only two macronuclear nodules. *Paramphisiella acuta* (FOISSNER, 1982) FOISSNER, 1988a, which also has more than 30 macronuclear nodules on average, differs from *Amphisiella multinucleata* by the generic characters and the lack of cortical granules (re-checked in protargol slides), the shorter amphisiellid median cirral row (40% vs. 53–71% of body length on average), and the distinctly lower number of adoral membranelles (about 15 vs. 28–30) and marginal cirri (45 left and 46 right vs. 69–88 and 72–95 on average). In vivo, *Amphisiella multinucleata* is characterized by the following combination of features: large and slender body (about 175–300 × 25–40 µm; ratio body length:width approximately 7–8:1), about 26–48 macronuclear nodules, cortical granules around cirri and dorsal bristles, amphisiellid median cirral row usually extending to posterior third of body.

Amphisiella polycirrata BERGER & FOISSNER, 1989 (Fig. 153a–d)

Since the original description, we have found this species in terrestrial habitats from Brasil, Republic of South Africa, Kenya, and Namibia, indicating that it is cosmopolitan. *Amphisiella polycirrata* is a conspicuous ciliate differing from *A. terricola* GELLÉRT, 1956, its presumed nearest relative, by body size (> 150 µm vs. < 150 µm), number of buccal cirri (4–8 vs. 1), and length of ventral cirral row (abutting on transverse cirri vs. more or less distinctly shortened). As these features are stable, *Amphisiella polycirrata* is easily identified.

The original description lacks an illustration of a living specimen because "in vivo this species looks so similar to *Amphisiella terricola* GELLÉRT, 1955, that we considered it unnecessary to draw the living aspect" (BERGER & FOISSNER 1989a). This is confirmed by the new observations. However, we want to emphasize several features, especially the lack of cortical granules in all six populations studied, and thus provide a description and a figure of the live aspect of the specimens from Namibian site (51).

Size about 170–200 × 40–60 µm in vivo. Elongate ellipsoidal (about 4:1) with both ends broadly rounded in ordinary specimens (Fig. 153a), bursiform when packed with large food inclusions (Fig. 153b); flattened dorsoventrally up to 3:1. Two ellipsoidal macronuclear nodules (30 × 15 µm in vivo) in usual position and several conspicuously large (6 µm across) micronuclei. Contractile vacuole with inconspicuous collecting canals in mid-body. Cortex

colourless, very flexible, without specific granules. Cytoplasm hyaline because free of refractive crystals, but frequently packed with lipid droplets up to 15 µm across postorally, making cells dark at low magnification (≤ ×100). Feeds on small (*Cyrtolophosis mucicola*) and medium-sized ciliates (*Colpoda*), and likely also on heterotrophic flagellates. Moves rather rapidly on microscope slide and between organic debris, showing great flexibility.

Cirri thick but not exceedingly long, marginal cirri 17 µm, transverse cirri (mostly four) about 23 µm long and hardly projecting from body proper because subterminally located. Six to eight buccal cirri form conspicuous row in all populations. Ventral cirral row extends to transverse cirri. Buccal cavity, although rather narrow, conspicuous because deep and extending to adoral zone of membranelles anteriorly. Buccal lip inconspicuous. About 45–50 adoral membranelles each in Brazilian, South African, and Namibian specimens, while only 35–38 ($\bar{x}$ = 37) membranelles in the few specimens analyzed from the Madeiran type population. However, the Madeiran population was weak, and thus such differences are to be expected.

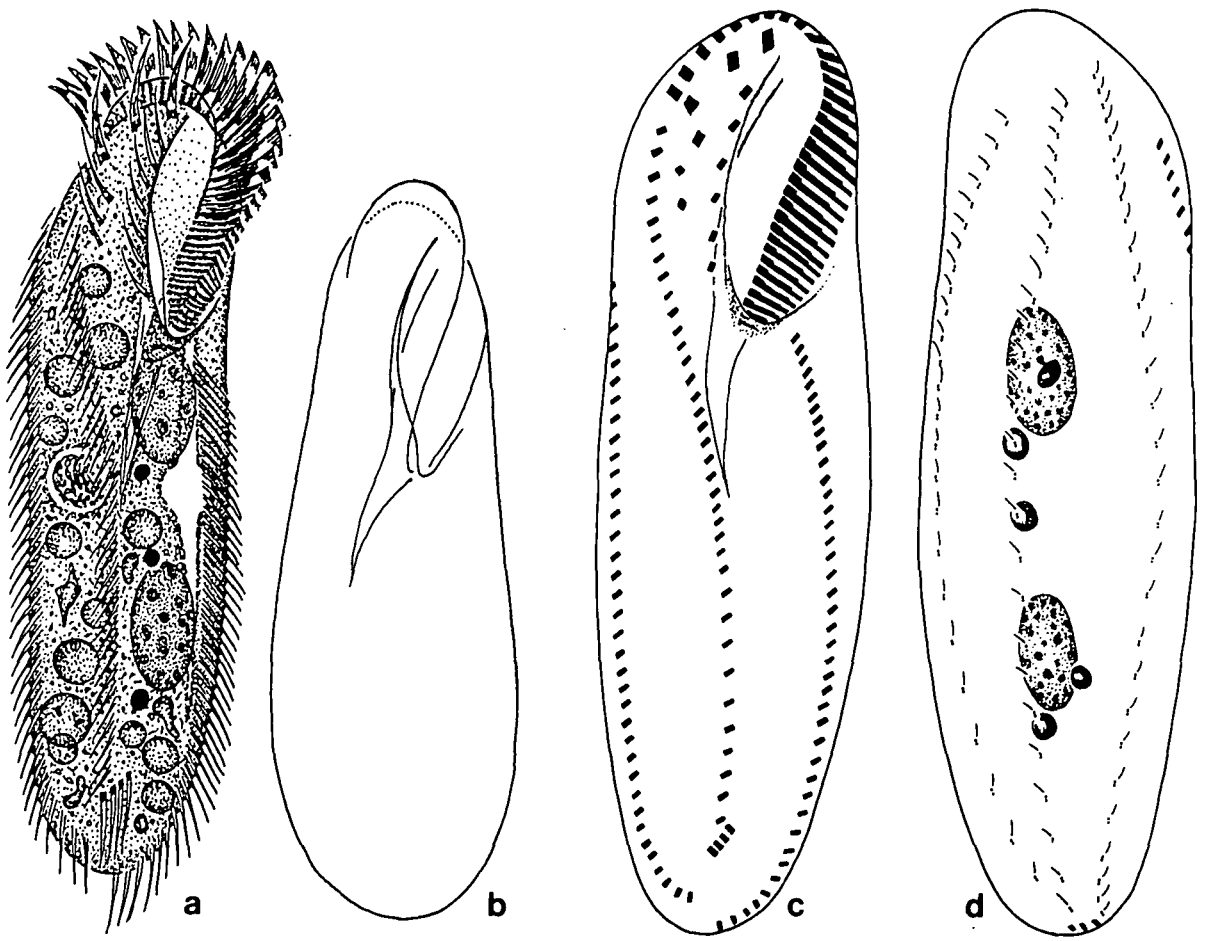

Fig. 153a–d. *Amphisiella polycirrata* from life (a, b) and after protargol impregnation (c, d; from BERGER & FOISSNER 1989a). **a:** Ventral view of a representative specimen from Namibian site (51), length 180 µm. **b:** Outline of a specimen packed with food inclusions from the Republic of South Africa. Such fat specimens occur also in Namibia. **c, d:** Infraciliature of ventral and dorsal side and nuclear apparatus of Madeiran holotype specimen, length 150 µm.

Amphisiella magnigranulosa FOISSNER, 1988a (Fig. 388a–e)

Since the original description, we have found this species in at least 100 samples from terrestrial biotopes world-wide; it is also common in Namibia (Table 4). *Amphisiella magnigranulosa* is readily identified by its cortical granules, which, however, are easily overlooked, although up to 3 µm across, because they are colourless and rather hyaline. Thus, and because there are several similar species with or without granules (Table 131), we provide several micrographs showing the granules and their arrangement in detail (Fig. 388a–e).

The cortical granules of *A. magnigranulosa* are restricted to the ciliature, that is, found only around the cirri, the dorsal bristles and in the wall of the buccal cavity. The clusters around the cirri are usually less distinct than those around the dorsal bristles. The buccal granules are conspicuous and have an intermediate size (~ 1 µm). Each granule cluster is composed of up to fifteen minute (< 1 µm) and one to three large (up to 3 µm, usually 1.5–2.5 µm) granules, which appear ring-shaped, indicating that they consist of two components of different refractivity. Although there is some variability in size and number of small and large granules are mixed, the granule clusters have a very similar pattern and appearance in populations from all main biogeographic regions. Thus, they are a highly constant and an important feature.

The nature of the cortical granules of *A. magnigranulosa* is unknown. On prolonged squeezing, they disappear, that is, are extruded, fading away without forming a coat around the cell. They do not, or only faintly, stain with methyl green-pyronin, but occasionally impregnate lightly with protargol.

Nudiamphisiella nov. gen.

Diagnosis: Amphisiellidae with several cirri left of amphisiellid median cirral row, which originates from the two rightmost anlagen. The rightmost dorsal kinety develops dorsomarginally. Transverse cirri and postperistomial cirrus lacking.

Type species: *Nudiamphisiella interrupta* nov. spec.

Etymology: Composite of the Latin adjective *nudus* (naked; because of the lack of transverse cirri) and the generic name *Amphisiella*. Feminine gender.

Classification and comparison with related genera: *Nudiamphisiella* is assigned to the Amphisiellidae because ontogenesis proceeds as in amphisiellids, for example, *Amphisiellides illuvialis* EIGNER & FOISSNER, 1994, that is, the median cirral row originates from the two rightmost anlagen (Fig. 154i). *Nudiamphisiella* is characterized by some cirri left of the anterior end of the amphisiellid median cirral row and the lack of transverse and postperistomial cirri (= cirri behind buccal vertex). This combination of features separates it from all other amphisiellids (including → *Afroamphisiella*), except for *Paragastrostyla*, as defined by EIGNER & FOISSNER (1994) and PETZ & FOISSNER (1996). However, *Paragastrostyla* HEMBERGER, 1985 lacks a buccal cirrus and dorsomarginal kinety, and produces the amphisiellid median cirral row from three fragments.

Nudiamphisiella interrupta nov. spec. (Fig. 154a–i; 398k; Table 138)

Diagnosis: Size about 150 × 50 µm in vivo; elongate ellipsoidal. Cortical granules globular, colourless to yellowish, form widely spaced rows. On average 2 macronuclear nodules, 27 adoral membranelles, 30 cirri in right and 23 in left marginal row, 14 cirri in discontinuous amphisiellid median cirral row (ACR), 3 cirri left of ACR, 1 buccal cirrus, 3 caudal cirri, and 4 dorsal kineties.

Type location: Mud and soil from road puddles in the Bambatsi Guest Farm, Namibia, 20°10'S 15°25'E (site 49 in figure 2 and chapter 2.1.2).

Etymology: The Latin participle *interruptus* (interrupted) refers to the discontinuous amphisiellid median cirral row.

Description: Size 120–170 × 35–55 µm in vivo, length:width ratio about 3:1 in vivo and protargol preparations (Fig. 154a, d–f; Table 138); very flexible but acontractile. Outline elongate elliptical with anterior end often somewhat obliquely truncated and posterior broadly rounded; left margin usually more convex than right. Two, rarely four macronuclear nodules slightly left of midline; individual nodules 20–25 × 10–15 µm in vivo, that is, ellipsoidal on average, sometimes globular or elongate ellipsoidal; nucleoli inconspicuous. Usually one globular, minute micronucleus attached to each macronuclear nodule. Contractile vacuole without collecting canals, near mid-body at left cell margin. Cortical granules inconspicuous and easily confused with cytoplasmic inclusions, form widely spaced longitudinal rows, do not distinctly impregnate with the protargol method used; when methyl green-pyronin is added, they become red but are not released (Fig. 154b); individual granules inconspicuous because only 0.5–1.0 µm across and almost colourless, most distinct in Benin cells (Fig. 398k), very indistinct in Venezuelan specimens; close beneath cortex ellipsoidal structures, likely mitochondria, as in most *Urosoma* species. Cytoplasm colourless and rather strongly granulated, contains ordinary crystals 1–6 µm in size, mainly in posterior body portion, some small lipid droplets, and 7–10 µm-sized food vacuoles with bacteria. Movement without peculiarities, that is, swims and glides rapidly on microscope slide and debris, showing great flexibility.

Cirral pattern and number of cirri rather variable (Fig. 154a, g, h; Table 138). All cirri about 15 µm long in vivo, those of marginal rows and amphisiellid median cirral row usually composed of two ciliary rows with four cilia each. Marginal rows open posteriorly, right row extends onto dorsolateral surface anteriorly and terminates about 5 µm ahead of rear body end, left row ends terminally near body midline. Frontal cirri distinctly enlarged, form transverse row, right cirrus, as is usual, behind distal end of adoral zone. Buccal cirrus enlarged (3 × 3–4 basal bodies), right of anterior end of paroral and ahead of endoral. Usually three slightly enlarged cirri behind right frontal cirrus, form short frontal row terminating on average at 25% of body length. Rare specimens have two short frontal rows. Amphisiellid median cirral row composed of an anterior portion and a posterior portion, shifted about 5 µm leftward, usually terminating at 53% of body length. Transverse and postperistomial cirri absent.

Dorsal bristles 3–4 µm long in vivo, arranged in four rows (Fig. 154h). Row 1 shortened anteriorly and less densely ciliated than row 2, which begins, like row 3, near anterior end;

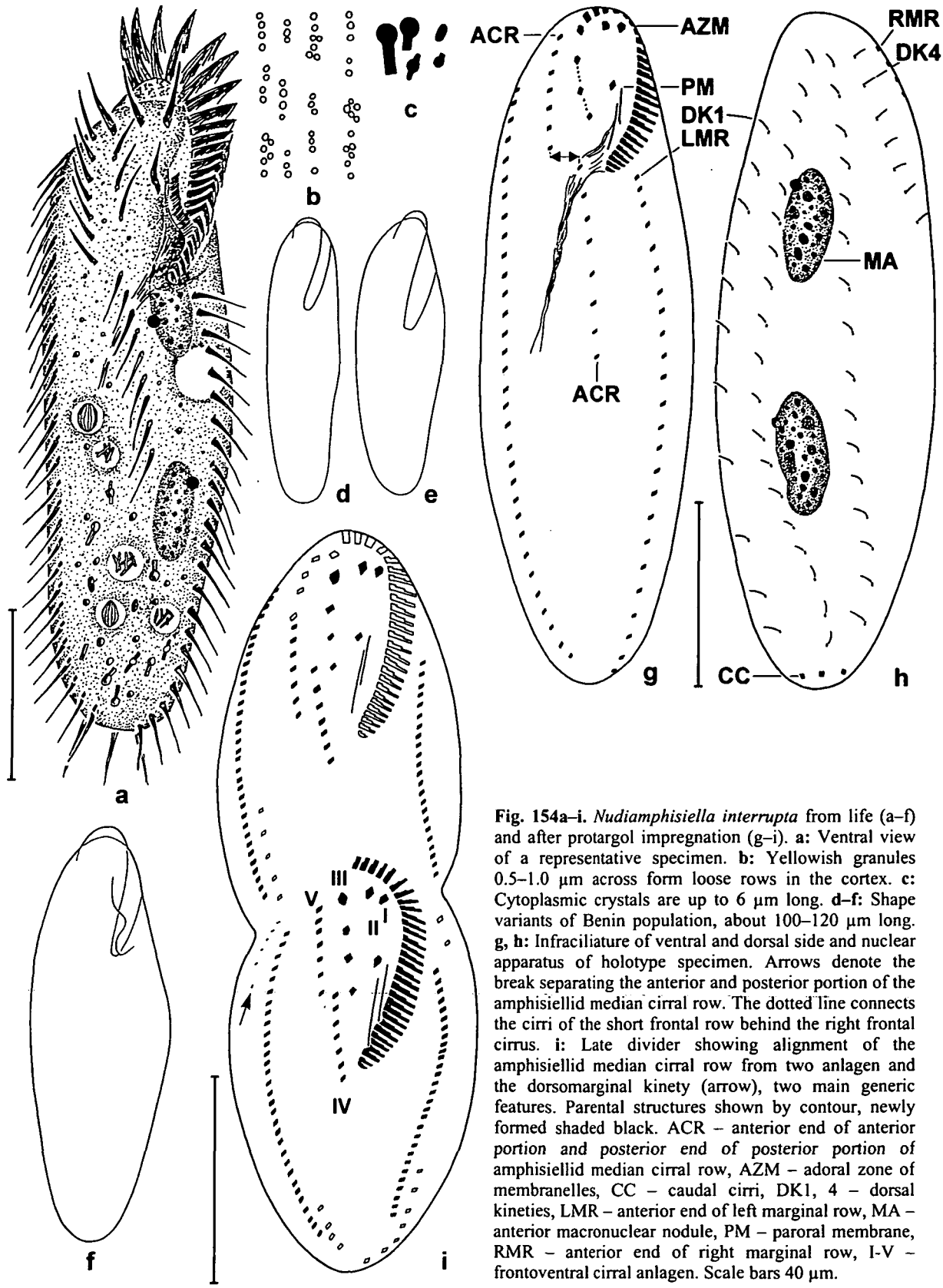

Fig. 154a–i. *Nudiamphisiella interrupta* from life (a–f) and after protargol impregnation (g–i). **a:** Ventral view of a representative specimen. **b:** Yellowish granules 0.5–1.0 µm across form loose rows in the cortex. **c:** Cytoplasmic crystals are up to 6 µm long. **d–f:** Shape variants of Benin population, about 100–120 µm long. **g, h:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrows denote the break separating the anterior and posterior portion of the amphisiellid median cirral row. The dotted line connects the cirri of the short frontal row behind the right frontal cirrus. **i:** Late divider showing alignment of the amphisiellid median cirral row from two anlagen and the dorsomarginal kinety (arrow), two main generic features. Parental structures shown by contour, newly formed shaded black. ACR – anterior end of anterior portion and posterior end of posterior portion of amphisiellid median cirral row, AZM – adoral zone of membranelles, CC – caudal cirri, DK1, 4 – dorsal kineties, LMR – anterior end of left marginal row, MA – anterior macronuclear nodule, PM – paroral membrane, RMR – anterior end of right marginal row, I-V – frontoventral cirral anlagen. Scale bars 40 µm.

row 4, a dorsomarginal kinety (Fig. 154i), composed of only 4–7 bristles and thus terminating distinctly ahead of mid-body. Caudal cirri inconspicuous in vivo because hardly longer than marginal cirri, composed of 2 × 2 basal bodies; usually one cirrus each associated with bristle rows 1–3, rarely two or three cirri with row 1 and two cirri with row 3.

Adoral zone of membranelles occupies 19–32%, on average 26% of body length, roughly in *Gonostomum* pattern, that is, extends straight along left body margin, performing right bend and slight clockwise rotation to plunge into buccal cavity; number of adoral membranelles unusually variable (Table 138), bases of largest membranelles about 7 µm wide in vivo. Buccal cavity flat and narrow. Buccal lip conspicuously projecting and extending from surface of cell at right angles, bears paroral membrane and covers posterior portion of buccal cavity and right half of rear end of adoral zone. Undulating membranes almost straight and both likely composed of a single row of basal bodies; paroral with about 5 µm long cilia, begins on average 3 µm ahead of endoral and is about 8 µm long; endoral usually alongside paroral, about 11 µm long, terminates near proximal end of adoral zone of membranelles. Pharyngeal fibres clearly recognizable in protargol preparations, of ordinary length and structure (Fig. 154a, g).

Table 138. Morphometric data on *Nudiamphisiella interrupta*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	136.0	138.0	13.7	2.9	10.1	111.0	158.0	23
Body, width	45.4	45.0	5.9	1.2	13.0	35.0	58.0	23
Body length:width, ratio	3.0	3.1	0.4	0.1	13.1	2.4	3.8	23
Anterior body end to rear end of adoral zone, distance	35.1	36.0	4.1	0.9	11.7	27.0	44.0	23
Body length:length of adoral zone, ratio	3.9	3.8	0.6	0.1	14.2	3.1	5.2	23
Anterior body end to buccal cirrus, distance	15.2	16.0	2.6	0.5	17.0	11.0	20.0	22
Anterior body end to short frontal cirral row, distance	10.2	10.0	2.1	0.4	20.9	6.0	14.0	23
Anterior body end to end of short frontal cirral row, distance	23.1	23.0	4.3	0.9	18.5	16.0	32.0	22
Anterior body end to ACR, distance	6.0	6.0	1.8	0.4	31.0	3.0	9.0	23
Anterior body end to end of anterior portion of ACR, distance	32.3	32.0	5.6	1.2	17.4	17.0	46.0	23
Interruption in ACR, lateral distance [b]	5.3	5.0	1.6	0.3	29.1	3.0	9.0	23
Anterior body end to posterior portion of ACR, distance	34.8	34.0	4.4	0.9	12.6	24.0	44.0	23
Anterior body end to end of ACR, distance	72.0	74.0	10.2	2.1	14.2	50.0	91.0	23
Body length:length of ACR, ratio	1.9	1.8	0.3	0.1	16.3	1.5	3.0	23
Anterior body end to right marginal row, distance	7.2	8.0	1.8	0.4	24.3	4.0	10.0	23
Posterior body end to right marginal row, distance	5.0	5.0	2.0	0.4	40.3	2.0	6.0	22
Anterior body end to paroral membrane, distance	16.8	17.0	3.0	0.6	17.7	11.0	22.0	23
Paroral membrane, length	8.0	8.0	1.1	0.2	14.3	6.0	10.0	23
Anterior body end to endoral membrane, distance	19.3	20.0	3.0	0.6	15.7	14.0	25.0	23
Endoral membrane, length	11.0	11.0	1.6	0.3	14.1	8.0	15.0	22
Posterior body end to middle caudal cirrus, distance	3.0	2.0	1.6	0.3	53.2	1.0	6.0	23
Anterior body end to first macronuclear nodule, distance	28.6	30.0	3.5	0.7	12.3	19.0	34.0	23
Nuclear figure, length	68.7	70.0	10.1	2.1	14.6	38.0	84.0	23
Macronuclear nodules, distance in between	26.2	26.0	6.4	1.3	24.2	17.0	38.0	23
Anterior macronuclear nodule, length	20.9	22.0	4.5	0.9	21.8	10.0	28.0	23
Anterior macronuclear nodule, width	9.2	9.0	1.3	0.3	14.6	6.0	12.0	23

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Anterior macronuclear nodule, length:width ratio	2.3	2.3	0.7	0.1	28.1	1.1	4.0	23
Posterior macronuclear nodule, length	21.6	22.0	4.9	1.0	22.8	10.0	30.0	23
Posterior macronuclear nodule, width	9.6	9.0	1.4	0.3	15.1	7.0	12.0	23
Macronuclear nodules, number [c]	2.0	2.0	0.0	0.0	0.0	2.0	2.0	22
Anterior micronucleus, diameter	2.8	3.0	–	–	–	2.5	3.0	23
Micronuclei near anterior macronuclear nodule, number	1.2	1.0	–	–	–	1.0	2.0	23
Micronuclei near posterior macronuclear nodule, number	1.0	1.0	–	–	–	0.0	2.0	23
Micronuclei, total number	2.2	2.0	0.7	0.1	30.3	1.0	4.0	23
Adoral membranelles, number	26.8	27.0	2.8	0.6	10.5	21.0	32.0	23
Frontal cirri, number	3.0	3.0	.0	0.0	0.0	3.0	3.0	23
Buccal cirri, number [d]	1.0	1.0	0.0	0.0	0.0	1.0	1.0	22
Short frontal row, number of cirri	2.7	3.0	0.6	0.1	24.4	1.0	4.0	23
Anterior portion of ACR, number of cirri	6.9	7.0	1.2	0.3	17.9	4.0	9.0	23
Posterior portion of ACR, number of cirri	7.0	7.0	1.4	0.3	19.7	4.0	10.0	23
ACR, total number of cirri	13.9	14.0	2.0	0.4	14.2	9.0	19.0	23
Right marginal cirri, number	30.0	30.0	4.2	0.9	14.1	20.0	37.0	23
Left marginal cirri, number	23.7	24.0	2.5	0.5	10.6	19.0	27.0	23
Caudal cirri, number	3.3	3.0	–	–	–	3.0	6.0	23
Dorsal kineties, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	23
Dorsal kinety 1, number of kinetids	11.9	12.0	1.0	0.4	8.3	11.0	14.0	8
Dorsal kinety 2, number of kinetids	17.4	17.0	1.1	0.4	6.5	16.0	19.0	9
Dorsal kinety 3, number of kinetids	14.4	14.0	1.6	0.6	11.1	12.0	17.0	8
Dorsal kinety 4, number of kinetids	5.5	5.5	0.9	0.3	16.8	4.0	7.0	8

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. ACR – amphisiellid median cirral row, CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] See Figure 154g (arrows).

[c] Rarely occur specimens with four macronuclear nodules.

[d] Rarely occur specimens without buccal cirrus.

Ontogenesis: Five cirral anlagen are recognizable in early and middle dividers, as in some other amphisiellids (EIGNER & FOISSNER 1994). In late dividers, **all** cirri of the rightmost anlage (V) migrate anteriad and produce the anterior portion of the amphisiellid median cirral row, while all cirri of anlage IV form the posterior portion (Fig. 154i). However, the alignment of the two portions is rather incomplete, that is, they are laterally separated by 3–9 µm in interphase specimens. Dorsal ontogenesis proceeds as usual, that is, dorsal kineties 1–3 develop within the parental kineties, while kinety 4 originates dorsomarginally, that is, from an anlage near the right marginal row (Fig. 154i).

Occurrence and ecology: To date found only at three sites of the southern hemisphere, namely the type location, where it occurred with high abundance; in Benin (Fig. 154d–f; soil sample from near the National University; kindly provided by Prof. Dr. Jean DRAGESCO); and in a soil sample from Venezuela.

Comparison with related species: *Nudiamphisiella interrupta* differs from all amphisiellids by the conspicuous discontinuity of the amphisiellid median cirral row (Fig. 154g, arrows), a feature recognizable even in live specimens. *Lamtostyla australis* (BLATTERER & FOISSNER, 1988), *Amphisiellides illuvialis* EIGNER & FOISSNER, 1994, and → *Gastrostyla* spp. have a similar habitus, but more or less distinct transverse cirri. *Paragastrostyla lanceolata* HEMBERGER, 1985 has 15–18 macronuclear nodules and lacks a buccal cirrus. *Orthoamphisiella grelli* EIGNER & FOISSNER, 1993 is smaller (60–90 × 20–30 µm vs. 120–170 × 35–55 µm), lacks caudal cirri and cortical granules, and has a continuous frontoventral row, two buccal cirri (vs. one), usually eight cirri left of the frontoventral cirral row (vs. three), and two dorsal kineties (vs. four). In vivo, *Nudiamphisiella interrupta* is thus identified by the discontinuous median cirral row, the cortical granules, and the lack of transverse cirri.

Afroamphisiella nov. gen.

Diagnosis: Amphisiellidae with one or several cirri left of amphisiellid median cirral row, which is involved in oral primordium formation. Transverse cirri, caudal cirri, and postperistomial cirri lacking.

Type species: *Afroamphisiella multinucleata* nov. spec.

Etymology: Composite of the Latin noun *Africa* and the generic name *Amphisiella*. Feminine gender.

Classification and comparison with related genera: *Afroamphisiella* likely belongs to the Amphisiellidae because the long ventral cirral row (= amphisiellid median cirral row; ACR) is involved in the formation of the oral primordium (Fig. 155k). Unfortunately, we could not find middle and late dividers showing the family character, namely, that the ACR is formed by two segments which align one after the other. By contrast, in *Orthoamphisiella* EIGNER & FOISSNER, 1991 - type of the Orthoamphisiellidae EIGNER, 1997 - the long ventral row does not participate in the origin of the oral primordium and develops from a single primordium within the central portion of the parental row (EIGNER & FOISSNER 1993).

Afroamphisiella is characterized by some cirri left of the anterior end of the ACR and the lack of transverse cirri, caudal cirri, and postperistomial cirri (= cirri behind buccal vertex). This combination of features separates it clearly from all other amphisiellids, as defined by EIGNER & FOISSNER (1994) and PETZ & FOISSNER (1996), which have transverse and/or caudal cirri. Accordingly, *Afroamphisiella* is probably the most derived member of the group.

Lamtostyla abdita FOISSNER, 1997d matches *Afroamphisiella multinucleata* both in interphase (lack of postperistomial, transverse, and caudal cirri) and early ontogenesis (participation of ACR in oral primordium formation). Thus, it is transferred to this genus: *Afroamphisiella abdita* (FOISSNER, 1997) nov. comb. FOISSNER (1997d) already emphasized the special position of this species.

Afroamphisiella multinucleata nov. spec. (Fig. 155a–k; 381j, k; Table 139)

Diagnosis: Size about 85 × 23 µm in vivo; outline elongate rectangular. Cortical granules in distinct rows, yellowish, about 1.0 × 0.5 µm. On average 18 macronuclear nodules, 17 cirri in left and 21 in right marginal row, 14 cirri in amphisiellid median cirral row, 1 cirrus behind right frontal cirrus, 1 buccal cirrus, and 2 dorsal kineties. Adoral zone composed of 17 membranelles on average, bipartited by an inconspicuous gap at left anterior margin of cell into a distal portion with 3–4 membranelles and a proximal portion with about 14 membranelles.

Type location: Highly saline soil from margin of Etosha Pan, Namibia, 19°10'S 15°55'E (site 61 in figures 2, 3 and chapter 2.1.2).

Etymology: The Latin adjective *multinucleata* (having many nuclei) refers to the numerous macronuclear nodules.

Description: Size 70–100 × 18–30 µm in vivo, length:width ratio 3.1–4.5:1, on average 3.7:1 in vivo, while 3:1 in protargol preparations; very flexible but acontractile. Outline usually elongate rectangular, that is, with parallel margins and broadly rounded ends, rarely other shapes occur (Fig. 155f–h); dorsoventrally flattened up to 1.5:1, ventral side flat, dorsal distinctly vaulted in mid-body or posterior half (Fig. 155a, d–h). Macronuclear nodules mainly left of midline (Table 139), ellipsoidal or dumb-bell-shaped, rarely globular, with few nucleoli 1–2 µm across. Micronuclei globular, attached or near macronuclear nodules. Contractile vacuole with two collecting canals slightly above mid-body at left cell margin. Cortical granules in longitudinal, rather widely spaced rows, do not impregnate with protargol, but when methyl green-pyronin is added, they become red, released, and swell to a voluminous, membranous coat; individual granules ellipsoidal, yellowish, highly refractive and thus conspicuous although only about 1.0 × 0.5 µm (Fig. 155b, c; 381j, k). Cytoplasm colourless, packed with granules about 1 µm across and, in posterior third, 2–5 µm-sized lipid droplets. Feeds on bacteria digested in vacuoles about 6 µm across. Glides slowly on microscope slide and soil particles.

Cirral pattern very constant, number of cirri of usual variability (Fig. 155a, i, k; Table 139). Frontoventral and marginal cirri about 8 µm long in vivo, fine because usually composed of four cilia only. Marginal rows widely open posteriorly, right row begins near level of buccal cirrus and ends subterminally, left row usually slightly shorter than right posteriorly. Most

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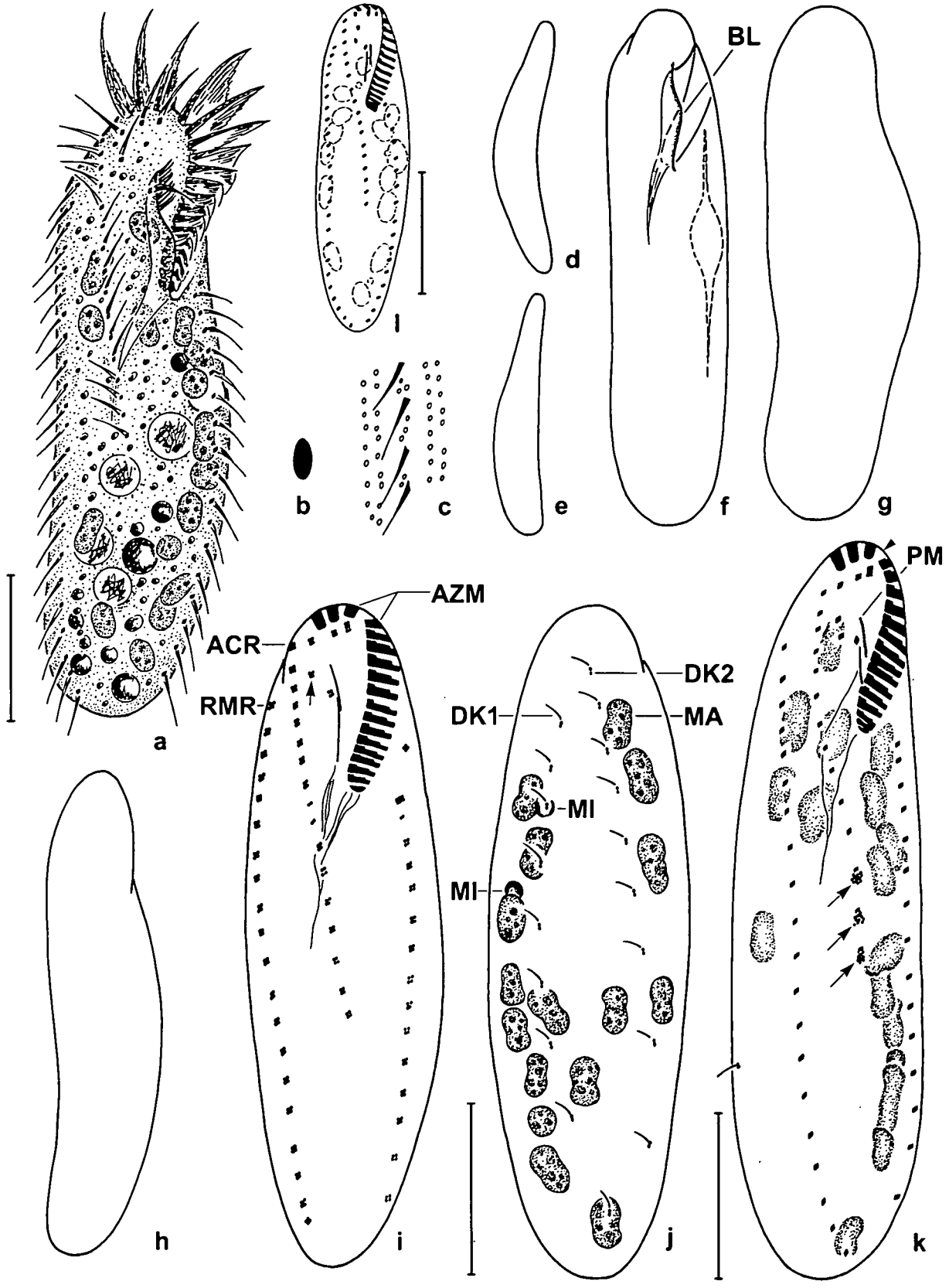
Fig. 155a–k. *Afroamphisiella multinucleata* from life (a–h) and after protargol impregnation (i–k). **a:** Ventral view of a representative specimen. **b, c:** The ellipsoidal cortical granules are about 1.0 × 0.5 µm, highly refractive, yellowish, and arranged in longitudinal rows. **d, e:** Right lateral views. **f–h:** Rare shape variants. **i, j:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. The arrow denotes a cirrus behind the right frontal cirrus. Note that most cirri consist of four cilia only. **k:** Very early divider showing the oral primordium originating from the posteriormost cirri (arrows) of the amphisiellid median cirral row. The arrowhead marks a gap in the adoral zone of membranelles, which is also recognizable in the type specimen (i). ACR – amphisiellid median cirral row, AZM – adoral zone of membranelles, BL – buccal lip, DK1, 2 – dorsal kineties, MA – anteriormost macronuclear nodule, MI – micronuclei, PM – paroral membrane, RMR – anteriormost cirrus of right marginal row. Scale bars 20 µm.

Fig. 155 l. *Uroleptoides kihni* sensu BORROR & EVANS (1979; protargol impregnation). This specimen is very likely an *Afroamphisiella multinucleata* (cp. with figure 155i). Scale bar 20 µm.


a
b
c
d
e
f
g
BL
l
ACR
AZM
RMR
h
i
DK1
DK2
MA
MI
MI
j
PM
k

specimens have five frontoventral cirri, that is, three frontal cirri with left cirrus often slightly enlarged, one buccal cirrus, and usually one cirrus (rarely two or three cirri) behind right frontal cirrus. Amphisiellid median cirral row (ACR) begins right of right frontal cirrus and extends to body midline at 55% of body length on average; straight, that is, does not have, as in some other species, a slight bow or interruption where the row fragments unite during late ontogenesis. Transverse and postperistomial cirri absent.

Dorsal bristles about 3 µm long in vivo, arranged in two rows with distances between dikinetids becoming wider from anterior to posterior, rarely a short third row between anterior portion of row 2 and right body margin. Row 1 anteriorly slightly more shortened than row 2; posteriormost dikinetid in cell's midline and thus not unequivocally assignable to one of the two rows. Caudal cirri absent (Fig. 155j).

Adoral zone occupies 26–42%, on average 31% of body length, composed of an average of 17 membranelles, bases of largest membranelles about 5 µm wide in vivo. Distalmost three or four membranelles separated from proximal segment of zone by more or less distinct gap (Fig. 155a, f, i, k; Table 139). Buccal cavity flat and narrow, anterior margin, however, rather distinct, forming bow with dorsal buccal wall (Fig. 155f). Buccal lip distinctly curved, covers right half of buccal cavity and proximal portion of adoral zone. Exact structure and arrangement of undulating membranes not unequivocally recognizable; paroral and endoral membrane short and almost straight, parallel to each other with posterior, respectively, anterior portion slightly overlapping; paroral cilia about 8 µm long in vivo. Pharyngeal fibres clearly recognizable in vivo and after protargol impregnation, of ordinary length and structure, extend obliquely backwards.

Occurrence and ecology: To date found only at type location, that is, a highly saline soil from the margin of the Etosha Pan. BORROR & EVANS (1979) found this or a very similar species in protargol slides made by Dr. E. SMALL during ecological investigations in the Chesapeake Bay estuary, Maryland, USA (Fig. 155 l; see also next paragraph).

Comparison with related species: *Afroamphisiella abdita* (FOISSNER, 1997d) has four macronuclear nodules, usually two buccal cirri, and two short frontoventral rows left of the amphisiellid median cirral row (ACR), which has on average about the same relative length as in *A. multinucleata* (55%). *Orthoamphisiella stramenticola* EIGNER & FOISSNER, 1991 and *O. grelli* EIGNER & FOISSNER, 1993 also lack transverse and caudal cirri; however, they have four, respectively, two macronuclear nodules (against 14–29 in *A. multinucleata*). → *Orthoamphisiella breviseries* has a dumb-bell-shaped macronucleus and very short frontoventral rows not extending beyond buccal vertex. *Uroleptoides kihni* WENZEL, 1953 sensu BORROR & EVANS (1979) is probably *Afroamphisiella multinucleata* because the nuclear and cirral pattern are very similar, even in details such as the beginning of the right marginal row at the level of the buccal cirrus (Fig. 155 l). The only difference worth mentioning is the number of dorsal kineties: three in BORROR & EVANS' population, usually two in *A. multinucleata*. However, we also found specimens with a short third row, indicating that this feature may be somewhat variable in this species. In vivo, *Afroamphisiella multinucleata* is easily identified by the following combination of features: rows of yellowish, cortical granules; many macronuclear nodules; single, long ventral cirral row, one buccal cirrus.

Table 139. Morphometric data on *Afroamphisiella multinucleata* (upper line) and *Orthoamphisiella breviseries* (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	71.5	72.0	6.5	1.2	9.1	59.0	84.0	29
	47.6	48.0	6.1	1.2	12.8	38.0	60.0	25
Body, width	24.0	24.0	2.4	0.4	9.9	18.0	29.0	29
	14.8	15.0	2.0	0.4	13.5	10.0	18.0	25
Body length:width, ratio	3.0	3.0	0.3	0.1	9.3	2.5	3.7	29
	3.3	3.2	0.5	0.1	14.5	2.5	4.0	25
Anterior body end to proximal end of adoral zone,	22.1	22.0	2.0	0.4	9.2	19.0	30.0	29
distance	13.6	13.0	1.7	0.3	12.6	11.0	17.0	25
Body length:length of adoral zone of membranelles, ratio	3.2	3.3	0.3	0.1	10.2	2.4	3.8	29
	3.5	3.6	0.5	0.1	12.9	2.6	4.6	25
Anterior body end to last cirrus of amphisiellid median	39.6	39.0	5.2	1.0	13.2	31.0	52.0	29
cirral row, distance	–	–	–	–	–	–	–	–
Anterior body end to end of frontoventral row 1, distance	–	–	–	–	–	–	–	–
	6.3	6.0	1.5	0.3	23.1	4.0	10.0	25
Anterior body end to end of frontoventral row 2, distance	–	–	–	–	–	–	–	–
	9.3	9.0	1.7	0.3	18.5	7.0	13.0	25
Anterior body end to (first) buccal cirrus, distance	10.3	10.0	1.3	0.2	12.4	7.0	15.0	28
	4.1	4.0	1.2	0.2	29.9	2.0	6.0	25
Anterior body end to anterior end of right marginal row,	9.2	9.0	2.0	0.4	21.4	6.0	15.0	29
distance	–	–	–	–	–	–	–	–
Anterior body end to anteriormost macronuclear nodule,	8.8	9.0	2.4	0.4	26.9	4.0	13.0	29
distance	9.3	9.0	2.4	0.5	25.5	5.0	15.0	25
Nuclear figure, length	57.6	58.0	5.3	1.0	9.2	47.0	66.0	29
	30.2	31.0	4.7	0.9	15.6	22.0	38.0	25
Anterior macronuclear nodule, length	5.5	6.0	1.1	0.2	19.1	3.0	7.0	29
	–	–	–	–	–	–	–	–
Anterior macronuclear nodule, width	3.0	3.0	0.4	0.1	14.1	2.0	4.0	29
	–	–	–	–	–	–	–	–
Macronuclear nodules, total number	18.4	17.0	3.7	0.7	20.0	14.0	29.0	29
				see text				
Macronuclear nodules, number right of midline	5.2	5.0	1.5	0.3	28.8	2.0	8.0	29
	–	–	–	–	–	–	–	–
Anterior micronucleus, length	2.1	2.0	–	–	–	1.5	3.0	28
	1.8	1.6	–	–	–	1.4	2.5	20
Anterior micronucleus, width	2.1	2.0	–	–	–	1.5	2.5	28
	1.7	1.6	–	–	–	1.4	2.0	20
Micronuclei, number	2.8	3.0	1.1	0.2	38.3	1.0	6.0	28
	1.6	2.0	–	–	–	1.0	3.0	19
Adoral membranelles, total number	17.5	17.0	0.9	0.2	5.0	16.0	19.0	29
	20.6	20.0	1.4	0.3	7.0	19.0	25.0	21
Proximal adoral membranelles, number	14.2	14.0	1.0	0.2	6.9	13.0	16.0	29
	–	–	–	–	–	–	–	–
Distal adoral membranelles, number	3.3	3.0	–	–	–	3.0	4.0	29
	–	–	–	–	–	–	–	–

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	28
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	24
Frontoventral rows, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	29
	2.1	2.0	–	–	–	2.0	3.0	25
Frontoventral (amphisiellid median cirral) row 1,	14.4	14.0	2.2	0.4	15.3	11.0	22.0	29
number of cirri	2.7	3.0	0.7	0.1	27.1	1.0	4.0	25
Frontoventral row 2, number of cirri	–	–	–	–	–	–	–	–
	4.8	5.0	0.7	0.1	15.4	3.0	7.0	25
Frontoventral row 3, number of cirri	–	–	–	–	–	–	–	–
	3.7	4.0	1.5	0.9	41.7	2.0	5.0	3
Cirri behind right frontal cirrus, number	1.3	1.0	–	–	–	1.0	3.0	29
	–	–	–	–	–	–	–	–
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	28
	2.5	2.0	–	–	–	2.0	4.0	25
Right marginal cirri, number	20.9	21.0	3.7	0.7	17.5	13.0	34.0	29
	31.6	31.0	2.1	0.4	6.7	26.0	37.0	25
Left marginal cirri, number	16.6	17.0	2.4	0.4	14.5	11.0	22.0	29
	28.5	28.0	2.6	0.5	9.2	20.0	32.0	25
Dorsal kineties, number [b]	2.1	2.0	–	–	–	2.0	3.0	29
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	24
Dorsal kinety 1, number of kinetids	9.2	9.0	1.5	0.3	16.8	6.0	13.0	27
	7.9	8.0	1.3	0.3	16.0	6.0	11.0	19
Dorsal kinety 2, number of kinetids	8.1	8.0	1.2	0.2	15.1	6.0	10.0	27
	7.6	8.0	1.0	0.2	13.6	5.0	9.0	18
Dorsal kinety 3, number of kinetids	3.3	2.0	–	–	–	2.0	6.0	3
	–	–	–	–	–	–	–	–

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Of 29 specimens analyzed, three have a short, third row.

Orthoamphisiella breviseries nov. spec. (Fig. 156a–k; 389a–d; Table 139)

Diagnosis: Size about 100 × 15 µm in vivo, that is, conspicuously elongate ellipsoidal. Macronucleus vermiform to dumb-bell-shaped. 20 adoral membranelles, 2 buccal cirri at anterior end of undulating membranes, and 8 frontoventral cirri in 2 short rows on average. 2 dorsal kineties.

Type location: Highly saline soil from margin of Etosha Pan, Namibia, 19°10'S 15°55'E (site 61 in figures 2, 3 and chapter 2.1.2).

Etymology: Composite of the Latin adjective *brevis* (short) and the Latin noun *series* (row), referring to the short rightmost frontoventral row.

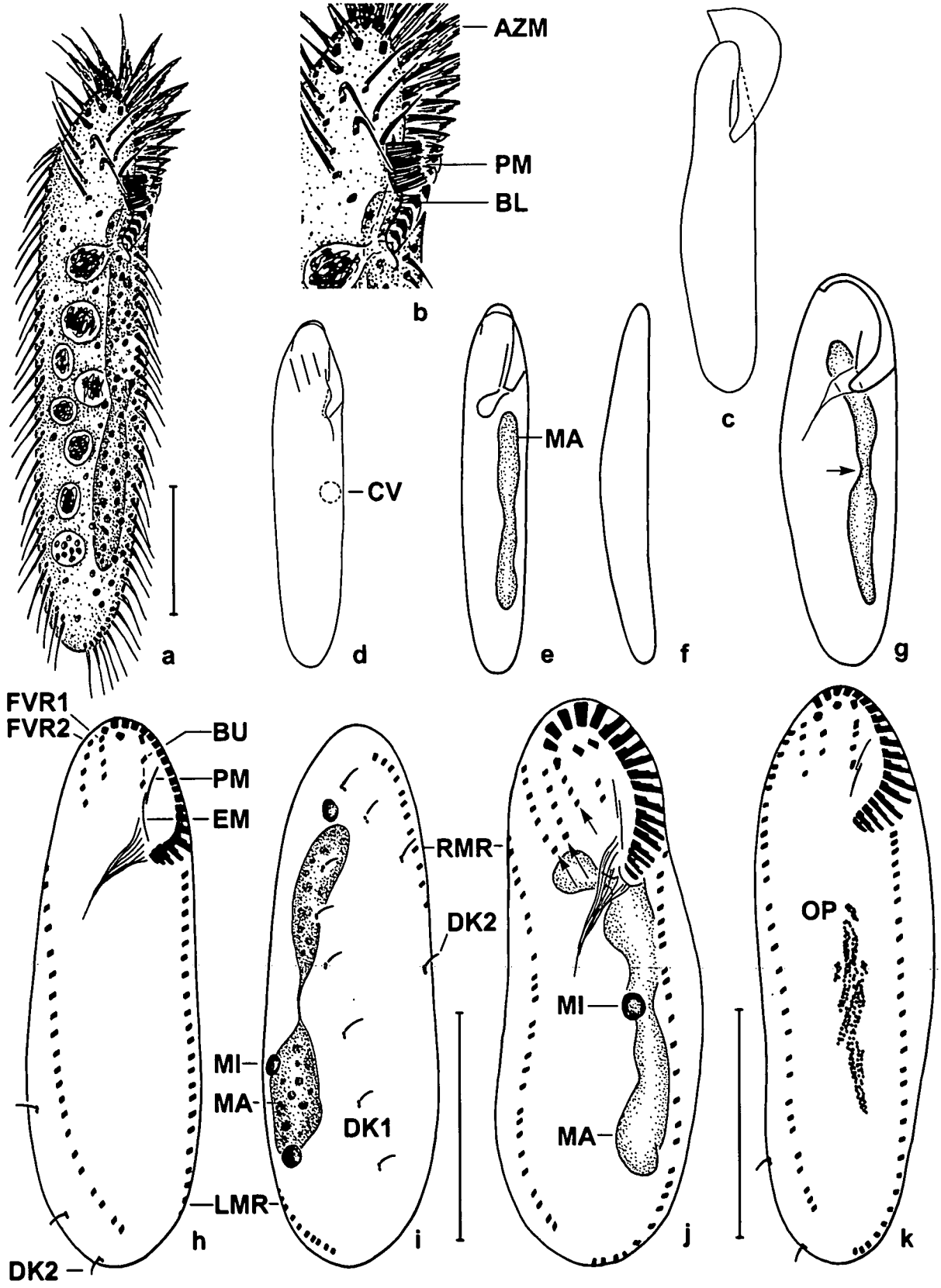
Description: Size 80–120 × 15–20 µm in vivo, length:width ratio about 5:1 in vivo, 2.5–4:1, on average 3.3:1 in protargol preparations, where specimens shrink longitudinally by up to 50%; width, in contrast, not changed significantly (Fig. 156a, f, h; Table 139). Very flexible but acontractile. Conspicuously elongate, overall shape ellipsoidal to slightly lanceolate with broadest site at buccal entrance, margins straight to slightly convex, ends rounded; dorsoventrally flattened up to 2:1, ventral side flat, dorsal slightly vaulted. Macronucleus in longitudinal axis of cell left of midline, very likely basically consists of two elongate nodules connected by an usually broad bridge providing the nucleus with a dumbbell-shaped or vermiform, wrinkled outline; nucleoli 1–3 µm across. Micronuclei globular, attached to or near macronucleus (Fig. 156a, e, g, i, j). Contractile vacuole near mid-body at left cell margin, disappears rapidly under cover glass pressure. No special cortical granules. Cytoplasm colourless, granulated by lipid droplets 1–2 µm across concentrated at left body margin; without crystals. Feeds on bacteria digested in slightly ellipsoidal and globular vacuoles 5–7 µm across. Movement without peculiarities.

Cirral pattern very constant, number of cirri of usual variability (Fig. 156a, b, d, h–k; Table 139). All cirri about 10 µm long in vivo. Marginal rows open widely posteriorly right of midline because right row ends subterminally and left curves to midline at end of cell, forming a J-shaped "tail" composed of closely spaced cirri. On average 13 cirri on frontal field, that is, three slightly enlarged frontal cirri, two buccal cirri near anterior end of undulating membranes, three cirri in frontoventral row 1, which is in line with right frontal cirrus, and five cirri in frontoventral row 2. Frontoventral rows invariably obliquely extending and shorter than adoral zone of membranelles. Postperistomial cirri, transverse cirri and caudal cirri definitely lacking. Ontogenesis commences apokinetally in mid-body (Fig. 156k).

Dorsal bristles 3–4 µm long in vivo and very widely spaced (10 µm), form two slightly oblique rows (Fig. 156h, i): row 1, which extends in midline, distinctly shortened anteriorly and posteriorly; row 2, which is bipolar, commences near cell's midline and extends on right dorsolateral surface to posterior end.

Adoral zone usually in *Gonostomum* pattern, that is, commences slightly right of midline and extends straight along left body margin, performing rather abrupt right bend to plunge into buccal cavity (Fig. 156g, h, k); conspicuously short, that is, occupies only about 25% of body length in vivo and 28% on average in shrunken protargol preparations; composed of an average of 20 membranelles, largest membranelles 4–5 µm wide in vivo. Buccal cavity very flat and narrow in vivo, often broadened in protargol preparations. Buccal lip conspicuously convex, covers buccal cavity and right half of rear end of adoral zone, bears paroral membrane at upper left margin. Exact arrangement and structure of undulating membranes unknown
because of preparation artifacts mentioned; paroral and endoral membrane of about same length, paroral ahead of endoral and in vivo composed of closely spaced, 7 µm long cilia (Fig. 156b). Pharyngeal fibres recognizable in vivo and after protargol impregnation, extend obliquely backwards.

Occurrence and ecology: To date found at type location and in a highly saline soil sample from Saudi Arabia. Thus, *Orthoamphisiella breviseries* very likely prefers saline inland soils. The congeners were also discovered in terrestrial habitats: *Orthoamphisiella stramenticola* in leaf litter from Austria and Japan, and *O. grelli* in moss and soil from a river bank on Gough Island. This indicates that *Orthoamphisiella*, although cosmopolitan, is con-


AZM
PM
BL
b
a
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FVR1
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RMR
DK2
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i
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fined to terrestrial biotopes, or at least prefers such habitats.

Generic classification and comparison with related species: The Namibian population matches *Orthoamphisiella* EIGNER & FOISSNER, 1991, except for the long ventral row, which is lacking. However, we cannot exclude that the rightmost frontoventral row of *O. breviseries* is a shortened, long ventral row. If ontogenetic data prove that this is not the case, then the Namibian species should be separated at subgeneric or generic level. This would also apply if ontogenesis shows that it belongs to the Amphisiellidae because all amphisiellid genera have transverse and/or caudal cirri (PETZ & FOISSNER 1996), except of → *Afroamphisiella* which, however, has a long ventral cirral row.

Orthoamphisiella breviseries differs from the congeners mainly by the lack of the long ventral cirral row. Furthermore, the macronucleus of *O. stramenticola* EIGNER & FOISSNER, 1991 and *O. grelli* EIGNER & FOISSNER, 1993 is separated into four, respectively, two distinct nodules, whereas it is a single, more or less dumb-bell-shaped mass in *O. breviseries*; this unique pattern separates it also from → *Afroamphisiella* spp. *Orthoamphisiella franzi* (FOISSNER, 1982) EIGNER, 1995 has 7–17 macronuclear nodules, two long ventral rows, a long (about 50% of body length) adoral zone, and three dorsal kineties. In vivo, *Orthoamphisiella breviseries* is easily identified by the following combination of features: rod-shaped macronuclear mass; few frontoventral cirri arranged in three to four short, oblique rows not extending beyond adoral zone of membranelles; short adoral zone of membranelles; very flat and narrow buccal cavity.

Lamtostyla halophila nov. spec. (Fig. 157a–v; 390a–e; Table 140)

Diagnosis: Size about 70 × 25 µm in vivo; slenderly ellipsoidal. On average 2 macronuclear nodules, 19 cirri in left and 24 in right marginal row, 4 cirri in amphisiellid median cirral row (ACR), 1–2 cirri left of ACR, 1 buccal cirrus, 3–4 transverse cirri, and 2–3 dorsal kineties. Adoral zone continuous, consists of 17–18 membranelles on average. Buccal cavity narrow and flat. The oral primordium develops postorally and independently of the ACR.

Type location: Highly saline soil from the margin of a pond in the surroundings of the town of Maltahöhe, Namibia, 24°55'S 16°55'E (site 18 in figure 2 and chapter 2.1.2).

Etymology: Composite of the Greek words *halós* (salt) and *philos* (preferring), referring to the saline habitats the species occurs.

Fig. 156a–k. *Orthoamphisiella breviseries* from life (a–f) and after protargol impregnation (g–k). **a, b:** Ventral view of a representative specimen and detail of oral apparatus. **c:** Outline of a freely motile specimen, drawn from video records. **d:** Outline showing oral apparatus and oblique frontoventral cirral rows. **e:** Outline showing macronucleus and oral apparatus with a forming food vacuole. **f:** Right lateral view showing dorsoventral flattening. **g:** A specimen with slightly constricted macronucleus (arrow). **h, i:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. **j:** Ventral side of a specimen with three frontoventral cirral rows (arrows). **k:** Early divider showing de novo formation of oral primordium. AZM – adoral zone of membranelles, BL – buccal lip, BU – buccal cirri, CV – contractile vacuole, DK1, 2 – dorsal kineties, EM – endoral membrane, FVR 1, 2 – frontoventral cirral rows, LMR – left marginal row, MA – macronucleus, MI – micronucleus, OP – oral primordium, PM – paroral membrane, RMR – right marginal row. Scale bars 20 µm.

Description: Two populations were studied, of which that from site (69) was much more variable than the type (Table 140). The diagnosis and description comprise both populations because conspecificity is beyond reasonable doubt.

Size 55–100 × 20–30 µm in vivo, usually about 70 × 25 µm. Ellipsoidal to slenderly ellipsoidal, length:width ratio 2.2–4:1 in vivo, 1.7–3.3:1, on average about 2.5:1 in protargol preparations, where specimens tend to become inflated; dorsoventrally flattened up to 2:1 (Fig. 157a, e, f; Table 140). Macronuclear nodules in middle third of cell left of midline, ellipsoidal to elongate ellipsoidal (up to 4:1), usually with rather irregular outline both in vivo and protargol preparations; nucleoli large and irregularly branched. Micronuclei globular, usually one attached to each macronuclear nodule, difficult to recognize in vivo and protargol preparations because hyaline and faintly impregnated. Contractile vacuole in mid-body at left margin. Cytopyge in posterior end left of midline, faecal clumps contain highly refractive bacterial spores embedded in fluffy material (Fig. 157e). Cortical granules loosely arranged, in vivo difficult to recognize because colourless and only 0.5–1 µm across, usually impregnate with protargol (Fig. 157e; 390a–c, e). Cytoplasm colourless, without crystals and lipid droplets. Feeds on long, spore-forming bacteria collected in ellipsoidal vacuoles up to 10 µm across (Fig. 157a). Glides slowly on microscope slide and organic debris.

Cirri about 12 µm long in vivo, very fine because composed of only two to four cilia, except for frontal cirri usually comprising six cilia each, first frontal cirrus often enlarged and composed of eight cilia. Marginal rows open widely posteriorly. Frontal cirral row (amphisiellid median cirral row, ACR) at right margin of rather distinct crest, shorter than adoral zone of membranelles because composed of only four cirri on average; likewise, transverse cirri insert at right margin of flat crest. Buccal cirrus invariably right of anterior end of paroral. Dorsal bristles 3–4 µm long, very loosely arranged, especially in left row, which is lacking in about 60% of specimens from site (69); no caudal cirri (Fig. 157a–c; 390a, d).

Oral apparatus inconspicuous because adoral zone narrow and occupying only 27% of body length; composed of an average of 18 membranelles, bases of largest membranelles 4 µm wide in vivo, only about 2 µm in anterior third of zone. Buccal cavity narrow and flat. Buccal lip rather conspicuous, arched, covers posterior third of adoral zone of membranelles. Paroral and endoral membrane very small, staggered in parallel, both near adoral zone of membranelles and very likely composed of a single row of cilia (basal bodies), often slightly obliquely arranged. Paroral cilia form distinct, triangular velum with cilia 12 µm long at anterior end and only 5 µm at posterior (Fig. 157a, b, d; 390a, d). Pharyngeal fibres distinct only in protargol preparations.

Ontogenesis: Division of *Lamtostyla halophila* is very similar to that of *L. australis* (FOISSNER, 1988a) PETZ & FOISSNER, 1996, as described by VOSS (1992); *Lamtostyla edaphoni* BERGER & FOISSNER, 1987, as described by PETZ & FOISSNER (1996); and *Lamtostyla perisincirra* (HEMBERGER, 1985) BERGER & FOISSNER, 1987, as described by BERGER et al. (1984). Thus, it will be not described in detail, but the reader is referred to the detailed figures and figure explanations (Fig. 157j–v). Three main differences should be noted: (i) the oral primordium does not develop near the transverse cirri but in mid-body (Fig. 157j, k); (ii) no patch of basal bodies develops at the posterior end of the ACR, which originates, as is typical for the family (EIGNER & FOISSNER 1994), by posterior-anterior alignment of the two rightmost anlagen 4 and 5 (Fig. 157s–u); (iii) the parental adoral zone of

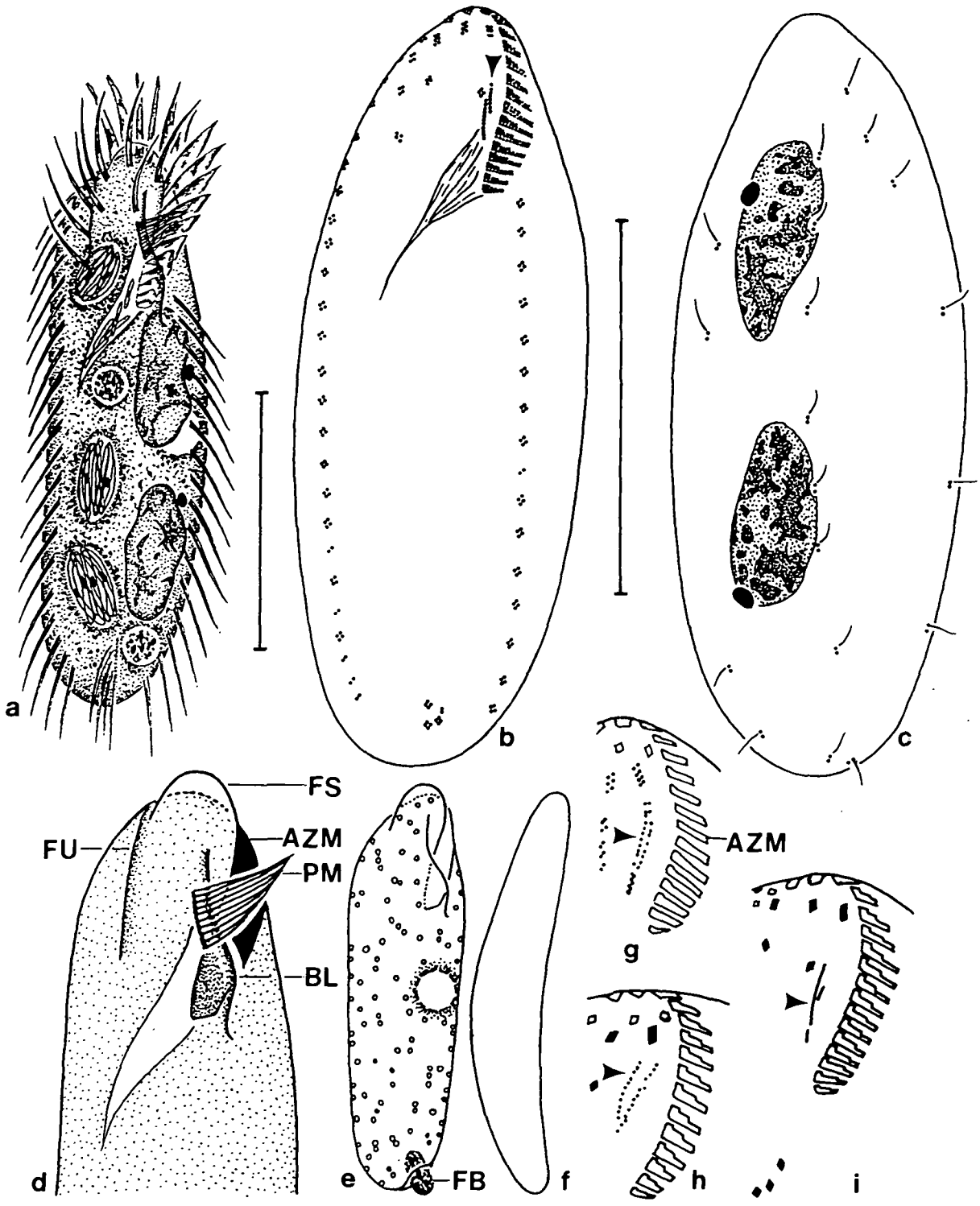

Fig. 157a–i. *Lamtostyla halophila* from life (a, d–f) and after protargol impregnation (b, c, g–i). **a:** Ventral view of a representative specimen. **b, c:** Infraciliature of ventral and dorsal side of holotype specimen. Arrowhead marks paroral. **d:** Oral apparatus. **e, f:** Ventral and lateral view of shape variant showing cortical granulation and dorsoventral flattening. **g–i** (details from Fig. 157q, s, t): Development of proter's paroral (arrowheads) and endoral. The paroral moves left of the endoral during shaping of the buccal cavity. AZM – adoral zone of membranelles, BL – buccal lip, FB – faecal mass, FS – frontal scutum, FU – furrow (crest) along amphisiellid median cirral row, PM – paroral membrane. Scale bars 30 μm.

Table 140. Morphometric data on *Lamtostyla halophila* from Namibian sites 18 (type location, upper line) and 69 (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	58.9	58.0	5.9	1.3	10.0	50.0	70.0	21
	66.5	65.0	6.2	1.9	9.3	60.0	77.0	11
Body, width	25.6	25.0	2.9	0.6	11.3	21.0	32.0	21
	25.2	25.0	5.6	1.7	22.3	19.0	36.0	11
Anterior body end to proximal end of adoral zone of membranelles, distance	16.3	16.0	1.2	0.3	7.3	15.0	19.0	21
	17.4	17.0	1.8	0.5	10.4	14.0	20.0	11
Anterior body end to proximal end of amphisiellid median cirral row, distance	12.0	12.0	1.2	0.3	10.1	10.0	15.0	21
	12.7	13.0	2.1	0.6	16.1	9.0	16.0	11
Macronuclear nodules, distance in between	5.8	6.0	1.7	0.4	30.0	3.0	10.0	21
	4.8	4.0	4.2	1.3	86.5	0.0	11.0	11
Posterior macronuclear nodule, length	15.3	15.0	1.8	0.4	11.5	12.0	19.0	21
	17.4	18.0	3.0	0.9	17.3	13.0	22.0	11
Posterior macronuclear nodule, width	7.8	7.0	1.1	0.2	14.1	6.0	10.0	21
	6.9	7.0	1.4	0.4	19.9	5.0	9.0	11
Posterior micronucleus, length	2.1	2.0	–	–	–	2.0	3.0	21
	2.2	2.0	–	–	–	2.0	3.0	11
Posterior micronucleus, width	1.8	2.0	–	–	–	1.5	2.0	21
	1.8	2.0	–	–	–	1.5	2.0	3
Adoral membranelles, number	17.0	17.0	0.8	0.2	4.8	15.0	18.0	21
	18.3	18.0	0.8	0.2	4.3	17.0	19.0	11
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
Micronuclei, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	2.0	2.0	–	–	–	2.0	2.0	3
Right marginal cirri, number	21.8	21.0	2.1	0.5	9.6	19.0	26.0	21
	27.1	26.0	3.8	1.2	14.1	22.0	33.0	11
Left marginal cirri, number	15.9	16.0	2.2	0.5	13.6	12.0	19.0	21
	22.6	22.0	6.0	1.8	26.8	16.0	34.0	11
Amphisiellid median row, number of cirri	3.6	4.0	0.6	0.1	16.7	3.0	5.0	21
	4.2	4.0	0.9	0.3	20.1	3.0	5.0	11
Cirri left of amphisiellid median cirral row, number	1.2	1.0	–	–	–	1.0	2.0	21
	1.7	2.0	0.8	0.2	45.5	1.0	3.0	11
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	1.4	1.0	–	–	–	1.0	3.0	11
Transverse cirri, number	3.7	4.0	0.6	0.1	15.8	2.0	4.0	21
	2.3	3.0	1.9	0.6	83.7	0.0	4.0	11
Dorsal kineties, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	2.5	2.0	–	–	–	2.0	3.0	11

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

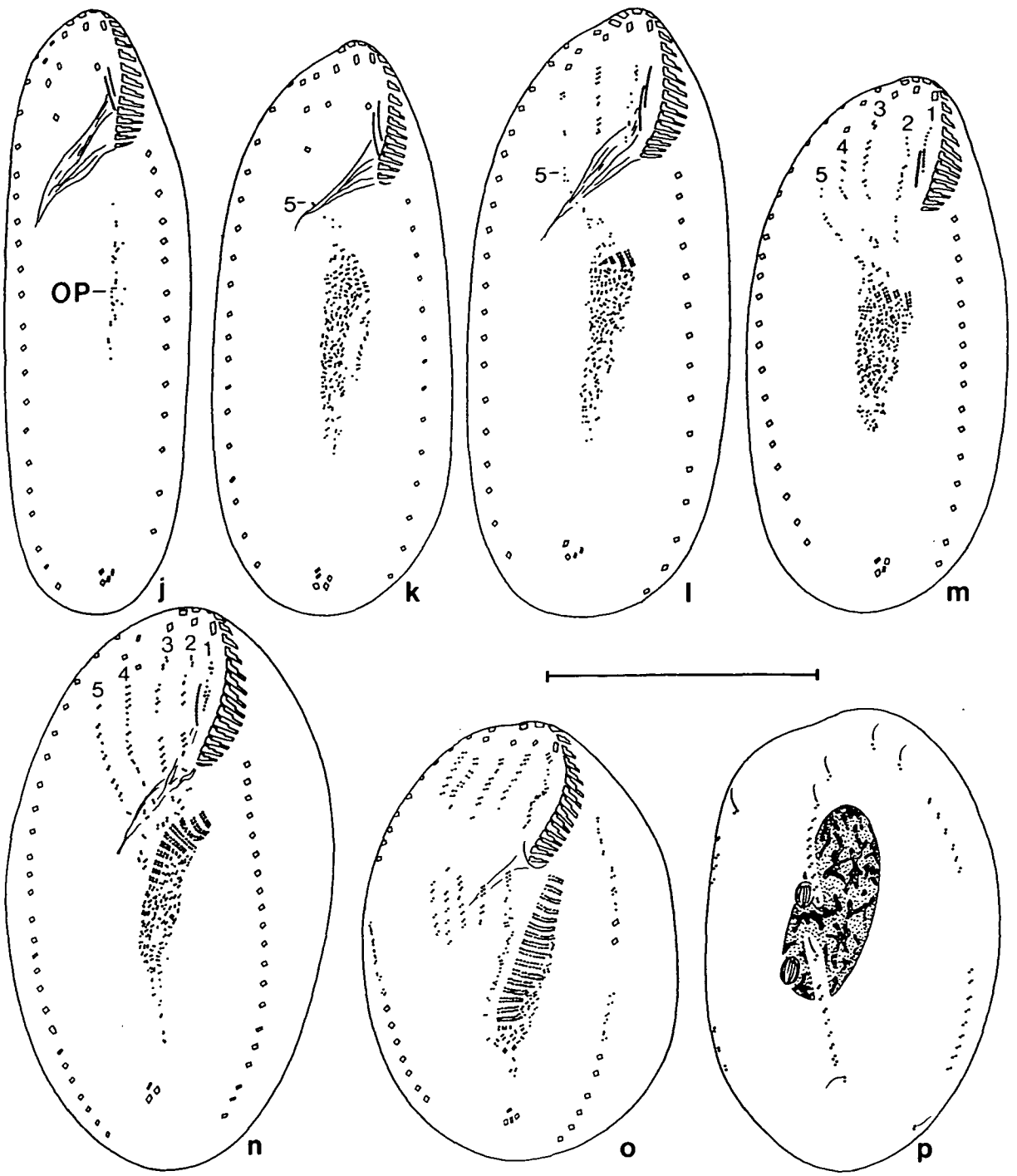

Fig. 157j–p. *Lamtostyla halophila*, ontogenesis of ventral (j–o) and dorsal (p) infraciliature after protargol impregnation. The oral primordium (OP) originates apokinetally in mid-body and produces five cirral streaks (numbers 1–5), which unite with streaks generated by parental frontoventral cirri (one each by the buccal cirrus, the cirrus left of the amphisiellid median cirral row, and the last cirrus of the amphisiellid median cirral row) to form long primary primordia (n). Streak 5, however, is generated entirely by the oral primordium (k–n). The primary primordia split in the middle to produce five cirral anlagen each in proter and opisthe (o). The dorsal kineties reproduce by intrakinetal proliferation of dikinetids (p; parental kinetids ciliated). Note that dividers become distinctly smaller and broader during the process. Drawn to scale 30 μm.

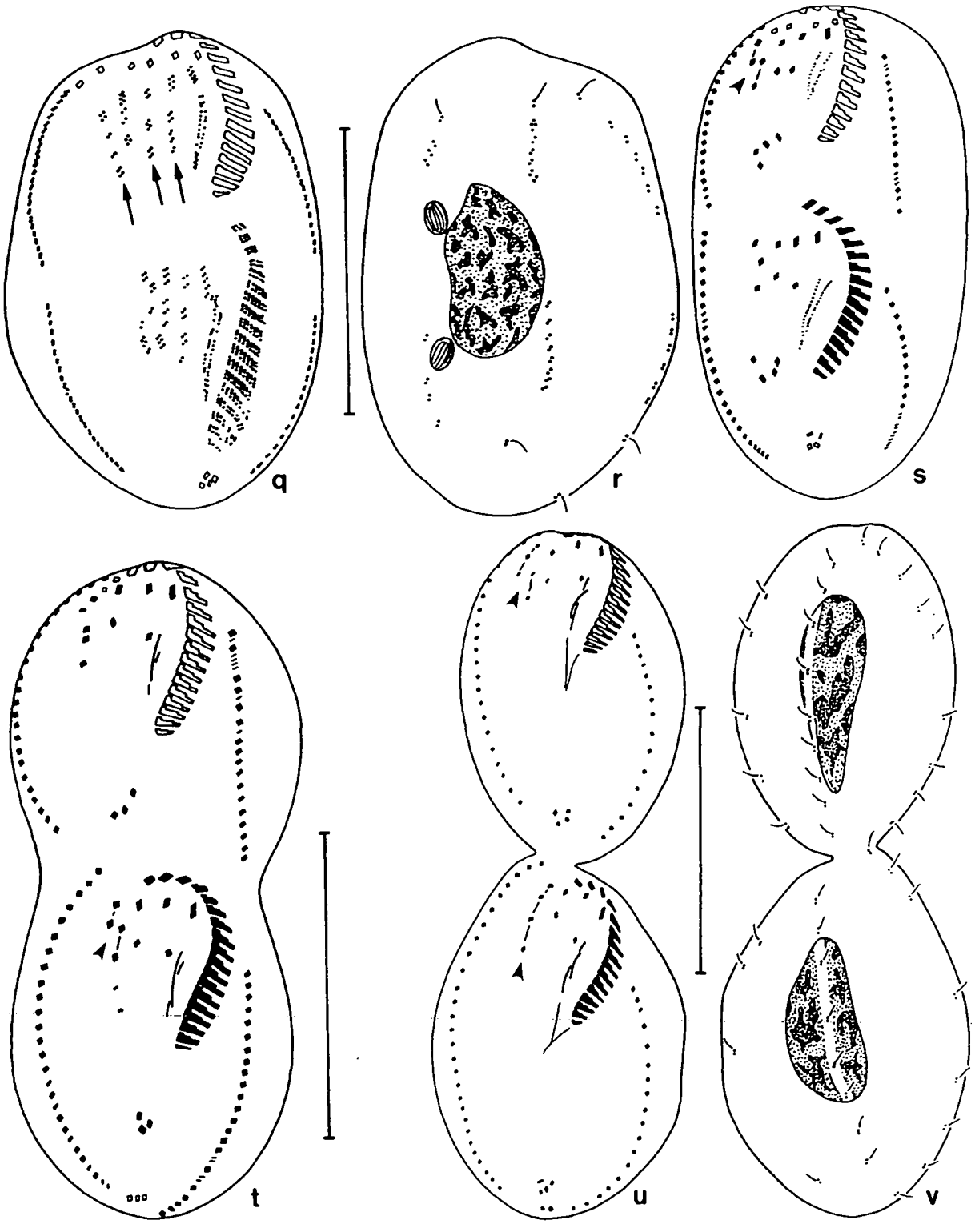

Fig. 157q–v. *Lamtostyla halophila*, ontogenesis of ventral (q, s–u) and dorsal (r, v) infraciliature after protargol impregnation. Transverse cirri (arrows) separate from the end of anlagen 2, 3, and 5, and the anlagen 4 and 5 align to the amphisiellid median cirral row (arrowheads). The paroral moves left of the endoral during shaping of the buccal cavity (for details, see figures 157g–i). Dorsal kineties reproduce by intrakinetal proliferation of kinetids (parental kinetids ciliated in [r], newly formed ciliated in [v]) and do not produce caudal cirri. Scale bars 30 µm.

membranelles performs a rather distinct internal reorganization in middle dividers (Fig. 157g, q).

Occurrence and ecology: To date found only in three highly saline soil samples from Namibia (sites 11, 18, 69), indicating that it is a halophilous species. The populations studied reproduced readily in the non-flooded Petri dish cultures.

Generic classification and comparison with related species: The populations belong, according to the recent revision by PETZ & FOISSNER (1996), to *Lamtostyla* because the oral primordium originates apokinetally and the amphisiellid median cirral row (ACR) commences anlagen formation at the posterior end. Morphologically, *Lamtostyla halophila* resembles, due to the cortical granules, *L. granulifera* FOISSNER, 1997d, which, however, is much larger (about 150 × 35 µm), has three cirri left of the frontal row, and possesses conspicuous, curved undulating membranes. *Lamtostyla edaphoni*, *L. kirkensis*, and *L. hyalina* (see BERGER & FOISSNER 1988a for authorships and dates) are highly similar to *L. halophila* in having only a single cirrus left of the ACR. However, they lack cortical granules, have a bipartited adoral zone of membranelles (*L. hyalina*) or many more cirri (6–13 vs. 3–5) in the ACR (*L. edaphoni*, *L. kirkensis*). Thus, *Lamtostyla halophila* is a distinct species easily separated from its congeners.

Lamtostyla decorata nov. spec. (Fig. 158a–m; 381 l; Table 141)

Diagnosis: Size about 140 × 25 µm in vivo. Oblong and usually twisted about main body axis. Cortical granules colourless, about 0.3 µm across, form conspicuous plaques around dorsal bristles. On average 2 macronuclear nodules, 32 cirri in left and 36 in right marginal row, 4 cirri in amphisiellid median cirral row (ACR), 3 cirri left of ACR, 1 buccal cirrus at summit of strongly curved undulating membranes, 7 transverse cirri, and 3 dorsal kineties. Adoral zone continuous, on average consists of 20 membranelles, with largest bases about 6 µm wide. Buccal cavity of ordinary width, deep.

Type location: Litter from *Welwitschia mirabilis* near the Welwitschia Drive in the central Namib Desert, Namibia, 22°45'S 15°25'E (site 31 in figure 2 and chapter 2.1.2).

Etymology: The Latin adjective *decorata* (ornamented) refers to the granule plaques.

Description: Three populations were studied, namely from Namibian sites (1) and (31) and from Australia. They agree in most, but not all features (see below). Thus, data are kept separate and the diagnosis and description contain only the type population.

Size 100–170 × 20–35 µm in vivo, length:width ratio about 5–6:1 (range 4–9:1) in vivo, on average 4.8:1 in protargol preparations, where cells are slightly inflated (Table 141). Body slender, often slightly sigmoidal, usually curved and/or even spiralized by half a turn about main body axis, distinctly flattened only in oral region (Fig. 158d, j, m); very flexible but acontractile, fragile and thus rather distorted in the preparations. Macronuclear nodules slightly left of midline, ellipsoidal, sometimes globular, with many medium-sized and small nucleoli; rarely specimens with four nodules occur. Micronuclei globular, attached to macronuclear nodules at variable positions. Contractile vacuole without distinct collecting canals above mid-body at left cell margin. Cortical granules scattered around bases of cirri

and in conspicuous plaques around dorsal bristles; individual granules inconspicuous because only about 0.3 µm across and colourless, neither impregnate with protargol nor stain or extrude when methyl green-pyronin is added (Fig. 158e, f; 381 l). Cytoplasm colourless with many fat globules 1–10 µm across, specimens thus dark at low magnification. Feeds on bacteria and small ciliates (*Pseudocohnilembus* sp.). Movement conspicuous because slow and serpentine.

Cirral pattern and number of cirri of usual variability (Fig. 158a–d, m; Table 141). Marginal cirri only about 8 µm long in vivo, arranged in two rows slightly shortened posteriorly, right row extends onto dorsolateral surface anteriorly. Frontal cirri slightly to distinctly enlarged, right one, as is usual, at distal end of adoral zone. Buccal cirrus close to summit of paroral membrane. Usually three cirri left of amphisiellid median cirral row, first cirrus often slightly dislocated to left and thus behind right frontal cirrus. Amphisiellid median cirral row usually composed of only four cirri, commences right of right frontal cirrus and terminates at 21% of body length on average; thus it is only slightly longer than the adoral zone, which occupies 19%; distance between second and third cirrus usually slightly enlarged. Transverse cirri about 15 µm long in vivo, near posterior body margin and thus distinctly projecting, form U-like pattern with one (pretransverse) cirrus in U-cavity (Fig. 158b, m). Dorsal bristles about 3 µm long in vivo, arranged in three rows; row 1 distinctly shortened anteriorly. No caudal cirri.

Gross and fine morphology of oral apparatus as in → *Amphisiella binucleata multicirrata* (Fig. 158a, b, d, t). Adoral zone occupies only 14–23%, on average 19% of body length, composed of about 20 membranelles, bases of largest membranelles about 6 µm wide in vivo. Buccal cavity deep and moderately wide, anterior cavity margin *Cyrtohymena*-like curved; right margin forms prominent lip, covers cavity and proximal adoral membranelles. Undulating membranes distinctly curved, both likely composed of closely spaced dikinetids and optically intersecting near mid. Pharyngeal fibres, likely mixed with long endoral cilia, prominent in vivo and after protargol impregnation, of ordinary length and structure, extend obliquely backwards.

Ontogenesis commences with the formation of a very narrow oral primordium extending from near the transverse cirri to the buccal vertex. Concomitantly, the posterior cirri of the amphisiellid median cirral row modify to anlagen.

Observations on Namibian site (1) specimens (Fig. 158n–w; Table 141): The Namibian site (1) specimens are distinctly larger than those from type locality (length 140–220 µm vs. 100–170 µm in vivo) and thus many morphometric features are considerably different, especially the almost doubled number of right and left marginal cirri. But there are also some rather distinct morphological features: (i) the micronuclei are conspicuously ellipsoidal

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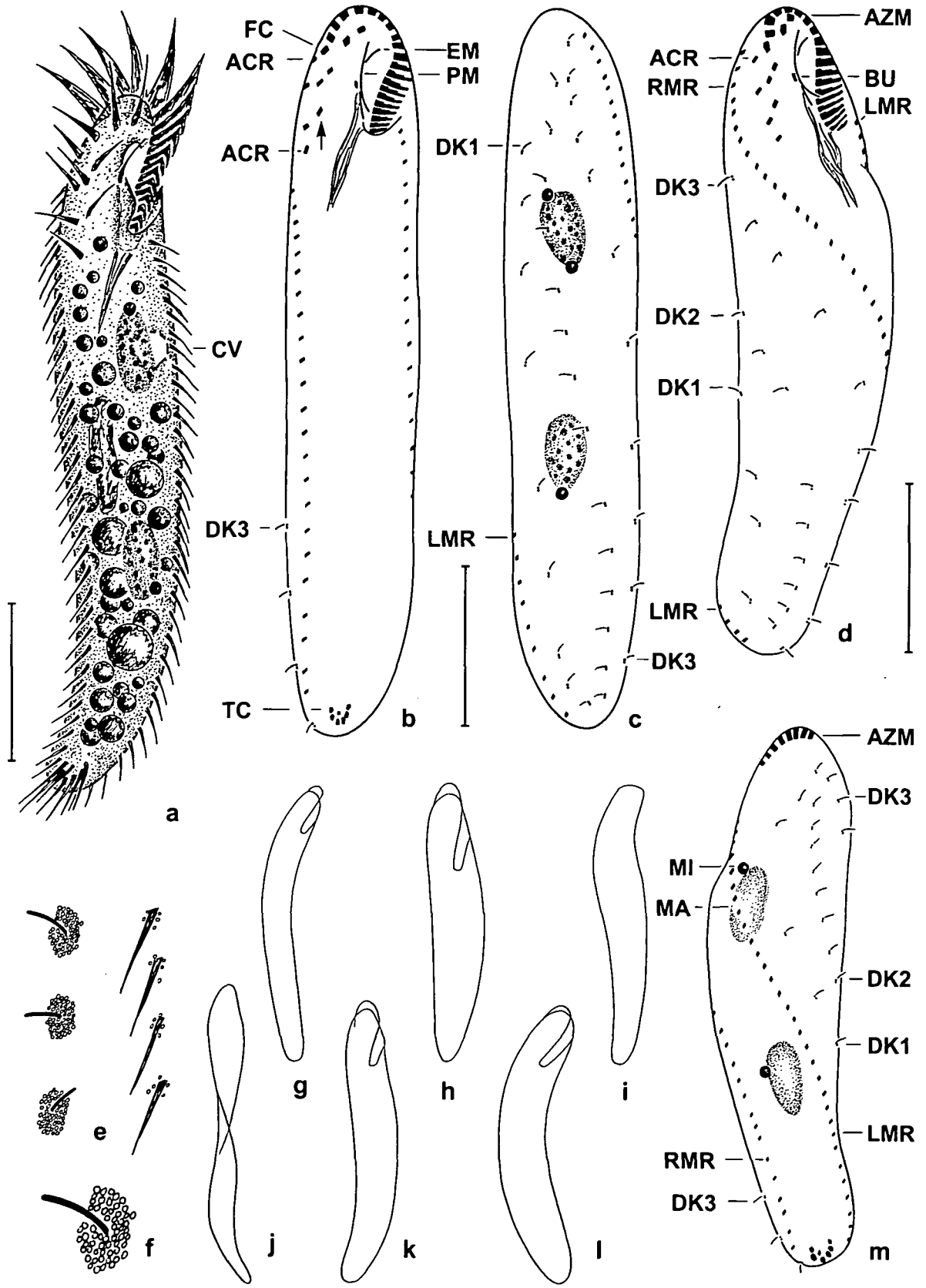
Fig. 158a–m. *Lamtostyla decorata* from life (a, e–l) and after protargol impregnation (b–d, m). **a:** Ventral view of a representative specimen with many lipid droplets. **b, c:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrow marks cirri left of amphisiellid median cirral row. **d, m:** Infraciliature of ventral and dorsal side and nuclear apparatus of a strongly twisted (about 180°) specimen. **e, f:** Tiny (0.3 µm), colourless cortical granules occur around the cirri and dorsal bristles, where they form conspicuous plaques. **g, j–l:** Shape variants. **h, i:** Same specimen in ventral and lateral view showing that *L. decorata* is usually unflattened. ACR – first and last cirrus of amphisiellid median cirral row, AZM – adoral zone of membranelles, BU – buccal cirrus, CV – contractile vacuole, DK1–3 – dorsal kineties, EM – endoral membrane, FC – right frontal cirrus, LMR – left marginal row, MA – macronuclear nodule, MI – micronucleus, PM – paroral membrane, RMR – right marginal row, TC – transverse cirri. Scale bars 30 µm.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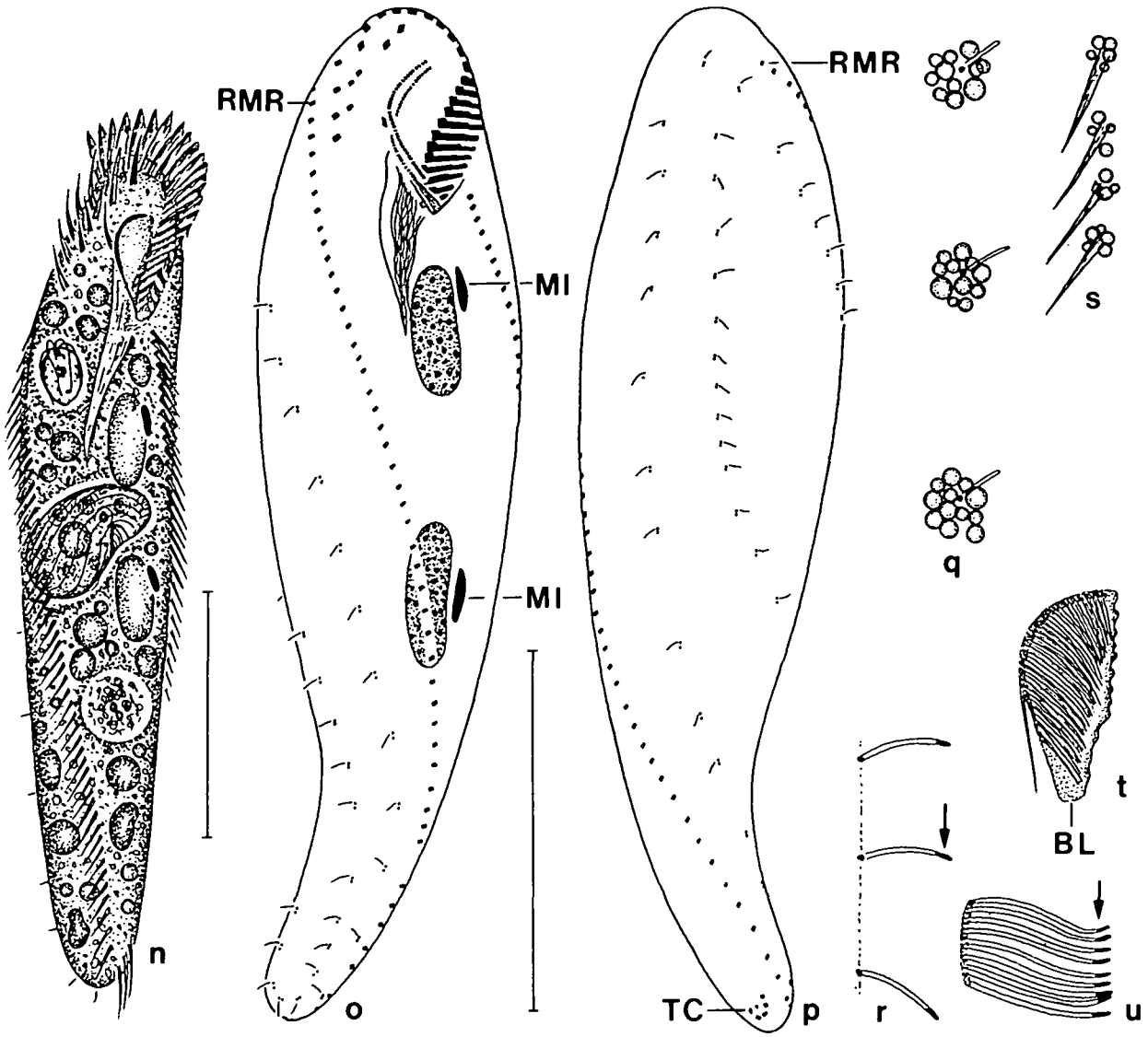


Fig. 158n–w. *Lamtostyla decorata* from Namibian site (1) in vivo (n, q, s, t) and after protargol impregnation (o, p, r, u–w). **n:** Ventral view of a representative, slightly twisted specimen having just ingested a *Colpoda maupasi*. Note the short, that is, about 8 µm long marginal cirri. **o, p:** Infraciliature of ventral and dorsal side and nuclear apparatus showing the conspicuous micronuclei. The species is very fragile and thus becomes inflated by the preparation procedures. **q, s:** The cortical granules, which are colourless and 0.5–2 µm across, form conspicuous plaques around the bases of the dorsal bristles. **t:** The buccal cavity is covered by the very hyaline buccal lip, which is roofed by the paroral cilia. **r, u:** The cilia of the cirri and paroral membrane (u) as well as the dorsal bristles (r) have a strongly argyrophilic distal end (arrows). **v, w:** Ventral and dorsal view of posterior body region showing lack of caudal cirri and the U-like arrangement of the transverse cirri. BL – buccal lip, F – fibres, LMR – left marginal row, MI – micronuclei, RMR – right marginal row, TC – transverse cirri. Scale bars 50 µm.

sometimes almost cylindroidal; (ii) the cortical granules around the bases of the cirri and dorsal bristles are a mixture of small (about 0.5 µm) and large (up to 2 µm) globules, as in the Australian specimens; and (iii) the distal 1–3 µm of all cilia/cirri and dorsal bristles are heavily argyrophilic, a curious property we never observed in any other hypotrich.

Observations on an Australian population (Table 141): A morphometric analysis of the Australian specimens, which have a size of about 110 x 20 µm in vivo, reveals two rather distinct differences to the type population, namely, (i) 6–8, on average 7 vs. 4–5, on average 4 cirri in the amphisiellid median cirral row; and (ii) 5–6, on average 5 vs. 6–9, on average 7 transverse cirri. Furthermore, the cortical granules are larger (1.0–1.5 µm vs. 0.3 µm across) and the plaques (granules groups) not confined to the ciliature, but occur throughout the cortex.

Table 141. Morphometric data on *Lamtostyla decorata* from Namibian site 31 (upper line; type), Australia (middle line), and Namibian site 1 (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	123.4	125.0	18.0	3.8	14.6	90.0	154.0	23
	88.7	86.0	9.2	2.8	10.4	72.0	102.0	11
	158.6	155.0	20.0	4.7	12.6	130.0	200.0	18
Body, width [most specimens of the Australian and	26.2	26.0	3.7	0.8	14.1	20.0	34.0	23
Namibian site (1) population are distinctly inflated]	23.3	23.5	2.8	1.4	11.8	20.0	26.0	4
	41.2	40.0	5.5	1.3	13.3	32.0	54.0	18
Body length:width, ratio	4.8	4.6	1.1	0.2	23.0	3.0	7.4	23
	3.8	3.8	0.4	0.2	9.6	3.4	4.3	4
	3.9	3.7	0.7	0.2	16.9	3.1	5.8	18
Anterior body end to proximal end of adoral zone, distance	23.0	24.0	2.0	0.4	8.9	19.0	26.0	23
	18.5	18.0	1.6	0.5	8.9	15.0	21.0	11
	29.8	30.0	1.8	0.4	5.9	27.0	34.0	18
Body length:length of adoral zone, ratio	5.4	5.2	0.8	0.2	14.1	4.4	7.0	23
	4.8	4.8	0.3	0.1	6.0	4.3	5.3	11
	5.3	5.3	0.6	0.2	12.1	4.4	6.7	18
Anterior body end to last cirrus of amphisiellid median	25.5	25.0	2.6	0.5	10.3	22.0	34.0	23
cirral row, distance	22.7	24.0	2.8	0.9	12.5	17.0	25.0	9
	20.2	20.0	2.6	0.6	12.6	18.0	28.0	18
Body length:length of amphisiellid median cirral row,	4.9	4.8	0.7	0.14	13.9	3.9	6.3	23
ratio	3.9	4.0	0.5	0.2	12.2	3.3	4.7	9
	7.7	7.8	1.1	0.3	14.9	6.1	10.1	18
Anterior body end to buccal cirrus, distance	12.4	12.0	1.3	0.3	10.2	10.0	14.0	23
	10.3	10.0	2.7	1.0	26.2	6.0	14.0	7
	15.8	16.0	1.4	0.3	8.6	14.0	19.0	18
Anterior end of paroral to buccal cirrus, distance	7.6	8.0	0.9	0.2	11.7	6.0	9.0	23
			not analyzed					
	7.9	8.0	2.2	0.5	27.8	5.0	14.0	18
Anterior body end to right marginal row, distance	6.9	7.0	1.8	0.4	25.7	4.0	11.0	23
	7.8	8.0	0.8	0.3	9.6	7.0	9.0	6
	7.8	8.0	2.6	0.6	33.8	2.0	12.0	18
Posterior body end to right marginal row, distance	6.1	7.0	2.5	0.5	40.6	1.0	11.0	21

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
			not analyzed					
	5.9	6.0	1.9	0.5	32.4	2.0	10.0	18
Posterior body end to left marginal row, distance	3.7	3.0	2.0	0.5	54.8	1.0	8.0	20
			not analyzed					
	2.0	1.0	1.8	0.4	87.5	0.0	7.0	18
Posterior body end to anteriormost transverse cirrus, distance	5.7	6.0	1.3	0.3	22.2	3.0	8.0	21
			not analyzed					
	4.6	4.0	0.9	0.2	18.8	3.0	6.0	18
Anterior body end to first macronuclear nodule, distance	33.5	34.0	4.7	1.0	14.1	23.0	42.0	23
	25.1	25.0	3.4	1.0	13.4	20.0	31.0	11
	44.5	42.0	8.4	2.0	18.9	33.0	65.0	18
Macronuclear nodules, distance in between	23.5	23.0	10.4	2.2	44.2	9.0	53.0	23
	11.8	12.5	3.5	1.0	30.2	6.0	17.0	12
	17.5	16.5	5.4	1.3	30.9	8.0	28.0	18
Anterior macronuclear nodule, length	14.7	15.0	3.4	0.7	22.9	7.0	20.0	23
	13.0	13.0	2.1	0.6	16.3	10.0	17.0	13
	18.2	18.5	2.4	0.6	13.1	11.0	21.0	18
Anterior macronuclear nodule, width	7.4	7.0	1.2	0.2	16.2	6.0	10.0	23
	6.5	6.0	1.0	0.3	15.0	5.0	8.0	13
	8.1	7.5	2.5	0.6	31.3	7.0	18.0	18
Macronuclear nodules, length:width ratio	2.0	2.2	0.5	0.1	24.7	1.0	2.7	23
	2.1	2.0	0.5	0.1	21.5	1.3	2.8	13
	2.4	2.5	0.5	0.1	22.2	1.0	3.0	18
Macronuclear nodules, number	2.3	2.0	0.6	0.1	27.6	2.0	4.0	23
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	13
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	18
Anterior micronucleus, length	2.7	2.5	–	–	–	2.5	3.0	21
	2.5	2.5	–	–	–	2.4	3.0	9
	6.2	6.5	0.8	0.2	12.4	5.0	7.0	18
Anterior micronucleus, width	2.5	2.5	–	–	–	2.0	3.0	21
	2.4	2.5	–	–	–	2.0	2.5	9
	2.2	2.0	–	–	–	2.0	3.0	18
Micronuclei, number	1.5	2.0	0.7	0.2	49.4	0.0	3.0	23
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	9
	2.1	2.0	0.8	0.2	35.9	1.0	4.0	18
Nuclear figure, length	52.1	53.0	11.6	2.4	22.3	33.0	79.0	23
	37.1	39.0	6.5	1.8	17.6	22.0	49.0	13
	53.4	53.5	6.5	1.5	12.1	38.0	63.0	18
Adoral membranelles, number	20.4	20.0	0.9	0.2	4.4	19.0	22.0	23
	19.6	19.0	1.0	0.3	4.9	18.0	21.0	13
	24.6	25.0	1.3	0.3	5.4	22.0	27.0	18
Frontal cirri, number (of 23 Namibian specimens analyzed, one has only two cirri)	3.0	3.0	–	–	–	2.0	3.0	23
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	18
Amphisiellid median cirral row, number of cirri	4.1	4.0	–	–	–	4.0	5.0	19
	7.2	7.0	0.6	0.2	8.8	6.0	8.0	10
	4.1	4.0	–	–	–	4.0	5.0	18
Cirri left of amphisiellid median cirral row, number	3.1	3.0	–	–	–	3.0	5.0	19

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10
	3.3	3.0	0.6	0.1	17.5	3.0	5.0	18
Cirri of amphisiellid median cirral row plus cirri left of it,	7.5	7.0	0.9	0.2	12.0	7.0	10.0	23
number	10.2	10.0	0.6	0.2	6.2	9.0	11.0	10
	7.3	7.0	0.7	0.2	9.4	7.0	9.0	18
Buccal cirri, number	1.0	1.0	0	0	0	1.0	1.0	23
	1.0	1.0	0	0	0	1.0	1.0	10
	1.0	1.0	0	0	0	1.0	1.0	18
Transverse cirri, number (including pretransverse cirri)	7.1	7.0	0.7	0.2	9.8	6.0	9.0	17
	5.1	5.0	–	–	–	5.0	6.0	9
	6.0	6.0	0.6	0.1	9.9	5.0	7.0	18
Right marginal cirri, number	36.4	36.0	2.5	0.5	6.9	32.0	41.0	22
	34.0	34.0	2.6	0.7	7.6	29.0	37.0	12
	60.3	61.5	7.1	1.7	11.8	51.0	70.0	18
Left marginal cirri, number	31.5	32.0	2.7	0.6	8.7	27.0	36.0	21
	34.2	34.0	2.6	0.7	7.6	29.0	37.0	12
	57.7	58.0	7.2	1.7	12.5	46.0	71.0	18
Dorsal kineties, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	22
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	18

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Occurrence and ecology: In Namibia as yet found at type location, that is, *Welwitschia* litter, and at site (1), where, however, a rather deviating population occurred (see above). Furthermore, it occurred at site (49), indicating a wide ecological range. The Australian population inhabited a highly saline soil from the shore of Lake Amadeus near the town of Alice Springs. Abundances were low in all samples, where *L. decorata*, interestingly, fed mainly on *Pseudocohnilembus* sp.; the Namibian site (1) specimens, however, ingested the flagellate *Polytomella* and medium-sized ciliates, such as *Colpoda maupasi* and *Urosomoida agiliformis*. In Austria, we found *L. decorata* in soil from Salzburg, but did not study it in detail. Thus, *L. decorata* is likely a euryoecious, euryhaline cosmopolitan.

Generic classification, comparison with related species, and ranking of populations: This species is classified in *Lamtostyla* BUITKAMP, 1977 because stomatogenesis commences apokinetally near the transverse cirri, as in *L. australis* (VOSS 1992). By contrast, in *Amphisiella* GOURRET & ROESER, 1888, which has the same interphase characteristics as *Lamtostyla*, the oral primordium originates in close contact with the amphisiellid median cirral row (PETZ & FOISSNER 1996, WICKLOW 1982). Interestingly, the transverse cirri are arranged U-like in most *Lamtostyla* species; even the *decorata* pattern with a single cirrus in the U-cavity is not unique, but also found in *L. hyalina* (for a review, see BERGER & FOISSNER 1988a). Furthermore, all large (≥ 100 µm) *Lamtostyla* species have a

deep buccal cavity and the undulating membranes side by side and distinctly curved. The small species, for instance → *L. halophila*, have a flat buccal cavity and short, almost straight undulating membranes, similar to *Gonostomum* (BERGER 1999). Accordingly, *L. decorata* and other large *Lamtostyla* species are probably misclassified. They might belong to a new genus or to *Amphisiella*. Further studies are necessary, especially on the oral apparatus with its unique buccal lip.

Lamtostyla decorata is obviously closely related to *L. granulifera* FOISSNER, 1997d; *L. longa* (HEMBERGER, 1985) BERGER & FOISSNER, 1988a; and *L. raptans* (HEMBERGER, 1985) FOISSNER, 1997d: all have seven cirri each in the frontal field and near the posterior end (transverse and pretransverse cirri). *Lamtostyla decorata* differs (i) from *L. granulifera* by body shape (elongate and often twisted about main axis vs. slenderly to rather broadly elliptical), cortical granules (0.3 µm across and packed around dorsal bristles vs. 1–2 µm across forming many closely spaced rows), number of right and left marginal cirri (36 and 32 vs. 44 and 45), and the width of the adoral membranelles (6 µm vs. 12 µm); (ii) from *L. longa* by body shape (elongate and often twisted about main axis vs. slenderly to rather broadly elliptical), number of right and left marginal cirri (36 and 32 vs. 23 and 21), number of dorsal kineties (3 vs. 5), and, most importantly, by the location of the buccal cirrus (about 8 µm behind anterior end of undulating membranes vs. at anterior end of undulating membranes); (iii) from *L. raptans* by size (100–170 × 20–40 µm vs. 200 × 40 µm), body shape (see *L. longa* above), number of right and left marginal cirri (32–41 and 27–36 vs. 57–68 and 60–62), number of adoral membranelles (19–22 vs. 33–36), and number of dorsal kineties (3 vs. 5). Possibly, *Lamtostyla longa* and *L. raptans* differ from *L. decorata* also by the lack of cortical granules. However, such granules might have been overlooked by HEMBERGER (1985), who did not study live specimens in detail.

Lamtostyla australis, which occurs in the same slides, is easily distinguished from *L. decorata* by body shape (elongate ellipsoidal, not twisted), the much longer amphisiellid median cirral row (8–15 cirri), the lower number of transverse cirri (usually 2), and the location of the buccal cirrus (near anterior end of paroral). In vivo, *Lamtostyla decorata* is characterized by the following combination of features: slender, usually twisted body; cortical granule plaques around dorsal bristles; short amphisiellid median cirral row hardly extending above buccal vertex.

The three populations, all studied independently because originally classified as distinct species, differ considerably in morphometrics and some morphological details, suggesting subspecies ranking. On the other hand, a biogeographic pattern is hardly recognizable (see cortical granules) and the cirral pattern is very similar in all specimens. Furthermore, one of the most important features, viz., the number of adoral membranelles, is rather similar, and the taxonomic value of some other characteristics (e.g., micronuclear shape) uncertain. Thus, we prefer to classify all populations in a single species at the present state of knowledge. The ambiguity of this decision becomes obvious when the species' diagnosis is amended to include all populations: "Size 110–220 × 20–30 µm in vivo. Oblong and usually twisted about main body axis. Cortical granules colourless, about 0.3–2 µm across, form conspicuous plaques around dorsal bristles. On average 2 macronuclear nodules and 2 globular to elongate ellipsoidal micronuclei; 32–58 cirri in left and 34–60 in right marginal row; 4–7 cirri in amphisiellid median cirral row (ACR) and 3 cirri left of ACR; 1 buccal cirrus at summit of strongly curved undulating membranes; 5–7 transverse cirri and 3 dorsal kineties. Adoral

zone continuous, consists of 20–25 membranelles on average with largest bases about 6 µm wide. Buccal cavity of ordinary width, deep".

Gastrostyla ENGELMANN, 1862[29]

Improved diagnosis: Adoral zone of membranelles formed like a question mark. Undulating membranes in *Oxytricha* pattern. Number of frontoventral and postoral cirri distinctly higher than 7; frontoventral cirri in more or less continuous, slightly sigmoidal row, usually except for cirri III/2 and IV/2. 4 or 5 transverse cirri and at least 2 pretransverse cirri. 1 right and 1 left row of marginal cirri. 5 or 6 dorsal kineties. Caudal cirri present. Proter and opisthe cirral anlagen develop independently, or at least partially so, from primary primordia. The amphisiellid median (frontoventral) cirral row originates from 3 anlagen with the middle portion consisting of a single cirrus or several cirri. Dorsal morphogenesis in *Oxytricha* pattern.

Type species: *Gastrostyla steinii* ENGELMANN, 1862.

Remarks: The diagnosis is adapted to fit the monograph of BERGER (1999). The ontogenetic data available and those presented below suggest that *Gastrostyla* should be split into three genera or subgenera. We prefer the latter because the interphase cirral pattern is rather similar in all species and the genus is still small, that is, contains only seven species (BERGER 1999).

Gastrostyla (*Gastrostyla*) ENGELMANN, 1862 **nov. stat.**

Diagnosis: Proter and opisthe cirral anlagen develop independently, and anlage II of the opisthe does not extend above proter's oral vertex. The middle portion of the amphisiellid median (frontoventral) cirral row consists of a single cirrus.

Type species: *Gastrostyla steinii* ENGELMANN, 1862.

Remarks: The following species, whose ontogenesis is unknown, remain in this subgenus: *Gastrostyla dorsicirrata* FOISSNER, 1982; *Gastrostyla muscorum* KAHL, 1932; *Gastrostyla setifera* (ENGELMANN, 1862) KENT, 1882; *Gastrostyla pulchra* (PEREYASLAWZEWA, 1886) KAHL, 1932.

[29] Cirral numbering and designation is partially borrowed from the oxytrichids, as explained in BERGER (1999) and figures 160q, r, although homology is uncertain [see discussion under *Gastrostyla (Spetastyla) mystacea*].

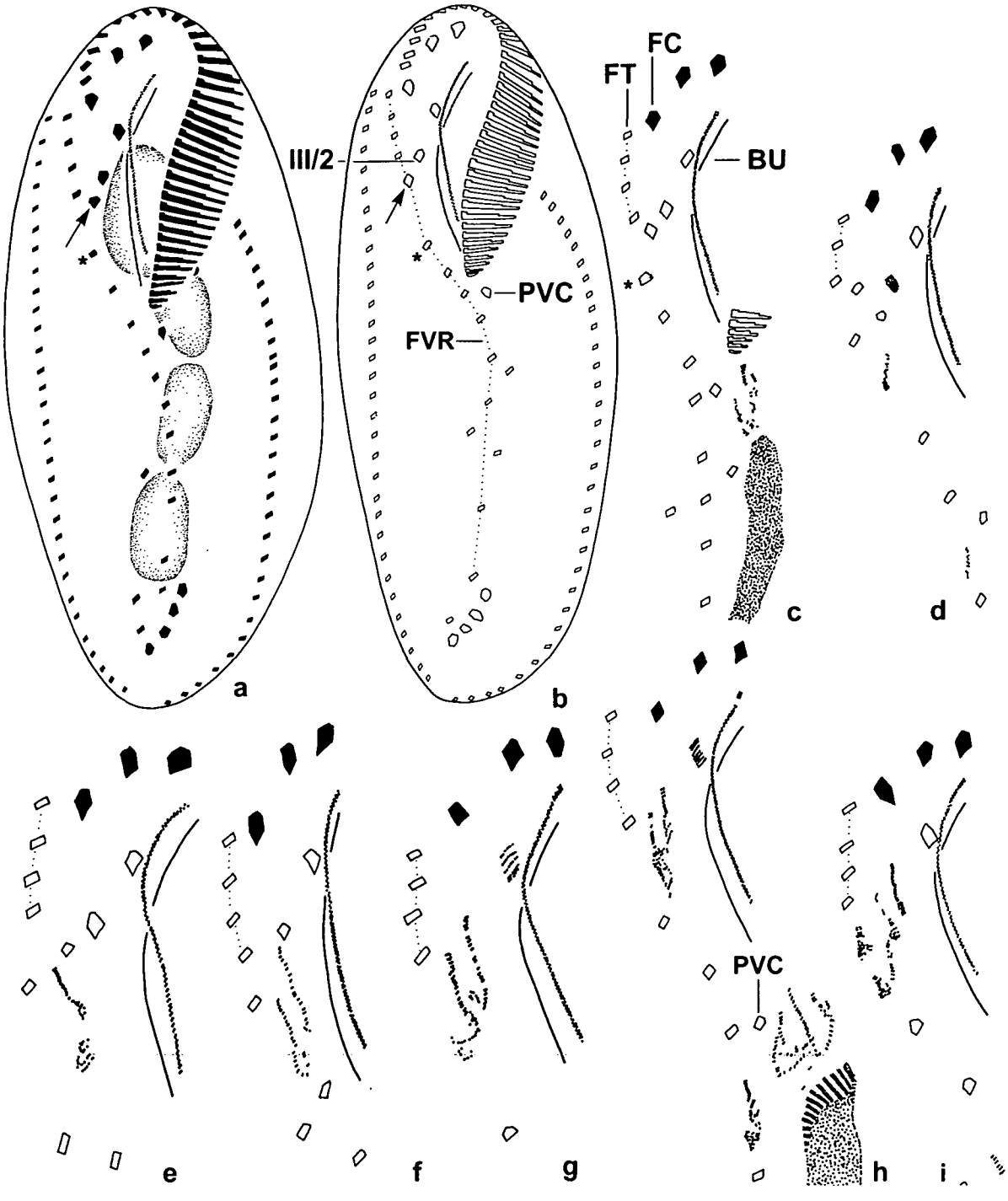


Fig. 159a–i. *Gastrostyla (Gastrostyla) steinii*, ventral side of morphostatic (a, b) and dividing (c–i) South African specimens. **a, b:** Specimens (both 136 µm) with cirrus IV/3 (arrows) distinctly left of frontoventral cirral row (a), respectively, in line with row (b). Asterisks mark anteriormost cirrus of posterior portion of frontoventral row. **c–i:** Anterior portion of early dividers showing variability of proter's cirral anlagen. Likely, no frontoterminal cirri are involved in anlagen formation. Possibly, anlagen IV–VI of the proter originate from cirrus IV/3 (arrows in a and b), as in *Sterkiella nova*; however, it cannot be excluded that the anteriormost cirrus of the posterior portion of the frontoventral row is involved (asterisks in a and b). BU – buccal cirrus, FC – right frontal cirrus, FT – anteriormost frontoterminal cirrus, FVR – frontoventral cirral row, PVC – postoral cirrus IV/2, III/2 – cirrus behind right frontal cirrus.

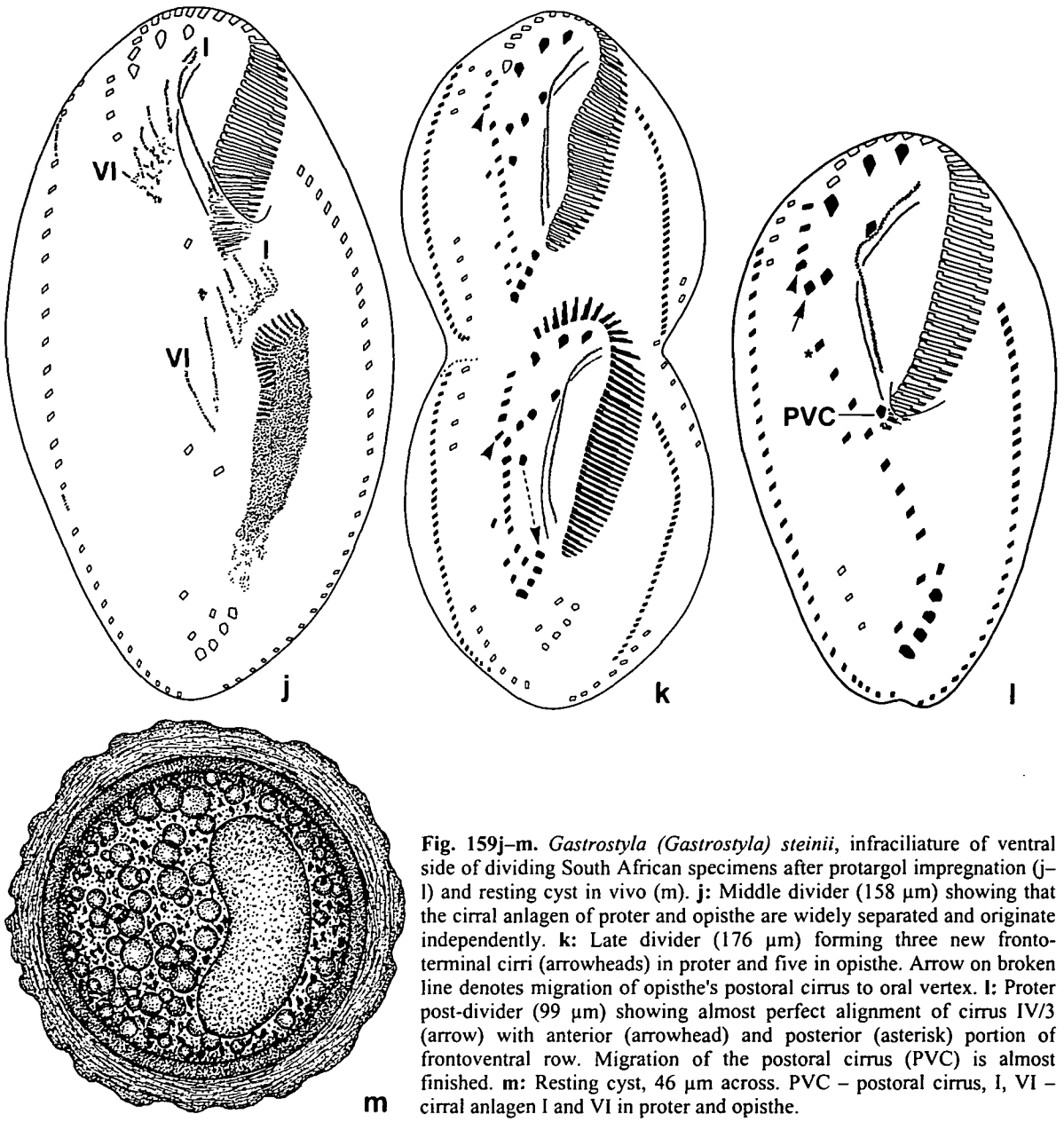


Fig. 159j–m. *Gastrostyla (Gastrostyla) steinii*, infraciliature of ventral side of dividing South African specimens after protargol impregnation (j–l) and resting cyst in vivo (m). **j:** Middle divider (158 µm) showing that the cirral anlagen of proter and opisthe are widely separated and originate independently. **k:** Late divider (176 µm) forming three new fronto-terminal cirri (arrowheads) in proter and five in opisthe. Arrow on broken line denotes migration of opisthe's postoral cirrus to oral vertex. **l:** Proter post-divider (99 µm) showing almost perfect alignment of cirrus IV/3 (arrow) with anterior (arrowhead) and posterior (asterisk) portion of frontoventral row. Migration of the postoral cirrus (PVC) is almost finished. **m:** Resting cyst, 46 µm across. PVC – postoral cirrus, I, VI – cirral anlagen I and VI in proter and opisthe.

Detailed data on the ontogenesis of *Gastrostyla steinii* were published by WALKER & GRIM (1973) and especially HEMBERGER (1982). We reinvestigated the morphology and morphogenesis of a South African population of *G. steinii* and document the features mentioned in the diagnosis by a few drawings and many micrographs (Fig. 159a–l; 287–293, 391a–y, 392a–n, p–r, 393a–g, l–y, 394a–j). Our data largely agree with those of the authors mentioned above. See figure explanations for details.

In the majority of our *Gastrostyla steinii* specimens cirrus IV/3 is 2–3 µm shifted leftwards so

that the amphisiellid median (frontoventral) cirral row seemingly consists of only an anterior and posterior portion (Fig. 159a). However, in about 30% of the specimens cirrus IV/3 is arranged exactly in line with the frontoventral row (Fig. 159b). Thus, it is reasonable to homologize this cirrus with the middle portion of the frontoventral row of the other subgenera.

The resting cysts of the cultivated (Eau de Volvic with some crushed wheat grains) population from the Republic of South Africa are colourless and globular with an outer (ectocyst) diameter of $\bar{x}$ = 47.4 µm (M = 46 µm, SD = 4.8 µm, SE = 1.1 µm, CV = 10.0%, Min = 40 µm, Max = 56 µm, n = 19) and an inner (mesocyst) diameter of $\bar{x}$ = 40 µm (M = 38 µm, SD = 3.7 µm, SE = 0.9 µm, CV = 9.3%, Min = 34 µm, Max = 46 µm, n = 19); rarely do ellipsoidal cysts occur. The meso- and endocyst are compact, smooth, and 1.5–2 µm thick. The ectocyst is less compact, has a wrinkled or indistinctly facetted surface, and is 3.6 µm thick on average. The macronuclear nodules are fused to a reniform mass. The plasm contains many pale fat globules 3–6 µm across and 1.5 × 1 µm-sized, refractive granules (Fig. 159m; 392o, 393i–k).

Gastrostyla (Kleinstyla) nov. subgen.

Diagnosis: Proter and opisthe cirral anlagen develop at least partially from primary primordia and anlage II of the opisthe extends beyond proter's oral vertex. The middle portion of the amphisiellid median (frontoventral) cirral row consists of more than one cirrus.

Type species: *Gastrostyla* (*Kleinstyla*) *bavariensis* nov. spec.

Dedication: We dedicate this new subgenus to Dr. h.c. Bruno M. KLEIN (1891–1968), an Austrian natural scientist, who discovered silver impregnation of protists and was the senior author's mentor.

Remarks: We consider the different number (one versus several) of cirri comprising the middle portion of the frontoventral cirral row as a subgeneric feature. Possibly, *Gastrostyla dorsicirrata* and *G. pulchra* also belong to *Gastrostyla (Kleinstyla)*, according to the incomplete ontogenetic data available (WALLENGREN 1900, BERGER 1999, HU & SONG 2000).

Gastrostyla (Spetastyla) nov. subgen.

Diagnosis: Proter and opisthe cirral anlagen develop at least partially from primary primordia and anlage II of the opisthe extends beyond proter's oral vertex. The middle portion of the amphisiellid median (frontoventral) cirral row consists of a single cirrus.

Type species: *Oxytricha mystacea* STEIN, 1859.

Dedication: We dedicate the new subgenus to Univ.-Doz. Hofrat Dr. Franz SPETA, director of the Biology Centre of the Upper Austrian Museum of Natural History in Linz, who made publishing this costly monograph possible.

Remarks: The anlagen V and VI are long streaks (primary primordia) dividing transversely in early-middle dividers, as in the oxytrichids *Stylonychia mytilus* and *Steinia sphagnicola*, providing proter and opisthe with two anlagen each.

Gastrostyla (Spetastyla) mystacea (STEIN, 1859) STERKI, 1878

Improved diagnosis: Size about 130 × 35–45 µm in vivo; outline elliptical to elongate elliptical. 2 macronuclear nodules. Cortical granules ellipsoidal, colourless, form closely spaced rows. On average 30–37 adoral membranelles, 27–32 left and 27–34 right marginal cirri, 5 transverse cirri, 13–19 cirri in frontoventral row, and 6 dorsal kineties having one caudal cirrus each associated with kineties 1 and 2 and one to three cirri with kinety 4. Frontoventral (amphisiellid median) cirral row terminates near transverse cirri, overlaps with pretransverse cirral row in subspecies *mystacea*.

Remarks: The cirral pattern of *Gastrostyla minima* HEMBERGER, 1985 matches that of *G. mystacea* (cp. figures 160e with 161a, b). Thus, FOISSNER et al. (1991) suggested synonymy. Furthermore, the fronto-ventral-transverse cirral anlage IV produces only one cirrus, which forms the middle portion of the amphisiellid median (frontoventral) cirral row (cp. figures 160m, o with 161f, g). However, exhaustive morphometric analyses revealed quite a lot of non-overlapping or only slightly overlapping features, most having low or ordinary variability coefficients (Table 142). Thus, we consider these allopatric taxa as subspecies of *G. mystacea*.

Gastrostyla (Spetastyla) mystacea mystacea (STEIN, 1859) STERKI, 1878 **nov. stat.** (Fig. 160a–p; 395a–t; Tables 142, 143)

Neotype material: Neotypified from Austrian population (see occurrence and ecology), according to reasons 1, 3, 4, 6 given in chapter 2.4.2.

Improved diagnosis: Size about 130 × 45 µm in vivo. On average 37 adoral membranelles and 19 cirri in frontoventral (amphisiellid median cirral) row, which distinctly overlaps pretransverse cirral row.

Redescription: Size 100–160 × 40–50 µm in vivo, length:width ratio about 2.5–3.0:1 in vivo, 2.1–2.8:1 in protargol preparations, where specimens are slightly inflated; very flexible but acontractile and flattened up to 2:1 dorsoventrally. Shape fairly constant, outline elliptical to elongate elliptical, posterior end often bluntly pointed, rarely broadly rounded (Fig. 160a,

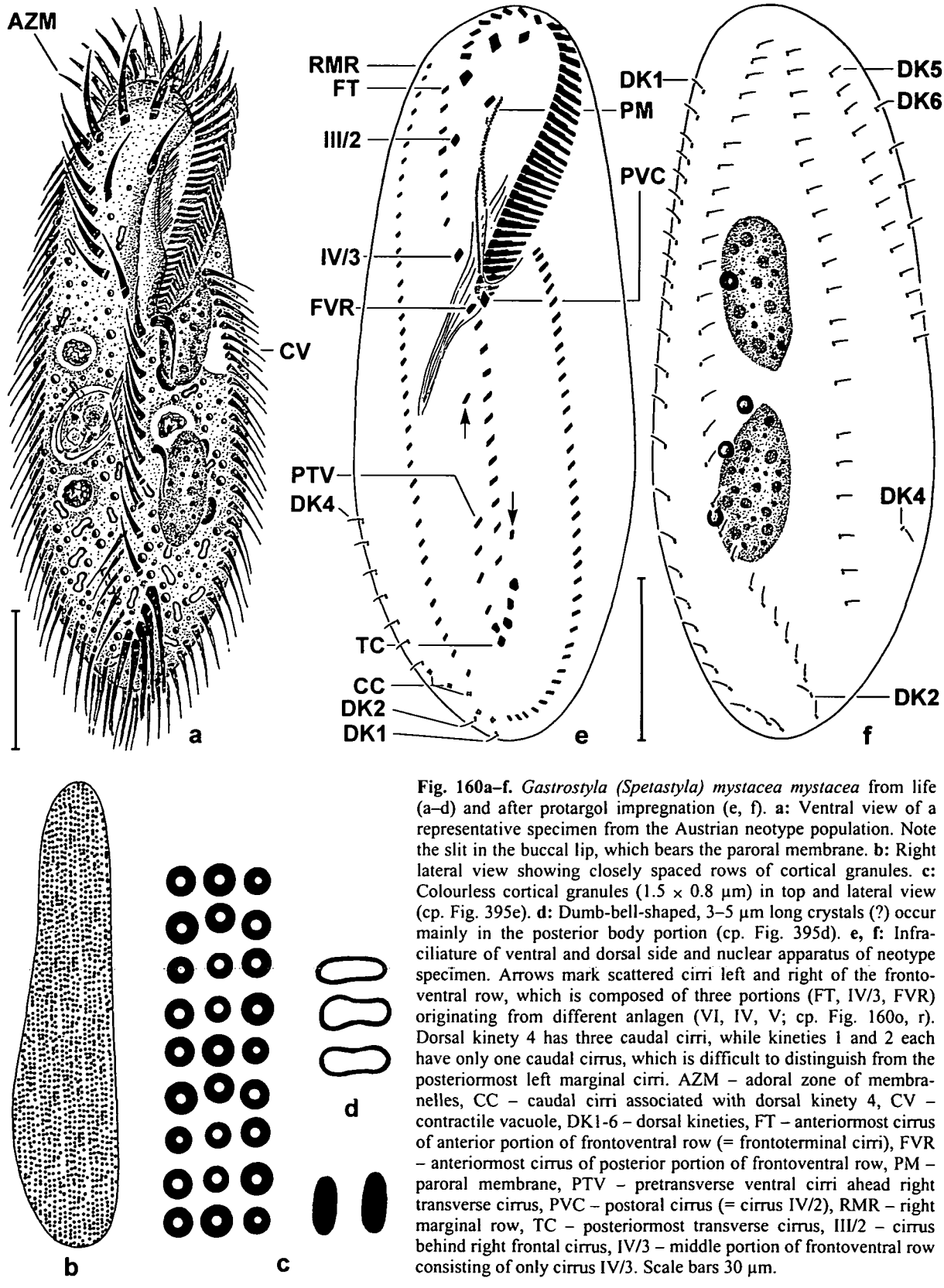


Fig. 160a–f. *Gastrostyla (Spetastyla) mystacea mystacea* from life (a–d) and after protargol impregnation (e, f). **a:** Ventral view of a representative specimen from the Austrian neotype population. Note the slit in the buccal lip, which bears the paroral membrane. **b:** Right lateral view showing closely spaced rows of cortical granules. **c:** Colourless cortical granules (1.5 × 0.8 µm) in top and lateral view (cp. Fig. 395e). **d:** Dumb-bell-shaped, 3–5 µm long crystals (?) occur mainly in the posterior body portion (cp. Fig. 395d). **e, f:** Infraciliature of ventral and dorsal side and nuclear apparatus of neotype specimen. Arrows mark scattered cirri left and right of the frontoventral row, which is composed of three portions (FT, IV/3, FVR) originating from different anlagen (VI, IV, V; cp. Fig. 160o, r). Dorsal kinety 4 has three caudal cirri, while kineties 1 and 2 each have only one caudal cirrus, which is difficult to distinguish from the posteriormost left marginal cirri. AZM – adoral zone of membranelles, CC – caudal cirri associated with dorsal kinety 4, CV – contractile vacuole, DK1-6 – dorsal kineties, FT – anteriormost cirrus of anterior portion of frontoventral row (= frontoterminal cirri), FVR – anteriormost cirrus of posterior portion of frontoventral row, PM – paroral membrane, PTV – pretransverse ventral cirri ahead right transverse cirrus, PVC – postoral cirrus (= cirrus IV/2), RMR – right marginal row, TC – posteriormost transverse cirrus, III/2 – cirrus behind right frontal cirrus, IV/3 – middle portion of frontoventral row consisting of only cirrus IV/3. Scale bars 30 µm.

b; 395c; Table 142). Macronuclear nodules left of midline, about 23 × 11 µm in vivo, ellipsoidal to elongate ellipsoidal, with many small and medium-sized nucleoli. Micronuclei about 5 × 3 µm in vivo, usually attached to macronuclear nodules. Contractile vacuole near mid-body at left cell margin. Cortical granules conspicuous at a magnification of ×1000 because in closely spaced, meridional rows; individual granules elliptical in lateral and ring-shaped in top view, about 1.5 × 0.8 µm, colourless, become blue but are not released when methyl green-pyronin is added; do not impregnate with the protargol method used (Fig. 160b, c; 395e–g). Cytoplasm colourless, contains lipid droplets 0.5–2 µm across and, especially in posterior half, many conspicuous crystal-like inclusions, which are 3–5 µm long, dumb-bell-shaped, colourless, and dissolve slowly when set free (Fig. 160a, d; 395d). Feeds on algae (mainly *Chlamydomonas*) digested in vacuoles 8–20 µm across, in pure cultures ingests small ciliates (*Urotricha* sp.) and starch grains. Movement without peculiarities, that is, swims and glides rapidly on microscope slide and debris, showing great flexibility.

Cirral pattern and number of cirri of usual variability (Fig. 160e; 395h–k; Table 142). Marginal and frontoventral cirri about 20 µm long, usually composed of two rows with 4–5 cilia each (4–5 × 2 pattern), posterior marginal cirri often distinctly smaller, sometimes composed of only a single row with 4–5 cilia. Right marginal row begins near level of distal adoral membranelle and terminates 5 µm before body end on average, left row usually J-shaped because terminating in midline. Frontal cirri distinctly enlarged and arranged as is usual. Buccal cirrus slightly enlarged (about 5 × 3 basal bodies), right of anterior end of paroral and ahead of endoral. Cirrus behind right frontal cirrus (= cirrus III/2) slightly enlarged because composed of about 4 × 4 basal bodies. Postoral cirrus (= postperistomial cirrus according to EIGNER & FOISSNER 1994) usually at margin of oral vertex and optically thus above proximal adoral membranelle, composed of 4–5 × 3 basal bodies on average. Frontoventral (amphisiellid median) cirral row conspicuous because extending from right frontal cirrus to near left transverse cirrus, slightly sigmoidal and interrupted by cirrus IV/3 right of proximal region of adoral zone; composed of three portions (see ontogenesis), namely, (i) an anterior portion commencing at 12% and terminating at 31% of body length on average; (ii) a middle portion composed of a single, usually enlarged (4–5 × 3 basal bodies) cirrus (IV/3) at 34% of body length; and (iii) a posterior portion commencing somewhat right and slightly behind level of postoral cirrus and terminating near left transverse cirrus. Frequently some scattered cirri left and/or right of posterior portion of frontoventral row. Ahead of right transverse cirrus a short row of pretransverse cirri invariably overlapping with posterior portion of frontoventral row. Transverse cirri in hook-shaped pattern, slightly enlarged and about 22 µm long in vivo, rather far subterminal and thus only the right cirri project beyond rear body end.

Dorsal bristles about 4 µm long in vivo, arranged in six rows (Fig. 160e, f): rows 1–3 as well as 5 and 6 slightly to moderately shortened anteriorly, row 5 terminates equatorially at right body margin, row 6 composed of only one to four bristles at right anterior corner; row 4 and its caudal cirri extend dorsoventrally in about 50% of impregnated specimens (Fig. 160e). Caudal cirri inconspicuous because not distinctly longer than marginal cirri and usually composed of only 2 × 2 basal bodies; one cirrus each associated with kineties 1 and 2 and usually two or three cirri with kinety 4. Caudal cirri of kineties 1 and 2 often difficult to distinguish from last cirri of left marginal row.

Table 142. Morphometric comparison of *Gastrostyla mystacea mystacea* (upper line) and *G. mystacea minima* (lower line). Asterisks mark non-overlapping or only slightly overlapping features, two (#) of which are considered as important for distinguishing the subspecies.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	123.1	119.0	14.8	3.2	12.0	92.0	147.0	21
	115.5	117.0	9.7	2.7	8.4	99.0	138.0	13
Body, width [b]	50.3	50.0	4.5	1.0	9.0	41.0	61.0	21
	35.7	36.0	4.2	1.2	11.7	27.0	42.0	13
Body length:width, ratio [b]	2.4	2.4	0.2	0.0	7.8	2.1	2.8	21
	3.3	3.2	0.4	0.1	11.0	2.8	3.9	13
Anterior body end to proximal end of adoral zone of membranelles, distance	51.4	52.0	6.0	1.3	11.6	41.0	63.0	21*
	35.5	35.0	2.4	0.7	6.9	33.0	40.0	13
Body length:length of adoral zone, ratio	2.4	2.4	0.1	0.0	6.2	2.2	2.8	21*
	3.3	3.2	0.2	0.1	5.6	2.9	3.6	13
Anterior body end to buccal cirrus, distance	14.5	14.0	3.0	0.6	20.5	10.0	21.0	21
	11.6	12.0	1.3	0.4	11.4	12.0	18.0	13
Anterior body end to frontoventral cirrus III/2, distance	22.9	23.0	3.4	0.8	15.1	18.0	30.0	21*
	15.8	16.0	2.2	0.6	14.0	12.0	18.0	13
Body length:distance between anterior body end and frontoventral cirrus III/2, ratio	5.4	5.3	0.7	0.2	13.1	4.5	6.8	21*
	7.4	3.2	0.2	0.1	6.1	2.9	3.5	13
Anterior body end to frontoventral cirrus IV/3, distance	42.4	42.0	5.2	1.1	12.2	34.0	53.0	21
	31.7	32.0	2.8	0.8	8.8	28.0	36.0	13
Anterior body end to postoral cirrus, distance	49.5	49.0	5.3	1.1	10.6	40.0	61.0	21*
	35.9	36.0	2.5	0.7	6.9	33.0	40.0	13
Body length:distance between anterior body end and postoral cirrus, ratio	2.5	2.5	0.1	0.0	5.3	2.3	2.8	21*
	3.2	3.2	0.2	0.1	6.1	2.9	3.5	13
Anterior body end to frontoventral row, distance	15.2	16.0	3.1	0.7	20.6	8.0	19.0	21
	10.2	10.0	2.8	0.8	27.2	7.0	16.0	13
Anterior body end to end of anterior portion of frontoventral row, distance	38.2	38.0	5.1	1.1	13.4	28.0	49.0	21*
	26.7	27.0	2.1	0.6	7.7	22.0	30.0	13
Body length:distance between anterior body end and end of anterior portion of frontoventral row, ratio	3.2	3.2	0.3	0.1	10.4	2.7	4.0	21*
	4.4	4.2	0.5	0.1	10.9	3.5	5.3	13
Anterior body end to posterior portion of frontoventral row, distance	51.8	50.0	5.2	1.1	10.0	42.0	61.0	21
	40.0	40.0	3.6	1.0	9.0	32.0	46.0	13
Anterior body end to end of posterior portion of frontoventral row, distance	99.0	97.0	12.3	2.7	12.4	74.0	119.0	21
	91.2	89.0	7.7	2.1	8.5	80.0	109.0	13
Anterior body end to anteriormost pretransverse cirrus ahead right transverse cirrus, distance	92.0	91.0	11.9	2.6	12.9	70.0	111.0	21
	93.3	91.0	7.9	2.2	8.4	79.0	110.0	13
Anterior body end to posteriormost pretransverse cirrus ahead right transverse cirrus, distance	106.9	106.0	12.9	2.8	12.1	82.0	126.0	21
	99.2	99.0	8.5	2.4	8.6	86.0	119.0	13
Anterior body end to paroral membrane, distance	13.8	14.0	3.1	0.7	22.3	9.0	20.0	21
	10.1	10.0	1.3	0.4	13.1	8.0	12.0	13
Paroral membrane, length	22.5	22.0	2.5	0.6	11.3	18.0	27.0	21*
	14.8	14.0	2.0	0.6	13.7	12.0	18.0	13
Body length:length of paroral membrane, ratio	5.5	5.3	0.5	0.1	9.8	4.6	6.9	21*
	7.9	7.8	0.8	0.2	10.3	6.8	9.0	13
Anterior body end to endoral membrane, distance	18.9	18.0	2.9	0.6	15.5	14.0	26.0	21
	14.5	15.0	1.2	0.3	8.2	12.0	16.0	13

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Endoral membrane, length	27.4	27.0	3.2	0.7	11.6	22.0	32.0	21*
	18.5	18.0	1.8	0.5	9.5	16.0	22.0	13
Body length:length of endoral membrane, ratio	4.5	4.5	0.4	0.1	8.7	3.9	5.6	21*
	6.3	6.5	0.4	0.1	7.0	5.3	6.9	21
Posterior body end to posteriormost transverse cirrus, distance	10.0	10.0	3.3	0.7	32.6	5.0	17.0	21
	11.6	11.0	2.0	0.6	17.4	9.0	15.0	13
Posterior body end to anteriormost transverse cirrus, distance	21.0	21.0	4.2	0.9	19.9	14.0	30.0	21
	21.1	21.0	3.2	0.9	15.2	16.0	26.0	13
Anterior body end to right marginal row, distance	11.6	11.0	3.2	0.7	27.4	4.0	17.0	21
	9.5	9.0	2.1	0.6	22.5	6.0	14.0	13
Posterior body end to right marginal row, distance	5.3	5.0	2.6	0.6	49.7	2.0	11.0	21
	3.2	3.0	1.5	0.4	48.2	1.0	6.0	13
Posterior body end to left marginal row, distance	0.6	0.0	–	–	–	0.0	3.0	21
	0.8	1.0	–	–	–	0.0	1.0	13
Anterior body end to first macronuclear nodule, distance	37.8	38.0	4.7	1.0	12.4	30.0	44.0	21
	29.2	30.0	2.4	0.7	8.4	24.0	33.0	13
Nuclear figure, length	58.0	59.0	6.9	1.5	11.9	44.0	71.0	21
	54.2	54.0	5.7	1.6	10.5	45.0	68.0	13
Macronuclear nodules, distance in between	8.5	12.0	1.7	0.4	14.5	9.0	14.0	21
	20.6	19.0	5.7	1.6	27.6	11.0	32.0	13
Anterior macronuclear nodule, length	24.3	25.0	3.9	0.9	16.1	18.0	31.0	21
	15.8	16.0	2.1	0.6	13.2	13.0	21.0	13
Anterior macronuclear nodule, width	11.9	12.0	1.7	0.4	14.5	9.0	14.0	21
	10.4	10.0	1.5	0.4	14.5	8.0	13.0	13
Posterior macronuclear nodule, length	25.1	25.0	4.1	0.9	16.1	18.0	33.0	21
	17.8	16.0	3.7	1.0	20.7	13.0	24.0	13
Posterior macronuclear nodule, width	12.9	13.0	2.0	0.4	15.2	10.0	16.0	21
	10.2	10.0	1.1	0.3	11.3	7.0	12.0	13
Anterior micronucleus, length	3.4	3.0	0.6	0.1	18.1	2.5	5.0	21
	–	–	–	–	–	2.5	4.0	2
Anterior micronucleus, width	3.0	3.0	0.3	0.1	10.5	2.5	4.0	21
	–	–	–	–	–	2.5	4.0	2
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	13
Micronuclei, number	3.0	3.0	1.0	0.2	31.9	2.0	5.0	21
	–	–	–	–	–	1.0	1.0	2
Adoral membranelles, number	36.5	38.0	3.5	0.8	9.7	27.0	42.0	21#
	29.5	29.0	1.4	0.4	4.7	28.0	32.0	13
Frontal cirri, number [c]	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13
Cirri behind right frontal cirrus, number [d]	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13
Anterior portion of frontoventral row (= fronto-terminal cirri), number of cirri	6.7	7.0	0.7	0.2	10.7	5.0	8.0	21
	5.1	5.0	0.8	0.2	15.0	4.0	6.0	13
Cirrus IV/3 (Fig. 160e), number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Postoral cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13
Posterior portion of frontoventral row, number of cirri [c]	11.4	12.0	1.1	0.2	9.4	9.0	13.0	21*
	7.2	7.0	0.7	0.2	9.6	6.0	8.0	13
Pretransverse ventral cirri ahead of right transverse cirrus, number	4.3	4.0	0.9	0.2	21.1	2.0	6.0	21*
	2.4	2.0	0.5	0.1	21.2	2.0	3.0	13
Transverse cirri, number	5.0	5.0	0.0	0.0	0.0	5.0	5.0	21
	5.0	5.0	0.0	0.0	0.0	5.0	5.0	13
Frontoventral cirri, number [f]	26.1	27.0	2.2	0.5	8.6	21.0	29.0	21*
	17.6	17.0	1.4	0.4	7.9	15.0	20.0	13
Frontoventral row, number of cirri [g]	19.1	20.0	1.6	0.4	8.6	16.0	21.0	21#
	13.2	13.0	1.3	0.4	9.8	11.0	15.0	13
Right marginal cirri, number	34.3	35.0	3.4	0.7	9.9	26.0	38.0	21
	26.9	27.0	3.9	1.1	14.4	16.0	32.0	13
Left marginal cirri, number	32.0	32.0	3.4	0.7	10.5	27.0	38.0	21
	26.6	26.0	2.3	0.6	8.7	24.0	30.0	13
Caudal cirri on dorsal kinety 1, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	20
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	9
Caudal cirri on dorsal kinety 2, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	20
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	9
Caudal cirri on dorsal kinety 4, number	2.3	2.0	–	–	–	1.0	3.0	19
				see text				
Dorsal kineties, number	6.0	6.0	0.0	0.0	0.0	6.0	6.0	21
	5.9	6.0	–	–	–	5.0	6.0	8
Dorsal kinety 1, number of bristles	22.4	23.0	2.1	0.5	9.5	18.0	26.0	17
	18.0	18.0	1.6	0.7	8.8	16.0	20.0	5

[a] Data based on protargol-impregnated and randomly selected specimens. Measurements in µm. *Gastrostyla mystacea mystacea*: specimens from a pure culture, as described in the text, impregnated with WILBERT's protargol method; *Gastrostyla mystacea minima*: specimens from a non-flooded Petri dish culture impregnated with FOISSNER's protargol method. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean, * – only slightly or non-overlapping features, (#) – features considered as important for distinguishing the subspecies.

[b] *Gastrostyla mystacea mystacea* slightly inflated due to the preparation method used.

[c] Specimens with four frontal cirri occur very rarely.

[d] Cirrus IV/3 not included. Specimens with two cirri behind the right frontal cirrus occur very rarely.

[e] Scattered cirri (arrows in figure 160e) left and/or right of row excluded.

[f] All cirri, except the three frontal cirri, the single buccal cirrus, the five transverse cirri, and the marginal and caudal cirri.

[g] Sum of frontoterminal cirri (= anterior portion of frontoventral row), cirrus IV/3, and cirri of posterior portion of frontoventral row (see dotted line in Fig. 160r).

Adoral zone occupies 36–45%, on average 42% of body length, of usual shape and structure; composed of an average of 37 membranelles, bases of largest membranelles about 10 µm wide in vivo (Fig. 160a, e; 395c, h–k; Table 142). Buccal cavity moderately wide and deep, right half covered by curved, hyaline lip bearing paroral membrane and covering proximal portion of adoral zone. Paroral slightly to distinctly curved, composed of zigzagging basal bodies having about 10 µm long cilia, begins about 5 µm ahead of endoral and terminates distinctly above proximal end of adoral zone. Endoral slightly curved, extends to proximal end of adoral zone, alongside posteriorly diverging paroral; in about half the specimens the anterior ends of the paroral and endoral optically overlap. Pharyngeal fibres clearly recognizable after protargol impregnation, of ordinary length and structure, extend obliquely backwards.

Occurrence and ecology: *Gastrostyla mystacea mystacea* was discovered by STEIN (1859) in a puddle containing percolating manure of a dunghill in the village of Tharandt near Dresden, Germany. Later, he found it in similar habitats near Berlin and Prague. We rediscovered this species in an ephemeric, eutrophic meadow pond near the Salzburg University (47°47'N 13°40'E) and could cultivate it in Eau de Volvic enriched with some squashed wheat grains and part of the natural microbial community. The data available indicate that *G. mystacea mystacea* prefers nutrient-rich habitats (FOISSNER et al. 1991). *Gastrostyla opisthoclada*, likely a junior synonym of *G. mystacea mystacea*, was discovered in China (SHI et al. 1999). For further records from Eurasia and Australia, all lacking illustrations, see BERGER (1999).

Comparison with original description and related species: Our specimens agree with the original description of *Gastrostyla mystacea* in most main features (cp. Fig. 160a, e with Fig. 395a, b), namely, body length (100–160 µm respectively 130–170 µm), length of adoral zone (about 42% of body length), number (20–30) of cirri in and near frontoventral row, the limnetic habitat, and geographic region (Austria respectively Germany and Czech Republic). Three differences are noteworthy: (i) STEIN figures two specimens both distinctly widened posteriorly (Fig. 395a, b). Our specimens are usually not widened, but bluntly pointed even when well-fed, that is, in cultures with many dividers. Possibly, STEIN's specimens were inflated due to the highly saprobic and likely oxygen-deficient milieu (liquid manure). (ii) STEIN (1859) did not mention cortical granules, although he described them in other hypotrichs, for example, *Paraurostyla weissei* and *Urostyla grandis* (for review, see FOISSNER et al. 1991). However, in these species the granules are coloured and make cells yellowish even at low magnification. By contrast, the granules of our specimens are colourless and thus recognizable only at high magnification, suggesting that STEIN (1859), who did not figure any details, overlooked them. (iii) According to STEIN's description, the transverse cirri do not project beyond rear body end, whereas they protrude slightly in our population (Fig. 160a). However, STEIN's illustrations show that he very likely underestimated the length of the transverse cirri, which are only 13–16 µm in his figures, while they are 22 µm long in our specimens.

Gastrostyla (Spetastyla) mystacea mystacea is the sole species of the genus which has distinctly more than 20 cirri in and near the frontoventral row (BERGER 1999). *Gastrostyla (Gastrostyla) dorsicirrata* lacks cortical granules, has 7–12 caudal cirri in three distinct rows, and 4–7 cirri originate from anlage IV, while only three do so in both subspecies of *Gastrostyla (Spetastyla) mystacea*. *Gastrostyla (Gastrostyla) setifera* possibly also lacks cortical granules, is about 270 µm long, and the transverse cirri form two distinct groups. *Gastrostyla*

(Gastrostyla) pulchra is a marine species with the transverse cirri near mid-body (HU & SONG 2000). In vivo, *Gastrostyla mystacea mystacea* is almost indistinguishable from the subspecies *minima*, which differs only in morphometric features (Table 142). Generally, both can be distinguished from other hypotrichs by the following combination of features: two macronuclear nodules; ellipsoidal, colourless cortical granules in inconspicuous rows; frontoventral row extending from frontal to transverse cirri.

Ontogenesis (Fig. 160g–p; 395 l–p): Ontogenesis commences with the formation of an oral primordium extending from near the anteriormost transverse cirrus to the buccal vertex. Some basal bodies of the right anterior portion of the oral primordium migrate towards the posterior end of the paroral (Fig. 160g, arrow), forming fronto-ventral-transverse cirral anlage II of the opisthe. No cirri participate in the formation of the oral primordium (Fig. 160g).

Somewhat later, the oral primordium becomes slightly wider anteriorly and anlage II extends to the rear end of the paroral (Fig. 160h); however, the streak very likely does not participate in the formation of proter's anlage II, which develops from the buccal cirrus (Fig. 160j). Simultaneously, the two or three anteriormost cirri of the posterior portion of the frontoventral row are transformed to anlagen V and VI for both the proter and opisthe (Fig. 160h, asterisks).

Next, the oral primordium begins with the formation of adoral membranelles in the usual manner (Fig. 160i). A slightly oblique, oblong field of basal bodies originates right of the anterior end of the oral primordium – likely by participation of the oral primordium and by incorporation of about three further cirri of the posterior portion of the frontoventral row – eventually forming the primordium for the opisthe's undulating membranes. Opisthe's anlage III inserts between opisthe's anlage II mentioned above and the postoral cirrus (Fig. 160i, arrow). Cirrus IV/3 (= middle portion of frontoventral row) transforms to anlage IV of the proter (Fig. 160i, arrowhead; 395 l). Anlagen V and VI become longer, that is, develop to primary primordia (Fig. 160i, asterisks).

Somewhat later, the postoral cirrus is transformed to anlage IV of the opisthe (Fig. 160j, arrow), cirrus III/2 to anlage III of the proter, and the buccal cirrus generates proter anlage II (Fig. 160j; 395 l). Anlagen V and VI are now conspicuously long primary primordia and commence to divide in an anterior portion for the porter and a posterior for the opisthe; on average, the two posteriormost parental cirri of the anterior portion of the frontoventral row are either resorbed or incorporated in anlage V of the proter. Anlage I of the proter originates from the anterior end of the reorganizing parental paroral membrane, while anlage I of the opisthe develops at the anterior end of the anlage for the undulating membranes (Fig. 160k; 395m). The origin of the anlagen is summarized in table 143.

In middle, late and very late dividers, the cirri commence to differentiate and migrate to their specific positions (Fig. 160 l, m, o; 395n–p). Figures 160m, o and 395p show that the frontoventral (amphisiellid median cirral) row is assembled from sections of the three rightmost cirral anlagen: the anterior section of anlage VI (= frontoterminal cirri), usually comprising six or seven cirri, forms the anterior portion of the frontoventral row; the middle portion is formed by the anterior section of anlage IV and consists of only one cirrus (IV/3) slipping between the frontoterminal cirri and the cirri of anlage V, which form the posterior portion of the frontoventral row. The postoral cirrus originates from anlage IV and migrates backwards to the oral vertex, while the posterior cirri of anlage VI become the pretransverse cirri ahead of the right transverse cirrus. No parental cirri are transmitted to the next generation.

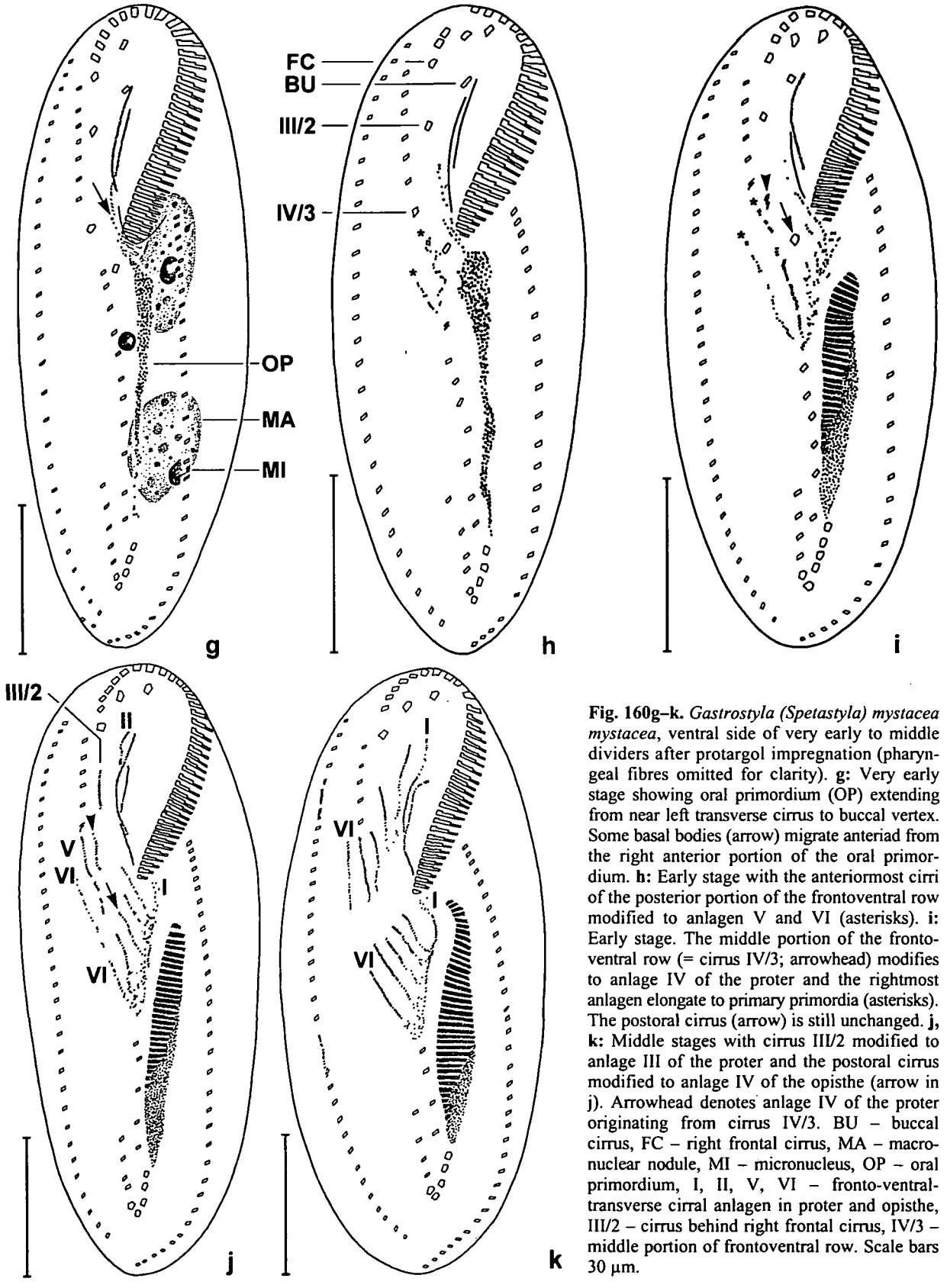


Fig. 160g–k. *Gastrostyla (Spetastyla) mystacea mystacea*, ventral side of very early to middle dividers after protargol impregnation (pharyngeal fibres omitted for clarity). **g:** Very early stage showing oral primordium (OP) extending from near left transverse cirrus to buccal vertex. Some basal bodies (arrow) migrate anteriad from the right anterior portion of the oral primordium. **h:** Early stage with the anteriormost cirri of the posterior portion of the frontoventral row modified to anlagen V and VI (asterisks). **i:** Early stage. The middle portion of the frontoventral row (= cirrus IV/3; arrowhead) modifies to anlage IV of the proter and the rightmost anlagen elongate to primary primordia (asterisks). The postoral cirrus (arrow) is still unchanged. **j, k:** Middle stages with cirrus III/2 modified to anlage III of the proter and the postoral cirrus modified to anlage IV of the opisthe (arrow in j). Arrowhead denotes anlage IV of the proter originating from cirrus IV/3. BU – buccal cirrus, FC – right frontal cirrus, MA – macronuclear nodule, MI – micronucleus, OP – oral primordium, I, II, V, VI – fronto-ventral-transverse cirral anlagen in proter and opisthe, III/2 – cirrus behind right frontal cirrus, IV/3 – middle portion of frontoventral row. Scale bars 30 μm.

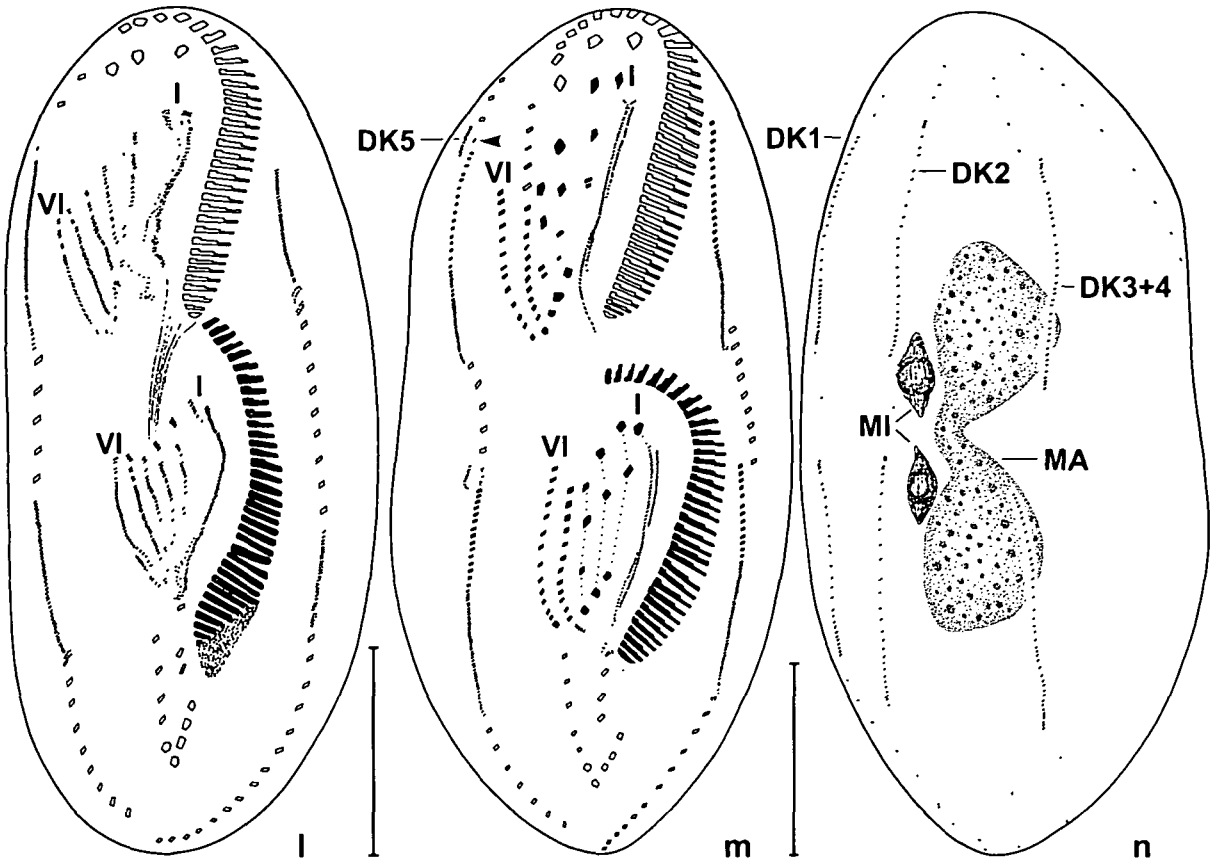


Fig. 160 l–n. *Gastrostyla (Spetastyla) mystacea mystacea*, infraciliature of a middle and a late divider after protargol impregnation. Parental structures shown by contour, newly formed shaded black. **l:** Middle stage showing six fronto-ventral-transverse cirral anlagen (I–VI) both in proter and opisthe. This specimen lacks parental frontoterminal cirri. **m, n:** Ventral and dorsal view of a late divider showing differentiation and migration of cirri as well as division of nuclear apparatus and dorsal kineties. Cirri which originate from the same anlage are connected by dotted lines (only shown in opisthe and for anlagen II–IV). The penultimate cirrus in anlage IV of the opisthe will form a scattered cirrus left of the posterior portion of the frontoventral cirral row (see left arrow in figure 160e). Arrowhead in figure 160m denotes new dorsal kinety 6 of the proter. Dorsal kineties 3 and 4 are not yet separated. DK1-5 – new dorsal kineties of proter, MA – macronucleus, MI – micronuclei, I, VI – fronto-ventral-transverse cirral anlagen. Scale bars 30 μm.

The marginal rows and the nuclear apparatus develop in the usual manner. The parental adoral zone of membranelles remains unchanged, while the paroral and endoral as well as the pharyngeal fibres are reorganized. Ontogenesis of the dorsal infraciliature occurs in the *Oxytricha* pattern (FOISSNER & ADAM 1983b, BERGER 1999), that is, kineties 1–3 originate by proliferation within the parental kineties, kinety 4 separates (fragmentates) from row 3 in late dividers, and kineties 5 and 6 originate dorsomarginally, that is, near or from the right marginal row (Fig. 160m–p).

Ontogenetic comparison: The ontogenesis of six *Gastrostyla* species has been investigated in protargol preparations, although in varying detail, namely of → *G. steinii* (HEMBERGER 1982, TUFFRAU 1969, 1970, WALKER & GRIM 1973; present study), *G. mystacea* (this study), → *G. bavariensis* (FOISSNER 1997b), *G. dorsicirrata* (BERGER 1999), *G. pulchra* (HU & SONG 2000), and *G. opisthoclada* (SHI et al. 1999). Unfortunately, illustration and description for *Gastrostyla pulchra* are so superficial that it is even impossible to

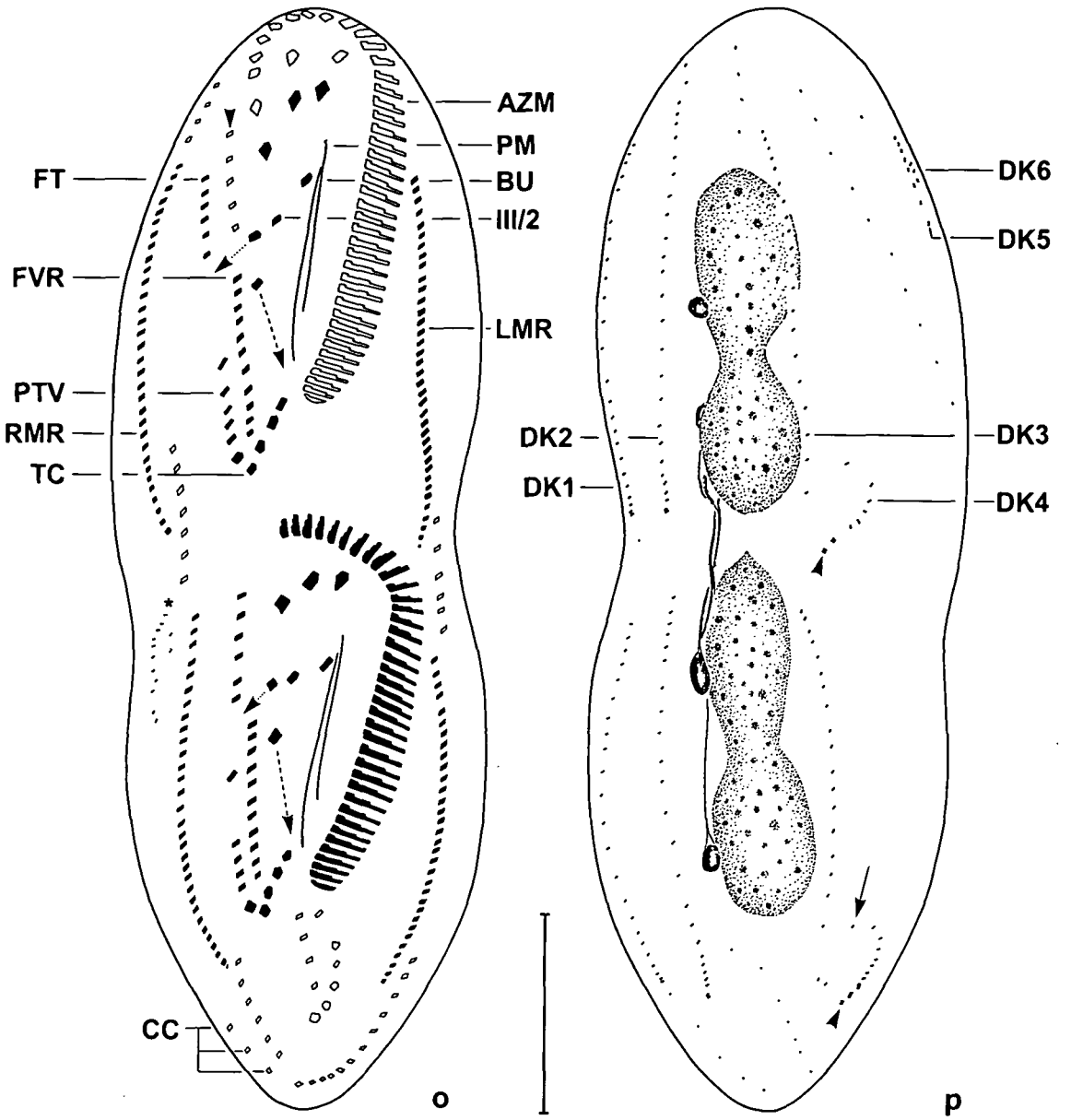


Fig. 160o, p. *Gastrostyla (Spetastyla) mystacea mystacea*, ventral and dorsal side and nuclear apparatus of a very late divider after protargol impregnation. Parental structures shown by contour, newly formed shaded black. **o:** Ventral side showing migration of cirri. Arrows on dotted lines mark migration of middle portion (= cirrus IV/3) of frontoventral row, arrows on broken lines show migration of postoral cirrus. Arrowhead denotes parental frontoterminal cirri. Asterisk marks opisthe's anlagen for dorsal kineties 5 and 6. **p:** Dorsal ciliary rows 1–4 originate by intrakinetal proliferation; vestiges of parental kineties are still present. Dorsal kinety 4 splits off (arrow) kinety 3 and is associated with two or three caudal cirri (arrowheads). Rows 5 and 6 are dorsomarginal kineties, which originate near or from the (new) right marginal row. AZM – parental adoral zone of membranelles, BU – buccal cirrus of proter, CC – parental caudal cirri associated with dorsal kinety 4, DK1-6 – dorsal kineties of proter, FT – anteriormost cirrus of anterior portion of frontoventral row of proter (= frontoterminal cirri), FVR – anteriormost cirrus of posterior portion of frontoventral row of proter, LMR – left marginal row of proter, PM – paroral membrane of proter, PTV – pretransverse ventral cirri ahead right transverse cirrus of proter, RMR – right marginal row of proter, TC – posteriormost transverse cirrus of proter, III/2 – cirrus behind proter's right frontal cirrus. Scale bar 30 μm.

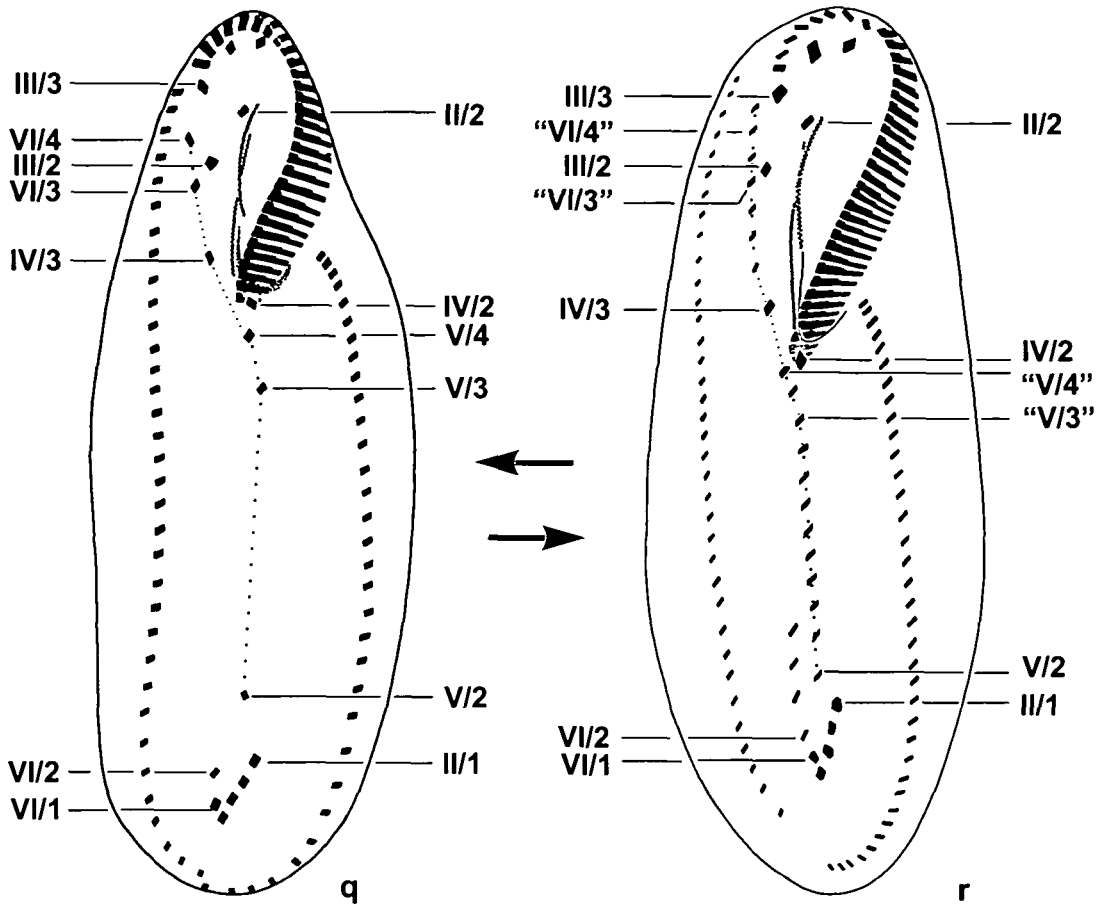


Fig. 160q, r. Homology of cirri in oxytrichids, *Gastrostyla*, and amphisiellids, exemplified in *Oxytricha granulifera* (q) and *Gastrostyla (Spetastyla) mystacea mystacea* (r). The cirri forming the frontoventral row are connected by dotted lines; those forming the anterior, respectively, posterior portion are connected by bold dotted lines. Designation of cirri is according to BERGER (1999). Briefly, Roman numerals I–VI designate fronto-ventral-transverse cirral anlagen; Arabic numerals designate cirri within individual anlagen beginning from rear end (thus, transverse cirri are numbered with 1). In *Gastrostyla mystacea mystacea* only those cirri of the frontoventral row are designated which are homologous with the cirri of *Oxytricha granulifera*. Cirri in quotation marks cannot be homologized unequivocally. The upper arrow between the two figures means "evolution of 18-cirri oxytrichids from a *Gastrostyla* by loss of cirri within the frontoventral row". The lower arrow means "evolution of a *Gastrostyla* from an 18-cirri oxytrichid by secondary increase of cirral number within the frontoventral row". Note that the postoral cirrus (IV/2) is at exactly the same location in both species and, for example, *Hemiamphisiella terricola*.

recognize the alignment of the frontoventral row; thus, this paper is not considered further. Here we focus on (i) the participation of postoral cirri in anlagen formation, (ii) the origin of the cirral anlagen I–VI, and (iii) the alignment of the frontoventral cirral row. The differences present in these features induced us to divide *Gastrostyla* in three subgenera.

(i) In *G. (Spetastyla) mystacea mystacea* (Fig. 160h–k) and *G. (Gastrostyla) steinii* (Fig. 31c–e in HEMBERGER 1982), only those cirri of the posterior portion of the frontoventral row which are close behind the oral vertex contribute to cirral anlagen. Even in late dividers some rear cirri of the parental frontoventral row are recognizable (Fig. 160m and 31e, f in HEMBERGER 1982). By contrast, in *G. (Kleinstyla) bavariensis* and *G. (Gastrostyla?) dorsicirrata* all cirri of the posterior portion of the frontoventral row transform to anlagen

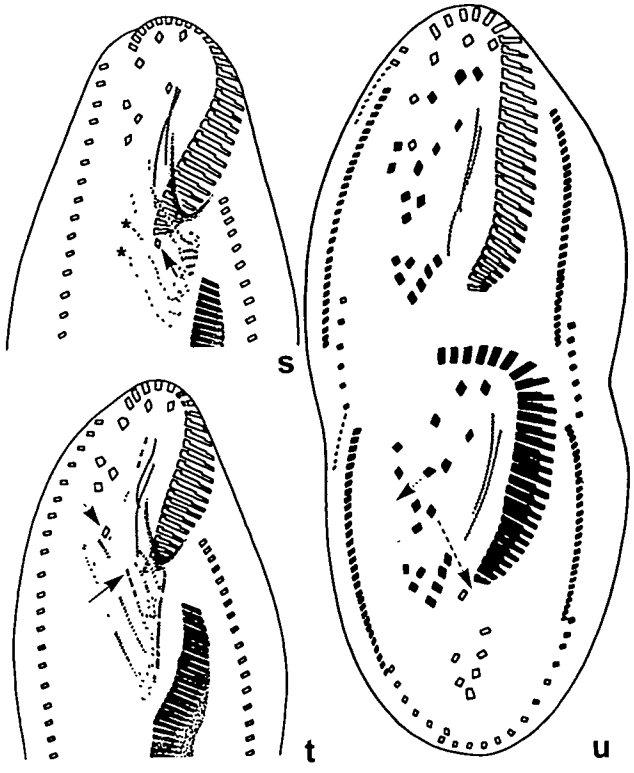


Fig. 160s–u. *Oxytricha granulifera*, dividing specimens after protargol impregnation (from FOISSNER & ADAM 1983b). The figures show that ontogenesis proceeds very similarly in *Oxytricha, Gastrostyla*, and amphisiellids (see text, corresponding figures 160h–i, m, o, and EIGNER & FOISSNER 1994). Asterisks in (s) mark anlagen V and VI for both the proter and the opisthe, that is, primary primordia; arrows on solid line denote postoral cirrus IV/2 unchanged (s) and modified to anlage IV (t) of the opisthe. Arrowhead in (t) marks cirrus IV/3, which forms the middle portion of the frontoventral row and modifies to anlage IV of the proter. Arrows in (u) mark rightward shift of cirrus IV/3 (dotted line) and migration of postoral cirrus (broken line) to oral vertex, showing that migration of cirri is the same in *Oxytricha, Gastrostyla*, and e.g., *Hemiamphisiella terricola*.

(Fig. 161b, c). Accordingly, only the anterior, ontogenetically active cirri of the posterior portion of the frontoventral row are retained in species with a short frontoventral row. This suggests that a long frontoventral row is the plesiomorphic state and a short row the apomorphic one. Unfortunately, secondary lengthening of the row cannot be excluded.

(ii) The origin of the fronto-ventral-transverse cirral anlagen I–VI of *G. (Spetastyla) mystacea mystacea* is summarized in table 143. *Gastrostyla (Kleinstyla) bavariensis* obviously has the same pattern (Table 143). Anlage IV of the proter originates, like in *G. (Spetastyla) mystacea mystacea*, from the middle portion of the frontoventral row; however, in *G. (Kleinstyla) bavariensis* this portion is composed of three (ontogenetically active) cirri, while of only cirrus IV/3 in *G. (Spetastyla) mystacea mystacea*. Unfortunately, most stages necessary for a proper comparison are lacking in *Gastrostyla opisthoclada*, which, however, is very likely a junior synonym of *Gastrostyla (Spetastyla) mystacea mystacea*. This is emphasized not only by the identical cirral pattern, but also by the frontoventral row, whose middle portion consists of a single cirrus only (SHI et al. 1999).

The formation of the cirral anlagen in *G. (Spetastyla) mystacea mystacea* differs from that in *Gastrostyla (Gastrostyla) steinii* in several respects (Fig. 160a–l; 391k–y, 392a–n, p–r, 393 l–y, 394a–j; HEMBERGER 1982, WALKER & GRIM 1973): first, anlage II of the opisthe of *G. (Spetastyla) mystacea mystacea* extends, like in some oxytrichids with 18 fronto-ventral-transverse cirri, above proter's oral vertex (Fig. 160h–j). By contrast, anlage II terminates behind the oral vertex in *G. (Gastrostyla) steinii* (Fig. 159c, h, j; 391u–y, 393o–r). Second, the anteriormost cirri of the posterior portion of the frontoventral row of *G. (Spetastyla) mystacea mystacea* are involved in anlagen formation for the opisthe. In *G. (Gastrostyla) steinii*, where the posterior portion of the frontoventral row extends above the oral vertex, the middle cirri are ontogenetically active. Third, anlagen V and VI of proter and opisthe have a common origin (primary primordia) in *G. (Spetastyla) mystacea mystacea* (Fig. 160h–j), while all cirral anlagen develop independently in *G. (Gastrostyla) steinii* (Fig. 159h, j).

(iii) *Gastrostyla* has a distinct frontoventral (amphisiellid median cirral) row extending from near the distal end of the adoral zone of membranelles to near mid-body or near the transverse cirri. In all species investigated ontogenetically, the row assembles from three portions originating from the three rightmost anlagen, IV, V and VI. The **anterior portion** is formed by the anteriorly migrating cirri of anlage VI. The **middle portion** of the frontoventral row originates from anlage IV. Due to a different number of cirri assembling this part of the frontoventral cirral row, two groups can be distinguished: group 1 with invariably only one cirrus (*Gastrostyla steinii* and *G. mystacea*) and group 2 with about three cirri (*G. bavariensis* and *G. dorsicirrata*). *Gastrostyla sterkii*, a synonym of *G. pulchra*, also belongs to group 2, according to the detailed observations by WALLENGREN (1900). We use this difference, in combination with other features, to distinguish two subgenera, *Gastrostyla (Spetastyla)* and *Gastrostyla (Kleinstyla)*. The middle cirrus is often not aligned with the anterior and posterior portion in *G. (Gastrostyla) steinii* (Fig. 159a; 391a, 393a), that is, dislocated up to 3 µm leftwards. However, the alignment is perfect in a considerable number of specimens (Fig. 159b; 391b, 393e, l) so that this feature cannot be used to distinguish *Gastrostyla (Gastrostyla)* from the other two subgenera. The **posterior portion** of the frontoventral row is generated by anlage V. This portion begins above the level of the oral vertex in *G. (Gastrostyla) steinii* (Fig. 159a, b), while it commences postorally in *G. (Spetastyla) mystacea*, *G. (Gastrostyla ?) dorsicirrata*, and *G. (Kleinstyla) bavariensis* (Fig. 160e, 161a, 162a). However, in both cases only postoral cirri contribute to the opisthe's anlagen formation, that is, some ontogenetically inactive cirri occur at the anterior end of the posterior portion of the frontoventral row of *G. (Gastrostyla) steinii*.

Systematic position of *Gastrostyla*: STEIN (1859) classified this species in *Oxytricha*. STERKI (1878) recognized the relationship to *Gastrostyla* ENGELMANN, 1862, but his proposal was abandoned by all later revisers (BORROR 1972a, KAHL 1932, KENT 1882), who put the species into the urostylid genus *Holosticha* because the frontoventral row resembles a midventral cirral pattern in STEIN's illustrations (Fig. 395a, b).

Recently, *Gastrostyla* was classified in the amphisiellids by EIGNER & FOISSNER (1994), in the parakahliellids by EIGNER (1997, 1999), and in the oxytrichids by TUFFRAU & FLEURY (1994) and BERGER (1999). Here, we shall compare *Gastrostyla* with typical representatives of the oxytrichids, namely *Oxytricha granulifera* and *Onychodromopsis flexilis*, and two representatives of the amphisiellids, namely *Amphisiella marioni*, type of the group, and *Lamtostyla australis*. All were characterized ontogenetically. Thus, it should be possible to find homologies and synapomorphies for a proper classification of *Gastrostyla*. The parakahliellids of EIGNER (1997, 1999) are, in our opinion, a polyphyletic group making a serious comparison impossible. Our comparison is subdivided in (i) oral primordium formation, (ii) origin of the cirral anlagen, (iii) participation of the anterior portion of the frontoventral cirral row in anlagen formation, (iv) alignment of the frontoventral cirral row, (v) ontogenetic activity and migration of the postoral cirrus, and (vi) ontogenesis of the dorsal ciliature.

(i) In *Gastrostyla*, the formation of the oral primordium commences, as in many oxytrichids, near the left transverse cirrus (for example, Fig. 160g; Fig. 202j in BERGER 1999). However, this pattern also occurs in the amphisiellid *Lamtostyla* (PETZ & FOISSNER 1996, VOSS 1992). The oral primordium of several other amphisiellids originates along the amphisiellid median cirral row (WICKLOW 1982, EIGNER & FOISSNER 1994). However, a similar pattern can be found in several oxytrichids, where the primordium originates near the postoral cirri or in the area between the postoral and transverse cirri (BERGER 1999). Accordingly, this feature

hardly provides insight into the systematic position of *Gastrostyla*.

(ii) *Gastrostyla mystacea mystacea* forms the fronto-ventral-transverse cirral anlagen from several distinct parts of the parental ciliature and the oral primordium. Surprisingly, the origin of the anlagen is largely identical to those of typical oxytrichids (Fig. 160q–u; Table 143) and amphisiellids. This indicates homology of the structures involved. In *Amphisiella marioni*, the exact origin of the anlagen is not known (WICKLOW 1982). Thus, we used *Hemiamphisiella terricola*, as described by EIGNER and FOISSNER (1994), as an example (Table 143). In *Gastrostyla mystacea* only two anlagen and in *G. steinii* none of the anlagen are formed via primary primordia. The same pattern occurs in amphisiellids (EIGNER & FOISSNER 1994). Thus, the origin of the cirral anlagen hardly provides insight into the systematic position of *Gastrostyla*, but suggests that both, oxytrichids and amphisiellids, are closely related.

(iii) In oxytrichids with 18 or less fronto-ventral-transverse cirri, the frontoterminal cirri (cirrus VI/3 and VI/4 in figure 160q) are never involved in cirral anlagen formation (for review, see BERGER 1999). The same applies to G. *steinii*, type of the genus, according to HEMBERGER (1985) and our investigations (Fig. 159a–j; 392a, b, 394v, x). The anterior portion of its frontoventral row is formed by 3–6, on average four cirri (median, n = 40). In most middle dividers, where anlagen formation is complete, four parental cirri (median, n = 40) are still recognizable, strongly suggesting that this portion of the frontoventral row is ontogenetically inactive. In *G. mystacea mystacea* the situation is less clear. In morphostatic specimens, the anterior portion of the frontoventral row is composed of seven cirri, while middle dividers have only five parental cirri in this position (Fig. 160j, k, m, o), indicating that, on average, two cirri are involved in anlagen formation or resorbed (Fig. 160g–j). Certainly, such details are difficult to study. However, we never found a *Gastrostyla* divider unequivocally showing cirral anlagen formation by cirri of the anterior portion of the frontoventral row, while this is common in several amphisiellids, such as *Paramphisiella caudata* and *Hemiamphisiella terricola* (EIGNER & FOISSNER 1994). Others, however, do not include these cirri in any anlagen, for instance, *Amphisiellides illuvialis*. Thus, this feature also does not provide reliable insight into the systematic position of *Gastrostyla*.

(iv) As described above and discussed in paragraph (iii) of the ontogenetic comparison, *Gastrostyla* forms a frontoventral row composed of three portions (Fig. 159k, 160o, r; 392f, 394h, i, 395p). This highly characteristic pattern is the key feature of the family Amphisiellidae as defined by EIGNER & FOISSNER (1994), strongly suggesting homology of the processes. In fact, this was the reason why EIGNER & FOISSNER (1994) transferred *Gastrostyla* to the Amphisiellidae. However, the three portions of the gastrostylid frontoventral row can also be plausibly correlated with the oxytrichid cirral pattern, although this is less obvious due to the strongly reduced number of cirri (Fig. 160q, r). In fact, this was already suggested by WALLENGREN (1900). Again, this feature does not provide insight into the systematic position of *Gastrostyla*.

(v) *Gastrostyla* has a rather prominent postoral cirrus originating from anlage IV and migrating towards the oral vertex in late dividers (Fig. 159k, 160e, o). In early dividers, this cirrus forms anlage IV of the opisthe (Fig. 160i, j). *Oxytricha granulifera* has a cirrus in the same position (Fig. 160q), and this cirrus also originates from anlage IV and migrates towards the oral vertex in late dividers (Fig. 160u). In early dividers, it also forms anlage IV of the opisthe (Fig. 160s, t; Table 143). At first glance, the agreement in position, migration, and ontogenetic potential indicates homology. However, the amphisiellids *Hemiamphisiella* and *Pseudouroleptus* also have a cirrus in the same position, and this cirrus also originates from

anlage IV and migrates towards the oral vertex in late dividers. In early dividers it is incorporated in the oral primordium, which forms cirral anlagen I–IV. Obviously, feature (v) hardly provides insight into the systematic position of *Gastrostyla*, but strongly suggests that both have a common ancestor, as emphasized by the dorsal ontogenesis discussed in the next paragraph.

Table 143. Origin of the fronto-ventral-transverse cirral anlagen and number of cirri produced per anlage in *Gastrostyla mystacea*, two oxytrichids with 18 fronto-ventral-transverse cirri, and the amphisiellid *Hemiamphisiella*.

Species	anlage [a] I	II	III	IV	V [g]	VI [g]
P r o t e r						
Gastrostyla (Spetastyla) mystacea mystacea and *Gastrostyla (Kleinstyla) bavariensis*	UM	II/2	III/2	IV/3	anterior cirri of posterior portion of frontoventral row	anterior cirri of posterior portion of frontoventral row
Oxytricha granulifera [b]	UM	II/2 and part of IIo	III/2	IV/3	V/4	V/3
Onychodromopsis flexilis [b]	UM	II/2	III/2	IV/3	V/4	V/3
Hemiamphisiella terricola [c]	UM	II/2	III/2	de novo	ACR [d]	ACR [d]
O p i s t h e						
Gastrostyla (Spetastyla) mystacea mystacea and *Gastrostyla (Kleinstyla) bavariensis*	OP	OP	OP	IV/2	anterior cirri of posterior portion of frontoventral row	anterior cirri of posterior portion of frontoventral row
Oxytricha granulifera [b]	OP	OP	OP	IV/2	V/4	V/3
Onychodromopsis flexilis [b]	OP	OP	OP	IV/2	V/4	V/3
Hemiamphisiella terricola [c]	OP	OP	OP	OP	ACR [d]	ACR [d]
Number of cirri produced per anlage						
Gastrostyla mystacea mystacea	1	3	3	3 [e]	13 (10–14) [f]	12 (8–15) [f]
Gastrostyla mystacea minima	1	3	3	3	8 (7–9) [f]	8 (7–10) [f]
Oxytricha granulifera [b]	1	3	3	3	4	4
Onychodromopsis flexilis [b]	1	3	3	3	4	4
Hemiamphisiella terricola [c]	1	2	2	4	> 10	> 10

[a] Designation of cirri according to the numbering system of WALLENGREN (1900) explained in BERGER (1999). OP – oral primordium, UM – undulating membranes (= paroral and endoral), IIo – anlage II of opisthe.

[b] From BERGER & FOISSNER (1997).

[c] From EIGNER & FOISSNER (1994).

[d] Anterior cirri of posterior portion, middle portion, and posterior cirri of anterior portion of amphisiellid median cirral row.

[e] Four or five when one or two scattered cirri present left of posterior portion of frontoventral row.

[f] Median values from table 142. Corresponding transverse cirri included. Minimum and maximum values in parentheses.

[g] Streaks are formed via primary primordia, a highly characteristic feature.

(vi) Dorsal ontogenesis is considered an important feature for reconstructing phylogenetic relationships in hypotrichs because the strongly reduced ciliature is likely subjected to reduced environmental pressure (MARTIN 1982, FOISSNER & ADAM 1983b, BERGER & FOISSNER 1997, BERGER 1999). In oxytrichids, the occurrence of dorsal kinety fragmentation is a highly characteristic feature (FOISSNER & ADAM 1983b, BERGER 1999). And exactly this special pattern is found in *Gastrostyla* (Fig. 160p; 392p, r, 393w, 394b–d). Unfortunately, many oxytrichid genera do not show dorsal kinety fragmentation and a "typical" amphisiellid, *Pseudouroleptus caudatus* HEMBERGER, 1985, has fragmentation like a "typical" *Oxytricha* (HEMBERGER 1982).While the first problem can be reasonably explained by assuming a secondary loss, the case of *Pseudouroleptus* remains enigmatic. BERGER (1999) "solved" the problem by classifying *Pseudouroleptus caudatus* with the oxytrichids, without, however, convincing evidence.

None of the features (i)–(vi) discussed in the previous paragraphs unequivocally assigns *Gastrostyla* to the amphisiellids or oxytrichids, but all can be homologized within these three groups, strongly suggesting a common ancestor. BERGER (1999) discusses two positions of *Gastrostyla* within the oxytrichids: (i) *Gastrostyla* is the sister group of the 18-cirrri oxytrichids, that is, the 18-cirral pattern evolved from the *Gastrostyla*-pattern by a reduction of the (ontogenetically inactive) cirri of the frontoventral row (Fig. 160r → 160q). This "primitive" position is widely assumed, for example, by KAHL (1932), MARTIN (1982), and WIRNSBERGER et al. (1986); (ii) *Gastrostyla* evolved from flexible 18-cirri oxytrichids (for example, *Oxytricha*) by an (secondary) increase of the number of cirri originating in anlagen IV to VI (Fig. 160q → 160r). Hopefully, gene sequence data will provide further insight into the proper relationships of oxytrichids, amphisiellids and *Gastrostyla*, which is certainly a key group within the hypotrichs.

Gastrostyla (Spetastyla) mystacea minima HEMBERGER, 1985 **nov. stat.** (Fig. 161a–g; Table 142)

1985 *Gastrostyla minima* HEMBERGER, Arch. Protistenk., 130: 406 (Abb. 12).

1991 *Gastrostyla mystacea* (STEIN, 1859) STERKI, 1878 — FOISSNER, BLATTERER, BERGER, KOHMANN, Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft, 1/91: 270 (pro parte, figures 3, 4 on p. 271).

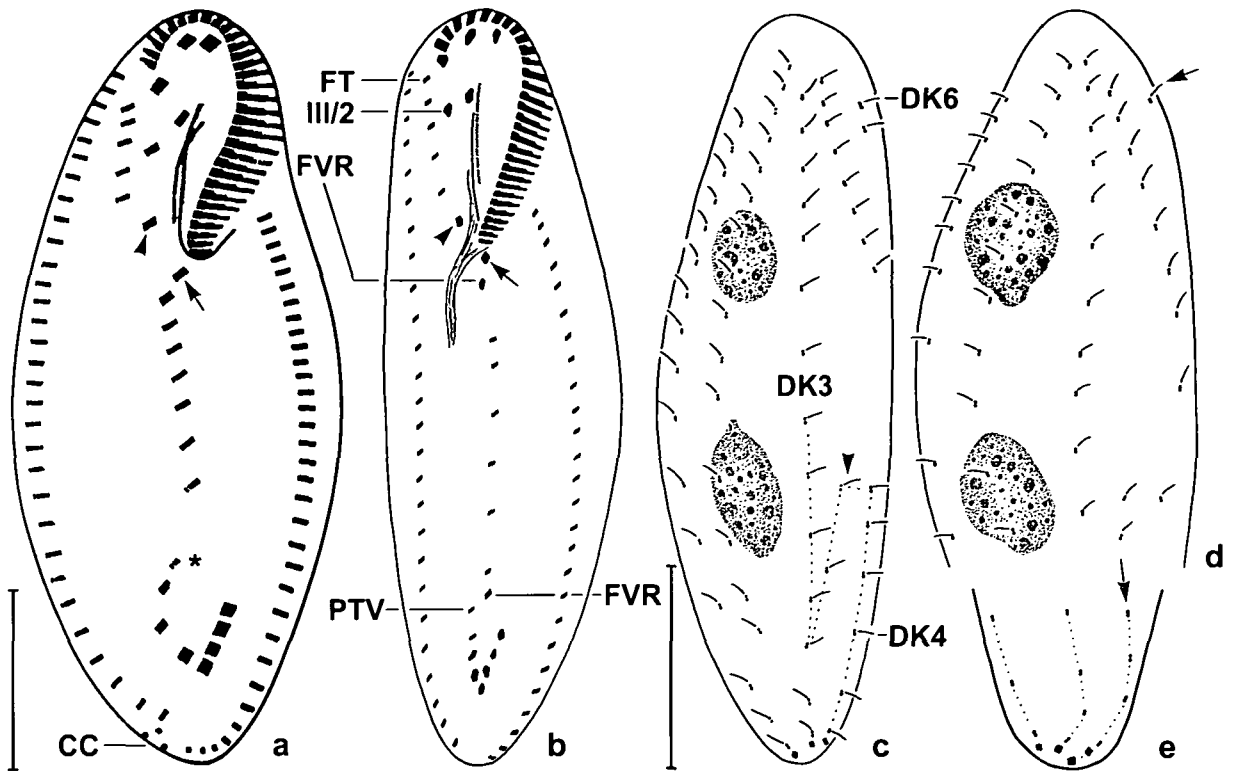
1997 *Gastrostyla minima* HEMBERGER, 1985 — FOISSNER, Limnologica, 27: 225 (misidentification; see *Gastrostyla (Kleinstyla) bavariensis*).

1999 *Gastrostyla minima* HEMBERGER, 1985 – BERGER, Monographiae biol., 78: 810 (pro parte, Fig. 203f).

Improved diagnosis: Size about 130 × 35 µm in vivo. On average 30 adoral membranelles and 13 cirri in frontoventral (amphisiellid median cirral) row. Posterior portion of frontoventral row and pretransverse cirral row not overlapping.

Remarks: For rank change, see remarks under *Gastrostyla (Spetastyla) mystacea*.

Brief description of Namibian site (73) population and comparison with original description: The in vivo aspect is indistinguishable from that of → *G.*



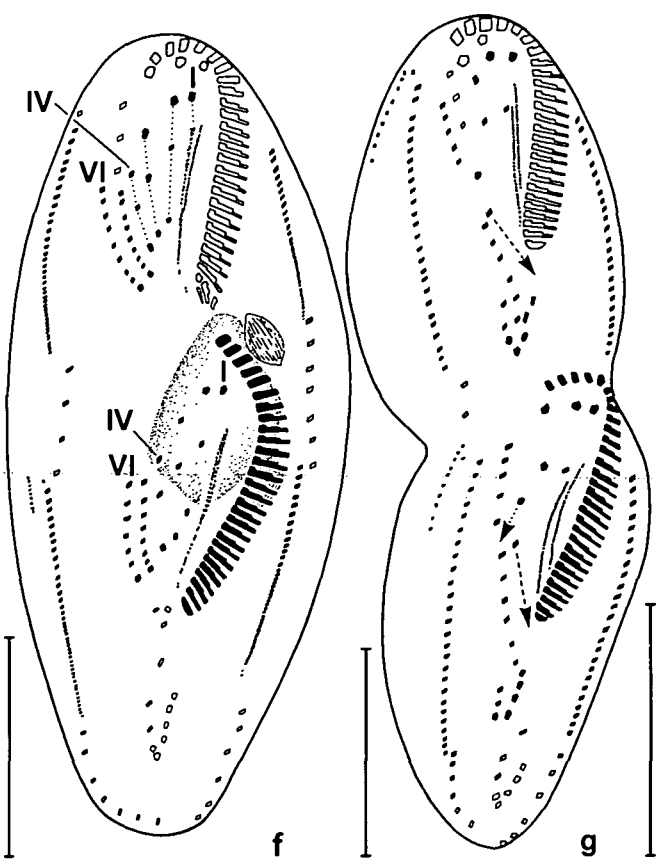


Fig. 161a–g. *Gastrostyla (Spetastyla) mystacea minima*, infraciliature of morphostatic (a–e) and dividing (f, g) Peruvian (161a; from HEMBERGER 1985) and Namibian site (73; 161b–g) specimens after protargol impregnation. **a, b:** Ventral views showing that the FVR and the PTV do not overlap. Arrows mark postoral cirrus, and arrowheads denote middle portion (= cirrus IV/3) of frontoventral cirral row. The cirrus marked with an asterisk in (a) is likely the posteriormost, slightly rightwardly dislocated cirrus of the posterior portion of the frontoventral row. **c:** Dorsal side and nuclear apparatus of specimen shown in figure (b). Dorsal kinety 4 is often indistinctly separated from kinety 3 (arrowhead). **d:** Dorsal side of a specimen with kinety 6 composed of only one bristle (arrow). **e:** Dorsal side of a specimen with two caudal cirri associated with kinety 4 (arrow). **f, g:** Ventral views of a middle and a late divider showing that the middle portion of the frontoventral cirral row is composed of cirrus IV/3 only (arrow on dotted line in figure 161g). Arrow on broken line marks migrating postoral cirrus. Cirri originating from same anlage connected by dotted lines. Parental structures shown by contour, newly formed shaded black. CC – caudal cirri, DK3, 4, 6 – dorsal kineties, FT – anteriormost cirrus of anterior portion of frontoventral row (= frontoterminal cirri), FVR – anteriormost and posteriormost cirrus of posterior portion of frontoventral row, PTV – pretransverse cirri ahead right transverse cirrus, III/2 – cirrus behind right frontal cirrus, I-VI – frontoventral-transverse cirral anlagen. Scale bars 30 µm.

mystacea mystacea, to which the reader thus is referred. The cirral pattern is also very similar in the two subspecies, except for the morphometrics marked in table 142. Separation of dorsal kinety 4 from kinety 3 is often incomplete (Fig. 161c), as in *Gastrostyla dorsicirrata* (BERGER 1999). The number of caudal cirri associated with dorsal kinety 4 is frequently difficult to ascertain because they are very close to the marginal cirri: the majority has one caudal cirrus (Fig. 161c), the rest have two (Fig. 161e). The formation of the amphisiellid median (frontoventral) cirral row proceeds as in *G. mystacea mystacea*, that is, the middle portion of the row is composed of cirrus IV/3 only (Fig. 161f, g).

The Namibian specimens agree with the original description of *G. minima* in most main features, namely, body length (130 µm respectively 120–145 µm), nuclear apparatus, length of adoral zone, number of adoral membranelles (28–32 respectively 32–35), arrangement of undulating membranes, arrangement and number (24–29 respectively 27 according to Fig. 161a) of fronto-ventral-transverse cirri (cp. figures 161a, b), number of right (16–32 respectively 28–33) and left (24–30 respectively 28–31) marginal cirri, habitat (soil respectively soil and freshwater), and Gondwanan distribution (Africa respectively South America). There are also, as is usual, some differences: (i) HEMBERGER's specimens are wider than ours (45–60 µm respectively 27–42 µm) and seemingly lack cortical granules. HEMBERGER used WILBERT's protargol method, where specimens sometimes become rather inflated and cortical granules rarely impregnate. In the specimens from Namibian site (73) the cortical granules impregnate only faintly, while they stain heavily in the site (49) specimens. HEMBERGER (1985), who obviously did not study live specimens in detail, likely simply overlooked the cortical granules. (ii) HEMBERGER invariably counted three caudal cirri, while about one third of our specimens has two cirri associated with dorsal kinety 4 and thus has four caudal cirri. HEMBERGER correctly stated that the caudal cirri are inconspicuous and the last cirri of the left marginal row are reduced in size. Thus, it cannot be excluded that he overlooked kinety 4 sometimes having two cirri. (iii) HEMBERGER counted "3 plus 2 × ½" dorsal kineties, indicating that his population lacks kinety 6, which is usually composed of only one or two bristles only in our population. However, we also found specimens which lack this short row (Table 142). (iv) The cirral bases in HEMBERGER's drawing (Fig. 161a) are distinctly larger than those in our figures, likely because he illustrated the individual basal bodies, which makes cirral bases larger due to spatial constraints. The slightly different number of caudal cirri and the lack of the short dorsal kinety 6 could also be interpreted as early speciation events of these geographically widely separated populations (Africa vs. South America). Generally, such details are largely unknown and should be investigated in combination with gene sequence and/or enzymatic data.

Occurrence and ecology: HEMBERGER (1985) discovered *Gastrostyla mystacea minima* in Peruvian freshwater; later, he observed high abundances in soil from this region. We found large numbers of *G. (Spetastyla) mystacea minima* at Namibian site (73), while it was sparse at site (49). The data indicate that the subspecies *minima* may be restricted to Gondwanaland (South America and Africa), whereas the subspecies *mystacea* possibly occurs in Eurasia only, at least according to the records substantiated by illustrations (STEIN 1859, SHI et al. 1999, present paper).

Comparison with related species: See *Gastrostyla bavariensis*.

Gastrostyla (Kleinstyla) bavariensis nov. spec. (Fig. 162a–d; 396a–c)

1997 *Gastrostyla minima* HEMBERGER, 1985 — FOISSNER, Limnologica, 27: 225 (misidentification).
1999 *Gastrostyla minima* HEMBERGER, 1985 — BERGER, Monographiae biol., 78: 810 (pro parte, Fig. 203e, g–q).

Diagnosis: Size about 70–120 × 25–40 µm in vivo; oblong. 2 macronuclear nodules. Cortical granules in closely spaced rows, in vivo hardly recognizable but deeply stained with methyl green-pyronin and silver nitrate. On average 32 adoral membranelles, each 32 right and left marginal cirri, 5 transverse cirri, and 12 frontoventral cirri forming a row terminating near mid-body. 6 dorsal kineties with one caudal cirrus each at kineties 1, 2, 4.

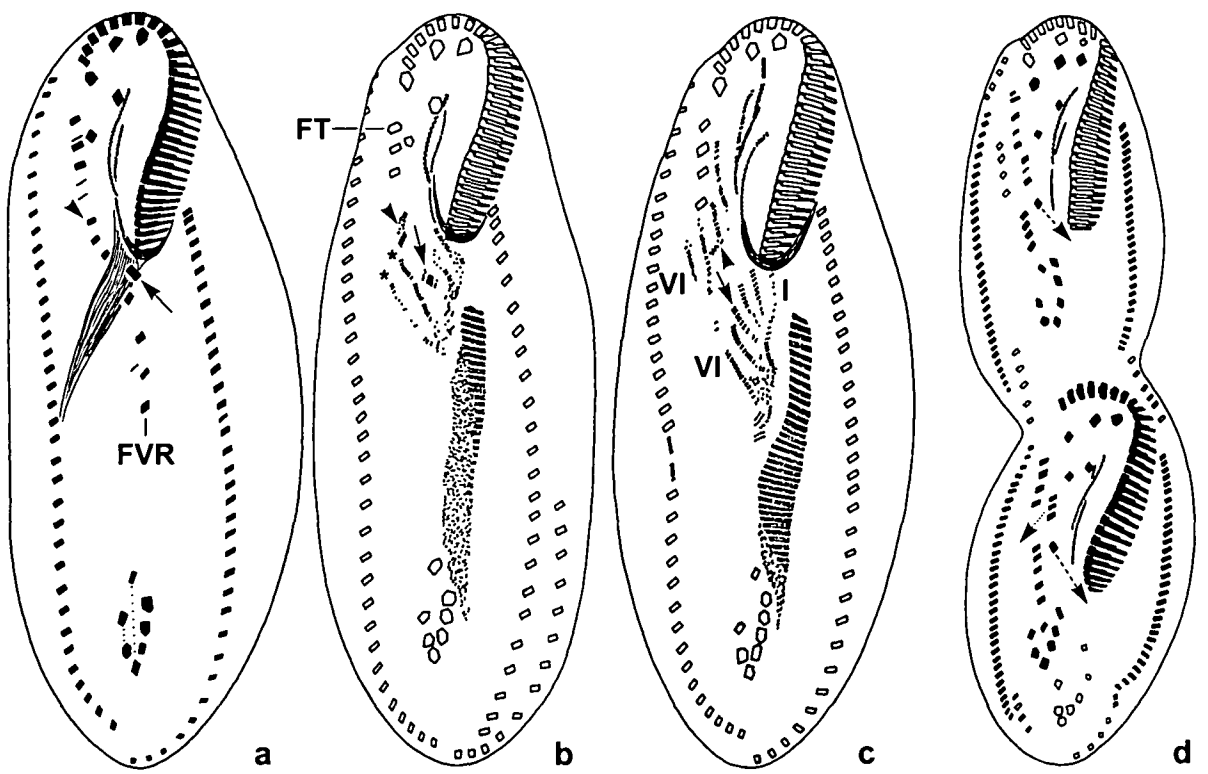


Fig. 162a–d. *Gastrostyla (Kleinstyla) bavariensis* (about 90 µm), ventral views of morphostatic (a) and dividing (b–d) specimens (from FOISSNER 1997b). This species is very similar to *G. (Spetastyla) mystacea minima* (Fig. 161a–g), but differs, inter alia, by the shorter frontoventral (amphisiellid median) cirral row (FVR) and the typical oxytrichid pretransverse/transverse cirral pattern composed of five transverse cirri and each one pretransverse cirrus ahead of the two rightmost transverse cirri (dotted lines). Figures (162b, c) show that anlagen formation is very similar to that of *G. (Spetastyla) mystacea mystacea* (Fig. 160i, j). Arrows on solid line mark postoral cirrus IV/2. The arrowheads denote the middle portion of the frontoventral row; in *G. (Kleinstyla) bavariensis* (Fig. 162a) and *G. (Gastrostyla?) dorsicirrata* (Fig. 162e, f), this portion is composed of three cirri, which are transformed to anlage IV of the proter (Fig. 162b, c). Asterisks in (b) mark anterior end of anlagen (primary primordia) V and VI for both the proter and the opisthe. Arrow on dotted lines in (d) denotes migration of middle portion of frontoventral row; arrows on broken lines denote migration of cirrus IV/2 to the oral vertex, to become the postoral cirrus. FT – anteriormost cirrus of anterior portion of frontoventral row, FVR – posteriormost cirrus of posterior portion of frontoventral row (the corresponding left pretransverse cirrus is not included in the number of cirri forming the frontoventral row in that species), I, VI – fronto-ventral-transverse cirral anlagen.

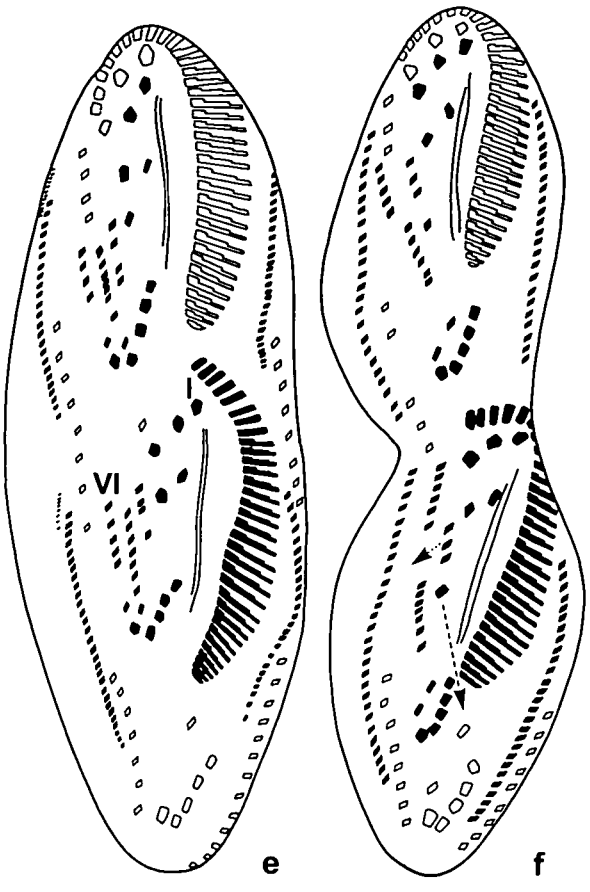


Fig. 162e, f. *Gastrostyla* (*Gastrostyla*?) *dorsicirrata*, infraciliature of ventral side of dividing specimens after protargol impregnation (from BERGER 1999). In this species, the middle portion of the frontoventral row is composed of three cirri (arrow on dotted line), as in *G. (Kleinstyla) bavariensis* (Fig. 162d); thus, it likely belongs to the subgenus *Kleinstyla*. Arrow on broken line denotes migration of opisthe's postoral cirrus to oral vertex. I, VI – fronto-ventral-transverse cirral anlagen. Body length 135 µm.

Type location: Benthos of the Röslau, a clean, periodically acidified brook in the Fichtelgebirge, Bavaria, about 2.5 km downstream the spring, 50°N 12°E.

Etymology: Named after the country discovered.

Description, discussion, and comparison with related species: Description, see FOISSNER (1997b), who identified, with some reservation, this population with *Gastrostyla minima* HEMBERGER [now → *G. (Spetastyla) mystacea minima*; Fig. 161a]. Our data show that HEMBERGER's species produces only one cirrus for the middle portion of the frontoventral (amphisiellid median cirral) row, while three or more cirri are generated in *G. bavariensis* (Fig. 162d) and *G. dorsicirrata* (Fig. 162f). For further details, see ontogenetic comparison under *G. (Spetastyla) mystacea mystacea*.

Morphologically, *Gastrostyla (Kleinstyla) bavariensis* and *G. (Spetastyla) mystacea minima* are distinguished by three rather sophisticated but distinct features, namely, the number of cirri in the posterior portion of the frontoventral row (5–6 vs. 6–8, usually 7), the length of the frontoventral row (ending near mid-body vs. near transverse cirri), and the number of pretransverse cirri (invariably one ahead of each of the two rightmost transverse cirri vs. 2–3 ahead the rightmost transverse cirrus, forming short but distinct row). These three features are recognizable also in a Venezuelan population studied recently (Fig. 396a–c). Furthermore, the cortical granules of *G. (Kleinstyla) bavariensis* are much less distinct in vivo than those of *G. (Spetastyla) mystacea mystacea* and *G. mystacea minima*. However, the most important feature is, of course, the subgeneric character, namely, the three cirri comprising the middle portion of the frontoventral row.

Occurrence and ecology: Possibly confined to freshwater. For some faunistic and ecological data, see FOISSNER (1997b). Recently found in a soil sample from Venezuela (Fig. 396a–c).

Oxytricha longa GELEI & SZABADOS, 1950 (Fig. 163a–d; 381p, 390g; Tables 144, 145)

The Namibian population of *Oxytricha longa* is highly similar to the original description (GELEI & SZABADOS 1950; Fig. 163f) and the redescription by GANNER et al. (1987; Fig. 163e), who originally identified their populations as *Urosomoida agiliformis* FOISSNER, 1982. BERGER & FOISSNER (1997) and BERGER (1999), however, classified populations 3 and 4 of GANNER et al. (1987) in *O. longa* because (i) primordia V and VI of the proter originate, as in *Oxytricha granulifera* FOISSNER & ADAM, 1983b (type of *Oxytricha*), from postoral cirri V/3 and V/4 (vs. de novo in *U. agiliformis*) and (ii) they have four transverse and two pretransverse cirri (vs. two, respectively, one in *U. agiliformis*). Now we found further morphometric differences between these species (Table 144). The smaller relative length of the nuclear figure in *Oxytricha longa* is due to the small distance between the macronuclear nodules. This feature and the higher number of transverse plus pretransverse cirri (usually 6 vs. usually 3) can be used to distinguish *Oxytricha longa* and *Urosomoida agiliformis* with high accuracy in vivo and in protargol preparations. Accordingly, the population recently described by OLMO & PÉREZ-UZ (2000) from a wastewater treatment plant in Spain belongs not to *U. agiliformis*, but to *O. longa*.

Table 144. Four morphometric differences between *Oxytricha longa* and *Urosomoida agiliformis*.

Characteristics [a]	*longa* 1	*longa* 2	*longa* 3	*agiliformis* 1	*agiliformis* 2
Length of adoral zone: body length, ratio	36% [b]	33% [g]	32% [c]	27% [g]	30% [g]
Anterior body end to rear postoral ventral cirrus:body length, ratio	43% [b]	48–49% [d]	47% [c]	35% [e]	37% [f]
Posterior body end to anterior pretransverse cirrus:body length, ratio	17% [b]	13% [d]	11% [c]	5% [e]	4% [f]
Length of nuclear figure:body length, ratio	39% [b]	38% [d]	39% [c]	49% [e]	53% [f]

[a] Data from protargol-impregnated specimens, unless otherwise indicated. *longa* 1 – type population from GELEI & SZABADOS (1950; mercuric chloride fixation), *longa* 2 – population 3 from GANNER et al. (1987); *longa* 3 – present population from Namibia; *agiliformis* 1 – type population from FOISSNER (1982); *agiliformis* 2 – from FOISSNER & ADAM (1983a).

[b] Single value from figure 163f.

[c] From table 145.

[d] Single value from figures 2, 3 and/or 5 in GANNER et al. (1987).

[e] Single value from figures 35b and 35c in FOISSNER (1982).

[f] Single value from figures 1 and 2 in FOISSNER & ADAM (1983a).

[g] From table I in GANNER et al. (1987).

Oxytricha similis ENGELMANN, 1862, which is also very similar to *O. longa* in size and shape, has five transverse cirri (Fig. 163i). However, this has to be confirmed by detailed data from protargol-impregnated specimens (BERGER 1999). *Oxytricha granulifera quadricirrata* BLATTERER & FOISSNER, 1988 has, like *O. longa*, only four transverse cirri (Fig. 163h); however, it is easily distinguished from *O. longa* by the cortical granules and the rear frontoventral cirrus (cirrus IV/3), which is distinctly set off from the other cirri (close to the other cirri in *O. longa*).

Taking the available (GELEI & SZABADOS 1950; GANNER et al. 1987, population 3; OLMO & PÉREZ-UZ 2000) and present data, *Oxytricha longa* can be characterized as follows: Size 60–100 × 20–40 µm in vivo (47–77 × 13–30 µm in protargol slides); outline elliptical to elongate elliptical; 2 almost abutting macronuclear nodules, 2 micronuclei; 18–25 adoral membranelles, 10–23 (M = 15–22) right marginal cirri, 14–23 (M = 16–20) left marginal cirri, 3 frontal cirri, 4 frontoventral cirri, 1 buccal cirrus, 3 postoral cirri, 2 pretransverse cirri, 4 transverse cirri, 2 caudal cirri, 4 dorsal kineties. The Namibian population stands out by its numerous cytoplasmic crystals (Fig. 163a; 381p) and the highly saline habitat. Thus, and to document the similarity of widely distant ciliate populations, we provide a detailed description.

Description of population from Namibian site (69): Size 70–90 × 20–35 µm in vivo, length:width ratio 2.8–4.9:1 in vivo, 2.3–3.4:1 after protargol impregnation. Elliptical to elongate elliptical, that is, both ends rounded (Fig. 163a, b); flexible but acontractile. Macronuclear nodules in body centre left of midline, ellipsoidal (2–3:1), on average near 2:1 and very close together. Two micronuclei about 3.5 µm across in vivo, one attached to each macronuclear nodule in variable positions. No cortical granules. Cytoplasm colourless, usually with many crystals of ordinary shape and size (Fig. 163a; 381p); crystals less abundant in specimens from site (58). Feeds on bacteria and flagellates digested in vacuoles about 7 µm across. Moderately fast gliding movement.

Cirral pattern rather constant, number of cirri of usual variability (Fig. 163c, d; 390g; Table 145). Transverse and caudal cirri 17–20 µm long and thus prominent, other cirri about 10 µm long in vivo. Right marginal row commences near level of last frontoventral cirrus and is slightly (5 µm) shortened posteriorly, left marginal row often terminates at rear, near midline. Frontal and transverse cirri slightly larger than other cirri. Buccal cirrus right of anterior end of paroral and ahead of endoral. Frontoventral cirri in ordinary, hook-shaped pattern. Postoral cirri also in ordinary pattern, occasionally the rear or the rear and the middle cirrus are lacking (specimens with only one postoral cirrus occur very rarely and were excluded from morphometry). Both pretransverse ventral cirri close to J-shaped transverse cirri.

Dorsal bristles about 4 µm long in vivo (6 µm in specimens from site 58), arranged in four rows: rows 1 and 2 distinctly, respectively, slightly shortened anteriorly and with a caudal cirrus each; row 3 slightly shortened at both ends; row 4, which is a dorsomarginal kinety, usually composed of only six dikinetids and thus terminating distinctly above mid-body (Fig. 163d).

Adoral zone occupies 28–36%, on average 32% of body length, of usual shape and structure (Fig. 163c; Table 145); composed of an average of 22 membranelles, bases of largest, about 12 µm long membranelles 7 µm wide in vivo. Buccal cavity very narrow and moderately deep, right margin conspicuously thickened; buccal lip distinctly projecting, covers posterior

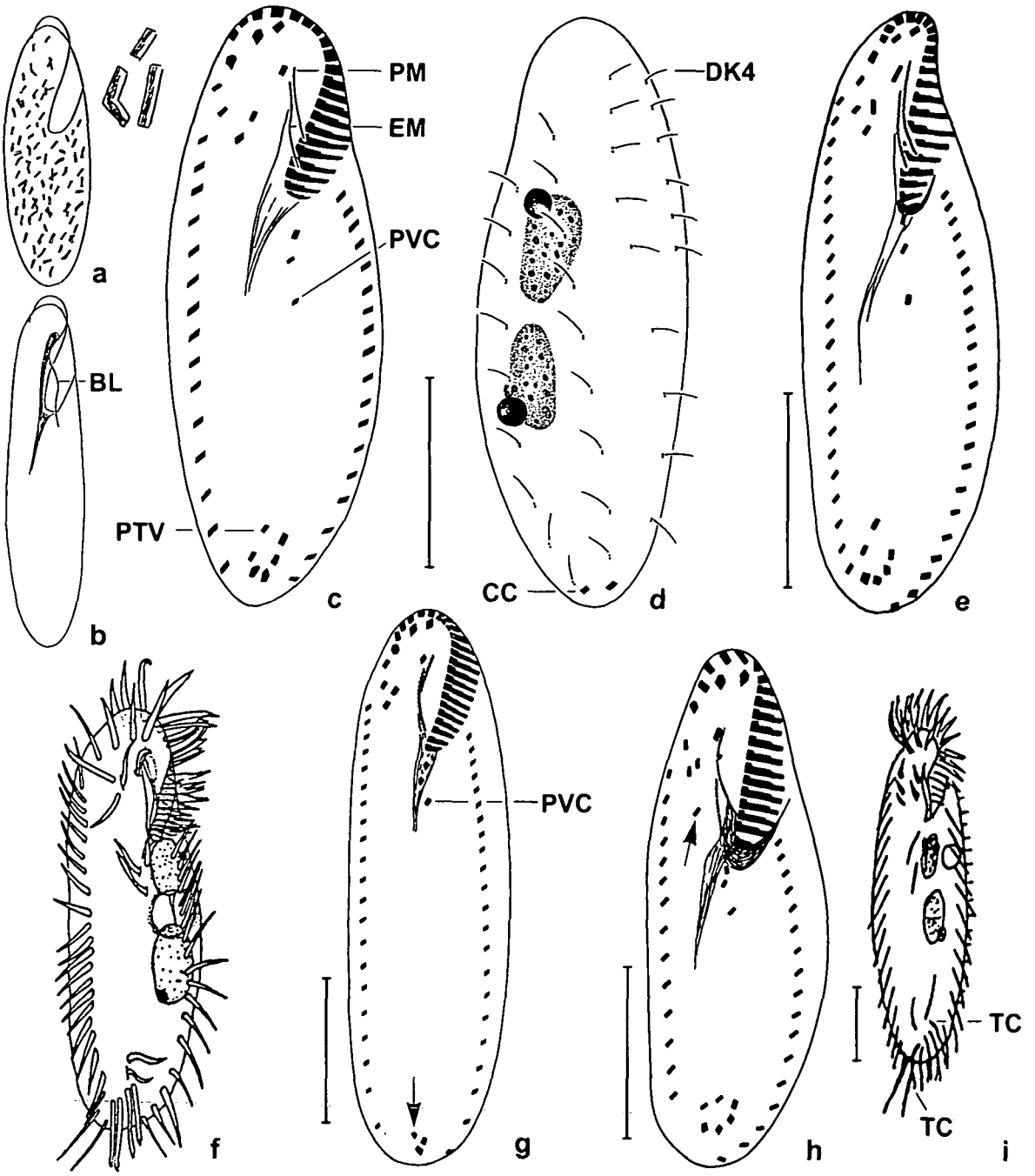


Fig. 163a–f. *Oxytricha longa* (a–d, Namibian specimens; e, from GANNER et al. 1987; f, from GELEI & SZABADOS 1950) from life (a, b), after protargol impregnation (c–e), and mercuric chloride fixation (f). **a, b:** Broad and slender specimen. Usually, specimens of this population are packed with cytoplasmic crystals, some shown at higher magnification at right side of figure (a). **c–f:** Infraciliature of ventral and dorsal side. Scale bars 20 µm. Length of (f) according to text 80–100 µm.

Fig. 163g–i. Ventral cirral pattern of *Urosomoida agiliformis* (from FOISSNER 1982), *Oxytricha granulifera quadricirrata* (from BLATTERER & FOISSNER 1988), and *Oxytricha similis* (from KAHL 1932) after protargol impregnation (g, h) and from life (i). Arrow in (g) denotes the single pretransverse ventral cirrus, arrow in (h) marks the rear frontoventral cirrus, which is distinctly set off from the other frontoventral cirri. Scale bars 20 µm.

BL – buccal lip, CC – caudal cirri, DK4 – dorsal kinety 4, EM – endoral membrane, PM – paroral membrane, PVC – rear postoral cirrus, PTV – front pretransverse cirrus, TC – right and left transverse cirrus.

portion of adoral zone almost completely and bears paroral membrane (Fig. 163b). Undulating membranes slightly curved and almost parallel to each other after protargol impregnation, endoral on average 10 µm long, paroral 8 µm and commencing about 2 µm ahead of endoral at level of buccal cirrus (Table 145); both membranes likely composed of dikinetids, paroral cilia about 5 µm long. Pharyngeal fibres of ordinary length.

Morphogenesis proceeds in the *Oxytricha* pattern (BERGER 1999) and as in population 3 of GANNER et al. (1987), that is, primordia V and VI of the proter originate from the postoral cirri. By contrast, these primordia originate de novo in *Urosomoida* (FOISSNER & ADAM 1983a). In the Spanish population, the relevant stages are not shown.

Occurrence and ecology: GELEI & SZABADOS (1950; Fig. 163f) discovered *Oxytricha longa* in a rain-water puddle in the town of Szeged, Hungary, while GANNER et al. (1987) found it in a polluted river in Salzburg, Austria (Fig. 163e) and a meadow soil from Israel. In Namibia, *Oxytricha longa* occurred in several highly saline, not strictly edaphic sites (Table 4). Abundances were high in the non-flooded Petri dish cultures showing that it is a truly euryhaline ciliate occurring both in limnetic and edaphic habitats.

Table 145. Morphometric data on *Oxytricha longa* from Namibian site (69).

Characteristics[a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	64.0	65.0	5.5	1.2	8.5	54.0	77.0	21
Body, width	23.1	22.0	3.5	0.8	15.2	18.0	30.0	21
Body length:width, ratio	2.8	2.8	0.3	0.1	11.7	2.3	3.4	21
Anterior body end to proximal end of adoral zone, distance	20.8	21.0	1.6	0.4	7.9	18.0	24.0	21
Body length:length of adoral zone, ratio	3.1	3.0	0.2	0.1	7.2	2.8	3.6	21
Anterior body end to last frontoventral cirrus, distance	13.1	13.0	1.4	0.3	10.5	10.0	16.0	21
Anterior body end to buccal cirrus, distance	6.2	6.0	0.6	0.1	10.0	5.0	8.0	21
Anterior body end to right marginal row, distance	14.6	15.0	1.8	0.4	12.2	10.0	18.0	21
Anterior body end to front postoral cirrus, distance	22.7	23.0	1.5	0.3	6.4	20.0	26.0	21
Anterior body end to rear postoral cirrus, distance	30.7	30.5	2.5	0.6	8.2	27.0	36.0	18
Posterior body end to rear transverse cirrus, distance	2.0	2.0	0.8	0.2	36.8	1.0	3.2	21
Posterior body end to right marginal row, distance	4.7	5.0	1.3	0.3	26.7	2.5	6.0	21
Posterior body end to left marginal row, distance	1.5	1.5	1.0	0.2	70.6	0.0	3.0	21
Posterior body end to front pretransverse ventral cirrus, distance	7.0	7.0	1.0	0.2	14.3	5.0	9.0	19
Anterior body end to paroral membrane, distance	5.7	6.0	1.1	0.2	19.3	4.0	8.0	21
Paroral membrane, length	8.0	8.0	0.8	0.2	10.5	6.0	9.0	21
Anterior body end to endoral membrane, distance	7.8	8.0	0.9	0.2	11.5	6.0	9.0	21
Endoral membrane, length	9.6	10.0	0.7	0.2	7.8	8.0	11.0	21
Anterior body end to first macronuclear nodule, distance	19.3	19.0	2.4	0.5	12.4	14.0	25.0	21
Macronuclear nodules, distance in between	2.0	2.0	1.2	0.3	62.2	0.0	6.0	21
Anterior macronuclear nodule, length	11.7	12.0	1.5	0.3	13.1	10.0	15.0	21
Anterior macronuclear nodule, width	5.8	6.0	0.7	0.2	12.9	4.0	7.0	21
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Anterior micronucleus, length	3.0	3.0	–	–	–	2.5	4.0	21
Anterior micronucleus, width	3.0	3.0	–	–	–	2.5	4.0	21
Micronuclei, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Nuclear figure, length	24.8	24.0	2.7	0.6	11.0	21.0	32.0	21

(continued)

Characteristics[a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Adoral membranelles, number	21.5	22.0	1.0	0.2	4.8	19.0	23.0	21
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Frontoventral cirri, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Postoral cirri, number	2.9	3.0	–	–	–	2.0	3.0	21
Pretransverse ventral cirri, number	1.9	2.0	–	–	–	1.0	2.0	21
Transverse cirri, number	3.9	4.0	–	–	–	2.0	4.0	21
Right marginal cirri, number	14.9	15.0	2.0	0.4	13.2	10.0	18.0	21
Left marginal cirri, number	16.0	16.0	1.4	0.3	8.7	14.0	18.0	21
Caudal cirri, number	1.9	2.0	–	–	–	1.0	2.0	21
Dorsal kineties, number	3.9	4.0	–	–	–	3.0	4.0	19

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. The species was abundant and exconjugants and reorganizers occurred. These and other aberrant specimens were excluded. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Vermioxytricha nov. gen.

Diagnosis: Oxytrichidae EHRENBERG, 1838 with bipartite adoral zone of membranelles, undulating membranes side by side, and frontoventral cirri in V-shaped pattern. Postoral, pretransverse, transverse, and caudal cirri lacking. Frontal and frontoventral cirri originate from 5 anlagen, the rightmost of which is a primary primordium. Dorsal morphogenesis in *Urosomoida* pattern.

Type species: *Vermioxytricha arenicola* nov. spec.

Etymology: Composite of the Latin noun *vermis* (worm) and the Greek generic name *Oxytricha* (pointed hair ≈ cirrus), referring to the slender body and the relationship with *Oxytricha* BORY DE SAINT-VINCENT, 1824. Feminine gender.

Comparison with related genera: *Vermioxytricha* is established for a new species described below and *Hemisincirra muelleri* FOISSNER, 1986. The overall features (slender body, reduced number of cirri, soil habitat) of these species are highly similar to *Hemisincirra*. However, the type species of that genus, *Uroleptus kahli* BUITKAMP, 1977b, has transverse cirri, which are lacking in *Vermioxytricha*, and the lack of a certain cirral group is commonly used as a generic feature (BERGER & FOISSNER 1997).

Vermioxytricha is very likely an oxytrichid ciliate because the frontal ciliature and ontogenesis are basically as in that group, except that not the usual six, but only five frontoventral cirral anlagen are generated. However, five anlagen also occur in two other new oxytrichid genera, namely → *Hemiurosoma* and → *Erimophrya*. An oxytrichid relationship is also emphasized by the urosomoid dorsal ontogenesis. All species of these three genera have a

reduced number of postoral cirri, namely 0, 1, or 2 vs. 3 in ordinary oxytrichids. In most oxytrichids, the postoral cirri (IV/2, V/3, V/4) are formed by the anlagen IV and V, while the frontoventral cirri (III/2, IV/3, VI/3, VI/4) originate from the anlagen III, IV, and VI (see figure 6a in BERGER 1999 for designation of cirri). Primordium V has a special position because all of its descendants are located postorally during interphase. This suggests that *Vermioxytricha*, which lacks postoral, pretransverse, and transverse cirri, secondarily lost anlage V. Furthermore, *Vermioxytricha* does not form cirrus IV/2, which is the third postoral cirrus in species with a full set of postorals. The fifth (= rightmost) anlage of *Vermioxytricha* is obviously homologous with anlage VI of ordinary oxytrichids, as indicated by the formation of the characteristic, ontogenetically inactive frontoterminal (migratory) cirri. *Vermioxytricha* is likely related to *Oxytricha*, as indicated by the V-like arranged frontoventral cirri and some ontogenetic features, for example, the formation of proter's anlage II from the buccal cirrus, anlage III from the cirrus behind the right frontal cirrus, anlage IV from the rear frontoventral cirrus (IV/3), and anlage V from anlage V of the opisthe (Fig. 165c). By contrast, *Hemiurosoma* is obviously closely related to *Urosoma* (*Urosoma* pattern of frontoventral cirri; almost all frontal, ventral, and transverse cirri originate from primary primordia). This suggests that the ordinary oxytrichid anlage V was lost independently at least twice. Accordingly, the feature cannot be used to split the family, which now contains almost 30 genera (BERGER 1999 and present study).

Vermioxytricha differs from *Hemiurosoma* by the lack of transverse and caudal cirri, the arrangement of the frontoventral cirri (V-shaped vs. *Urosoma* pattern), and the lower number of primary primordia (1 vs. 4). *Erimophrya* species have postoral, transverse, and caudal cirri, and are thus also easily distinguished from *Vermioxytricha* species. *Circinella* species, which, like *Vermioxytricha* lack, transverse and caudal cirri, usually have a rather long frontoventral row composed of many cirri. Thus, they resemble amphisiellids. Furthermore, the type species, *Circinella arenicola*, generates an oral primordium extending from mid-body to proter's frontal area, and the frontoventral cirri originate from only four anlagen (FOISSNER 1994a). Thus, *Circinella* and *Vermioxytricha* are distinct taxa, likely even belonging to different families.

Vermioxytricha species not only have a strongly reduced ventral ciliature (no postoral, pretransverse, and transverse cirri), but also a sparse dorsal infraciliature, namely only one bipolar kinety and a very short row near the anterior end. In spite of this, ontogenesis matches the *Urosomoida* pattern, that is, the single bipolar kinety (vs. three in the ordinary *Urosomoida* pattern) divides by within-proliferation, while the short row is generated dorsomarginally.

As mentioned above, a *Hemisincirra* species has to be transferred to the new genus: *Vermioxytricha muelleri* (FOISSNER, 1986) nov. comb. (basionym: *Hemisincirra muelleri* FOISSNER, 1986). We checked all other *Hemisincirra* species listed by BERGER (2001) to see whether or not some of them belong to *Vermioxytricha*. However, most of them have, like the type species of *Hemisincirra*, transverse cirri and thus cannot be included in *Vermioxytricha*. The absence of transverse cirri in *Hemisincirra vermiculare* HEMBERGER, 1985 is uncertain, and → *Hemisincirra rariseta* very likely lacks a buccal cirrus; hence, both species should remain in *Hemisincirra*, which includes mostly small, slender species that do not fit into any other genus well.

Vermioxytricha arenicola nov. spec. (Fig 164a–z, 165a, b; 397a–n; Table 146)

Diagnosis: Size about 170 × 17 µm in vivo; vermiform. Usually 13–16 macronuclear nodules in single strand left of midline. Cortical granules around cirri and dorsal bristles and scattered in short rows, about 1 µm across and yellowish. On average 43–46 right and 39 left marginal cirri. Adoral zone occupies 12–14% of body length, comprises 3 frontal and 14–15 ventral membranelles. Invariably 1 bipolar and 1 very short dorsal kinety near anterior end.

Type location: Humous sand under *Acacia erioloba* trees (Camel thorn) in the Sossus Vlei of the Namib Desert, 24°50'S 15°20'E (site 24 in figure 2 and chapter 2.1.2).

Etymology: The Latin adjective *arenicola* (living in sand) refers to the preferred habitat.

Description: Two populations were studied, namely from Tunisia and from Namibian site (24). They agree so well in all features that conspecificity is beyond reasonable doubt (Table 146). Thus, the diagnosis and description contain data from both populations.

Size 120–220 × 12–25 µm in vivo, usually about 170 × 17 µm, length:width ratio around 10:1 on average both in vivo and in protargol preparations (Table 146), flattened only in oral area; acontractile, occasionally slightly twisted about main body axis. Vermiform with anterior portion slightly narrowed and inconspicuously bulged where the adoral zone enters the buccal cavity; posterior region usually tail-like and more or less distinctly curved with slight, but typical subterminal notch at right side (Fig. 164a–g; 397a, g). Nuclear apparatus in central quarters of cell. Macronuclear nodules in single strand left of midline, individual nodules usually elongate ellipsoidal, rarely globular or ellipsoidal; nucleoli minute. Usually 2–4 globular micronuclei along macronuclear strand. Contractile vacuole with distinct collecting canals above mid-body at left cell margin. Cortex thin and flexible, contains granules around cirral and dorsal bristles bases, but also scattered in bare areas; individual granules about 1 µm across and yellowish, usually impregnate distinctly with the protargol method used; when methyl green-pyronin is added, they become red but are not released; underneath cortex ellipsoidal, about 2 µm-sized, pale structures, likely mitochondria (Fig. 164h, i; 397g, i, j). Cytoplasm colourless, packed with lipid droplets 1–2 µm across and some vacuoles with a single crystal each. Food vacuoles 5 µm across, contain rod-shaped bacteria, yeast cells, short fungal hyphae, and debris. Moves rapidly and serpentinely on microscope slide and between soil particles, showing great flexibility; if numerous, the whirling bodies produce a curious spectacle.

Cirral pattern and number of cirri of usual variability, except for the number of marginal cirri, which varies distinctly in the Tunisian specimens (Fig. 164a, j–l, o–q; 397a, f, g, h; Table 146). Most cirri only about 8–10 µm long and fine, each usually consisting of only two or four cilia. Right marginal row slightly shortened and extending dorsolaterally anteriorly, ends subterminally; left row of Tunisian specimens usually terminates with three closely spaced cirri at rear end. Frontal cirri of about same size as other cirri, in subapical, oblique row, first (= left) cirrus invariably in or near gap between frontal and ventral adoral membranelles. Frontoventral row right of midline, ends slightly to distinctly above oral vertex, usually composed of only three cirri, namely the two frontoterminal cirri and the single cirrus originating from anlage IV. Majority of specimens with a single cirrus left of frontoventral row, rarely specimens without cirrus or with two cirri occur. Buccal cirrus in corner of

undulating membranes, usually composed of two cilia only. Postoral and transverse cirri lacking.

Dorsal bristles about 2 µm long in vivo, arranged in two rows: row 1 bipolar, slightly shortened anteriorly and posteriorly; row 2 usually composed of only two basal body pairs near anterior right end of cell. Caudal cirri lacking (Fig. 164m, p; 397a, c–e; Table 146).

Adoral zone inconspicuous because occupying only 12–14% of body length, three frontal and 14–15 ventral membranelles of ordinary fine structure separated by a distinct gap at left anterior body corner. Buccal field narrow and flat; buccal lip covers proximal adoral membranelles. Paroral and endoral membrane almost straight, close together, staggered, and likely composed of monokinetids. Pharynx without peculiarities (Fig. 164a, b, e, j–l, o, p; 397a–e, g, h; Table 146).

Table 146. Morphometric data on *Vermioxytricha arenicola* from Namibian type location (N) and Tunisia (T).

Characteristics[a]	Pop[a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	N	162.7	162.0	15.3	4.0	9.4	138.0	192.0	15
	T	163.6	160.0	24.9	6.9	15.2	132.0	215.0	13
Body, width	N	15.7	15.0	2.7	0.7	17.1	12.0	22.0	15
	T	15.5	15.0	2.2	0.6	14.1	12.0	20.0	13
Body length:width, ratio	N	10.5	10.3	1.3	0.3	12.8	7.9	12.8	15
	T	10.7	10.7	2.3	0.6	21.2	8.0	16.5	13
Anterior body end to proximal end of adoral zone, distance	N	21.2	21.0	1.9	0.5	8.8	18.0	26.0	15
	T	21.8	22.0	1.3	0.4	6.0	20.0	24.0	13
Body length:length of adoral zone, ratio	N	7.7	7.8	1.0	0.2	12.4	6.4	9.6	15
	T	7.5	7.5	1.0	0.3	12.6	6.1	9.1	13
Anterior body end to paroral membrane, distance	N	8.9	9.0	1.6	0.4	18.0	7.0	13.0	13
Anterior body end to endoral membrane, distance	N	10.8	10.5	1.2	0.4	10.8	9.0	12.0	8
Paroral membrane, length	N	5.3	5.0	0.9	0.3	17.2	4.0	7.0	11
Endoral membrane, length	N	5.9	6.0	–	–	–	5.0	6.5	7
Anterior body end to right marginal row, distance	N	11.5	11.0	1.2	0.3	11.6	8.0	12.0	15
Anterior body end to proximal end of frontoventral cirral row, distance	N	15.6	16.0	1.7	0.4	10.8	11.0	18.0	15
Anterior body end to buccal cirrus, distance	N	10.1	10.0	1.2	0.3	11.6	8.0	12.0	15
Anterior body end to first macronuclear nodule, distance	N	26.9	27.0	3.5	0.9	13.0	19.0	33.0	15
Nuclear figure, length	N	97.3	93.0	13.7	3.5	14.1	78.0	118.0	15
Anterior macronuclear nodule, length	N	9.7	9.0	2.4	0.6	25.2	5.0	14.0	15
	T	7.8	7.0	1.5	0.4	19.1	6.0	10.0	13
Anterior macronuclear nodule, width	N	2.9	2.5	0.6	0.2	21.1	2.4	4.0	15
	T	2.8	3.0	0.5	0.1	18.1	2.0	4.0	13
Macronuclear nodules, number	N	12.8	13.0	2.4	0.7	18.4	8.0	16.0	13
	T	15.6	16.0	2.0	0.6	13.0	13.0	18.0	13
Anterior micronucleus, length	N	1.8	1.6	–	–	–	1.6	2.5	15
	T	1.9	1.9	–	–	–	1.7	2.0	13
Anterior micronucleus, width	N	1.6	1.6	–	–	–	1.0	1.6	15
	T	1.9	1.9	–	–	–	1.7	2.0	13

(continued)

Characteristics[a]	Pop[a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Micronuclei, number	N	3.6	4.0	0.9	0.2	24.1	2.0	5.0	13
	T	2.6	2.0	1.2	0.3	45.6	1.0	5.0	13
Frontal adoral membranelles, number	N	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
	T	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13
Ventral adoral membranelles, number	N	14.3	14.0	1.2	0.3	8.6	13.0	17.0	15
	T	14.5	15.0	1.1	0.3	7.7	12.0	16.0	13
Adoral membranelles, total number	N	17.3	17.0	1.2	0.3	7.1	16.0	20.0	15
	T	17.5	18.0	1.1	0.3	6.4	15.0	19.0	13
Frontal cirri, number	N	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
	T	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13
Buccal cirri, number	N	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
	T	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13
Frontoventral row, number of cirri	N	2.9	3.0	–	–	–	1.0	3.0	15
	T	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13
Cirri left of frontoventral row, number	N	1.1	1.0	–	–	–	1.0	3.0	15
	T	1.2	1.0	–	–	–	0.0	2.0	13
Right marginal cirri, number	N	43.3	44.0	5.4	1.4	12.4	29.0	50.0	15
	T	46.4	44.0	10.1	2.8	21.9	36.0	78.0	13
Left marginal cirri, number	N	39.2	39.0	4.9	1.3	12.6	30.0	48.0	15
	T	39.2	37.0	7.2	2.0	18.4	30.0	56.0	13
Dorsal kineties, number	N	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15
	T	2.0	2.0	0.0	0.0	0.0	2.0	2.0	13
Dorsal kinety 1, number of bristles	N	16.5	17.0	1.6	0.4	9.4	14.0	19.0	13
Dorsal kinety 2, number of bristles	N	1.8	2.0	–	–	–	1.0	2.0	15

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, Pop – population, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Ontogenesis (Fig. 164o–z, 165a, b; 397k–n): Division, studied in specimens from type location, is similar to that of oxytrichids (for a review, see BERGER 1999), but simpler due to the reduced number of anlagen and cirri.

Ontogenesis commences with the formation of a long, narrow oral primordium slightly above mid-body (Fig. 164n, o). Then, four cirral anlagen streaks in forked pattern arise from the anterior end of the oral primordium, where adoral membranelles are already assembled (Fig. 164r–t; 397k, l). Next, the rightmost cirral anlage splits transversely to produce an anlage each for the frontoterminal cirri of the proter and opisthe; thus, this streak is a primary primordium (Fig. 164t, u; long arrow; 397 l). Furthermore, the parental undulating membranes begin to reorganize, and the buccal cirrus, the cirrus behind the right frontal cirrus, and the rear frontoventral cirrus modify to proter's anlagen I to IV.

In middle dividers, five frontoventral cirral anlagen streaks are recognizable both in proter and opisthe (Fig. 164v, x, y; 397 l). In late dividers, frontoventral cirri begin to segregate and arrange to the species-specific pattern, showing that neither postoral nor pretransverse and transverse cirri are formed (Fig. 164z, 165a; 397m). On average, the following number of cirri

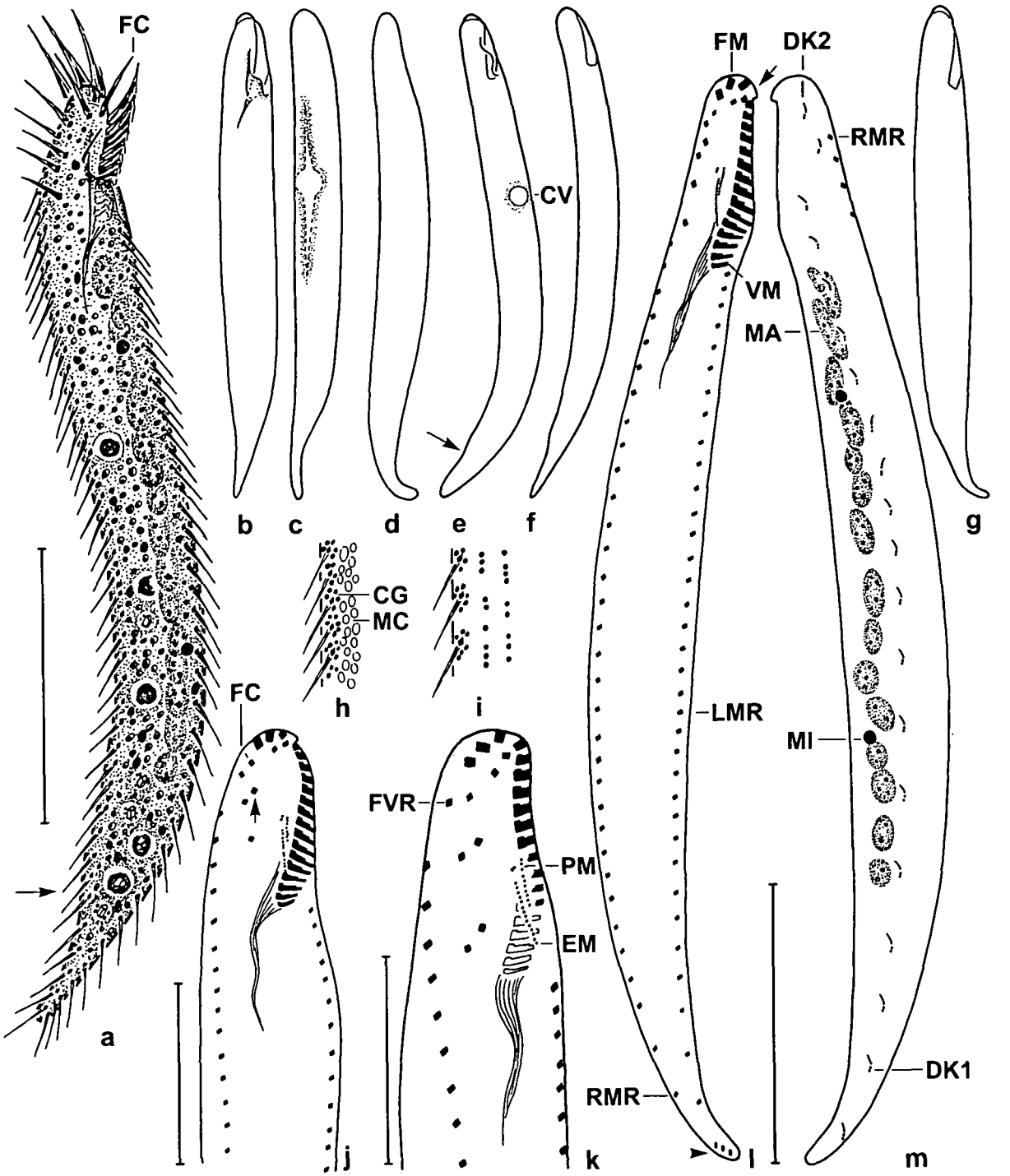


Fig. 164a–m. *Vermioxytricha arenicola*, Tunisian and Namibian specimens from life (a–i) and after protargol impregnation (j–m). **a–g:** Ventral view of a representative specimen (a) and shape variants. Arrows mark notch at right posterior margin. **h, i:** Cortical granulation and mitochondria underneath cortex. **j–m:** The overview (l, m) shows the infraciliature and nuclear apparatus of a representative Tunisian specimen. Arrow marks gap between frontal and ventral membranelles, arrowhead denotes closely spaced cirri near body end. Usually there is only one cirrus (j, arrow), rarely two (k) left of the frontoventral row. CG – cortical granules, CV – contractile vacuole, DK1, 2 – dorsal kineties, EM – endoral membrane, FC – left (a) or right (j) frontal cirrus, FM – frontal membranelles, FVR – frontoventral row, LMR – left marginal row, MA – macronuclear nodules, MC – mitochondria, MI – micronucleus, PM – paroral membrane, RMR – right marginal row, VM – ventral membranelles. Scale bars 50 µm (a, l, m) and 20 µm (j, k).

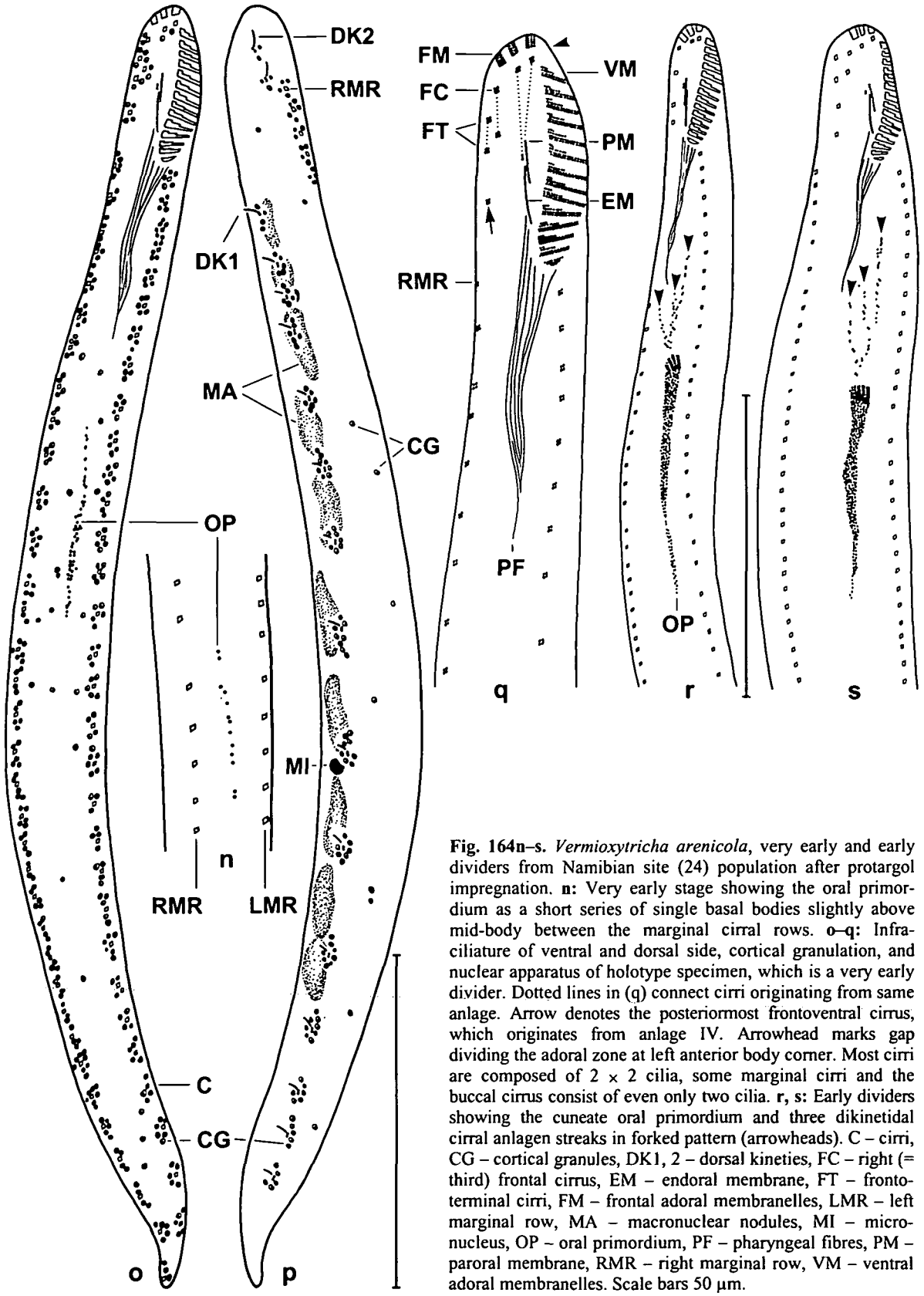


Fig. 164n–s. *Vermioxytricha arenicola*, very early and early dividers from Namibian site (24) population after protargol impregnation. **n:** Very early stage showing the oral primordium as a short series of single basal bodies slightly above mid-body between the marginal cirral rows. **o–q:** Infraciliature of ventral and dorsal side, cortical granulation, and nuclear apparatus of holotype specimen, which is a very early divider. Dotted lines in (q) connect cirri originating from same anlage. Arrow denotes the posteriormost frontoventral cirrus, which originates from anlage IV. Arrowhead marks gap dividing the adoral zone at left anterior body corner. Most cirri are composed of 2 × 2 cilia, some marginal cirri and the buccal cirrus consist of even only two cilia. **r, s:** Early dividers showing the cuneate oral primordium and three dikinetidal cirral anlagen streaks in forked pattern (arrowheads). C – cirri, CG – cortical granules, DK1, 2 – dorsal kineties, FC – right (= third) frontal cirrus, EM – endoral membrane, FT – frontoterminal cirri, FM – frontal adoral membranelles, LMR – left marginal row, MA – macronuclear nodules, MI – micronucleus, OP – oral primordium, PF – pharyngeal fibres, PM – paroral membrane, RMR – right marginal row, VM – ventral adoral membranelles. Scale bars 50 µm.

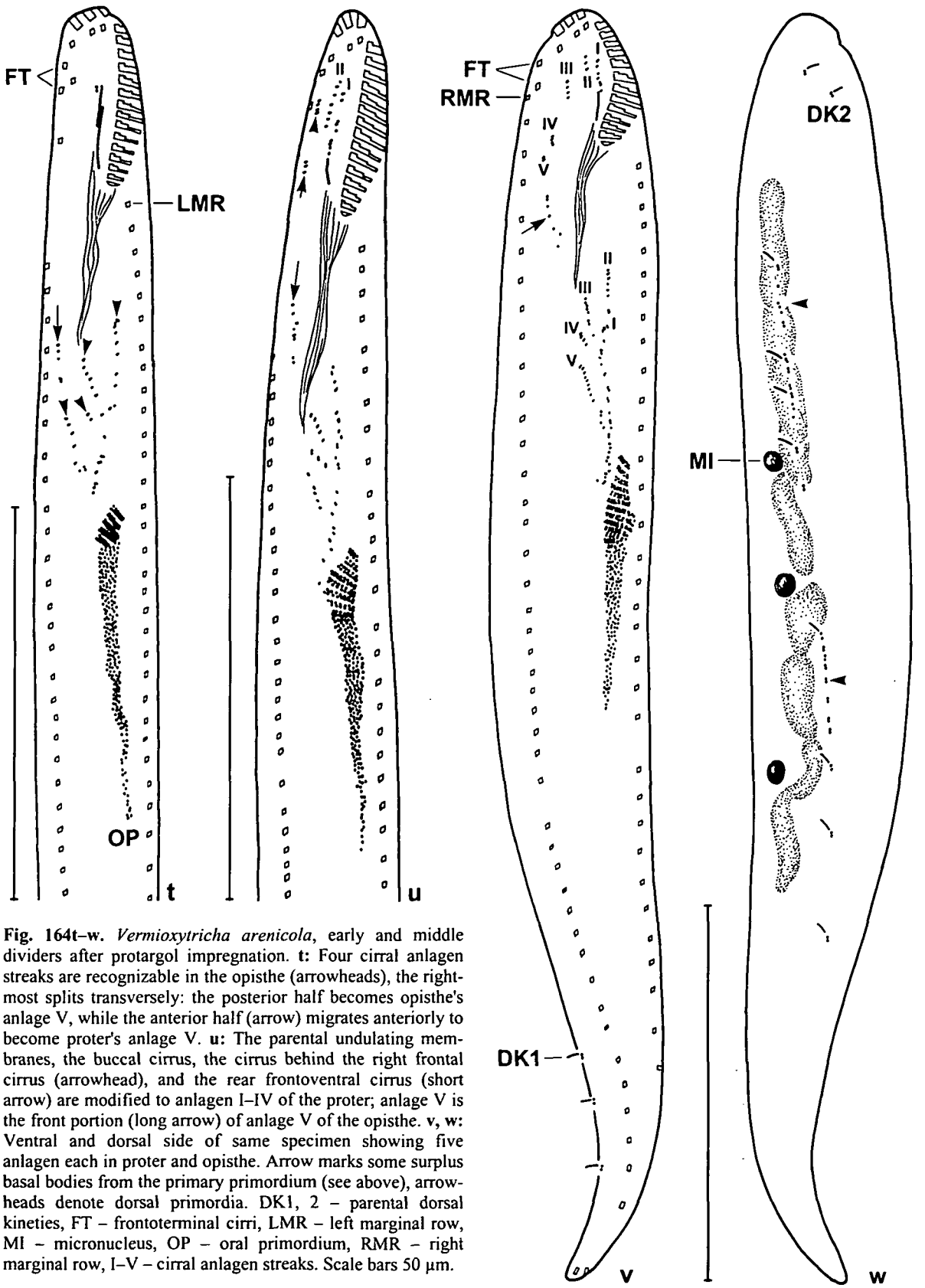


Fig. 164t–w. *Vermioxytricha arenicola*, early and middle dividers after protargol impregnation. **t:** Four cirral anlagen streaks are recognizable in the opisthe (arrowheads), the rightmost splits transversely: the posterior half becomes opisthe's anlage V, while the anterior half (arrow) migrates anteriorly to become proter's anlage V. **u:** The parental undulating membranes, the buccal cirrus, the cirrus behind the right frontal cirrus (arrowhead), and the rear frontoventral cirrus (short arrow) are modified to anlagen I–IV of the proter; anlage V is the front portion (long arrow) of anlage V of the opisthe. **v, w:** Ventral and dorsal side of same specimen showing five anlagen each in proter and opisthe. Arrow marks some surplus basal bodies from the primary primordium (see above), arrowheads denote dorsal primordia. DK1, 2 – parental dorsal kineties, FT – frontoterminal cirri, LMR – left marginal row, MI – micronucleus, OP – oral primordium, RMR – right marginal row, I–V – cirral anlagen streaks. Scale bars 50 μm.

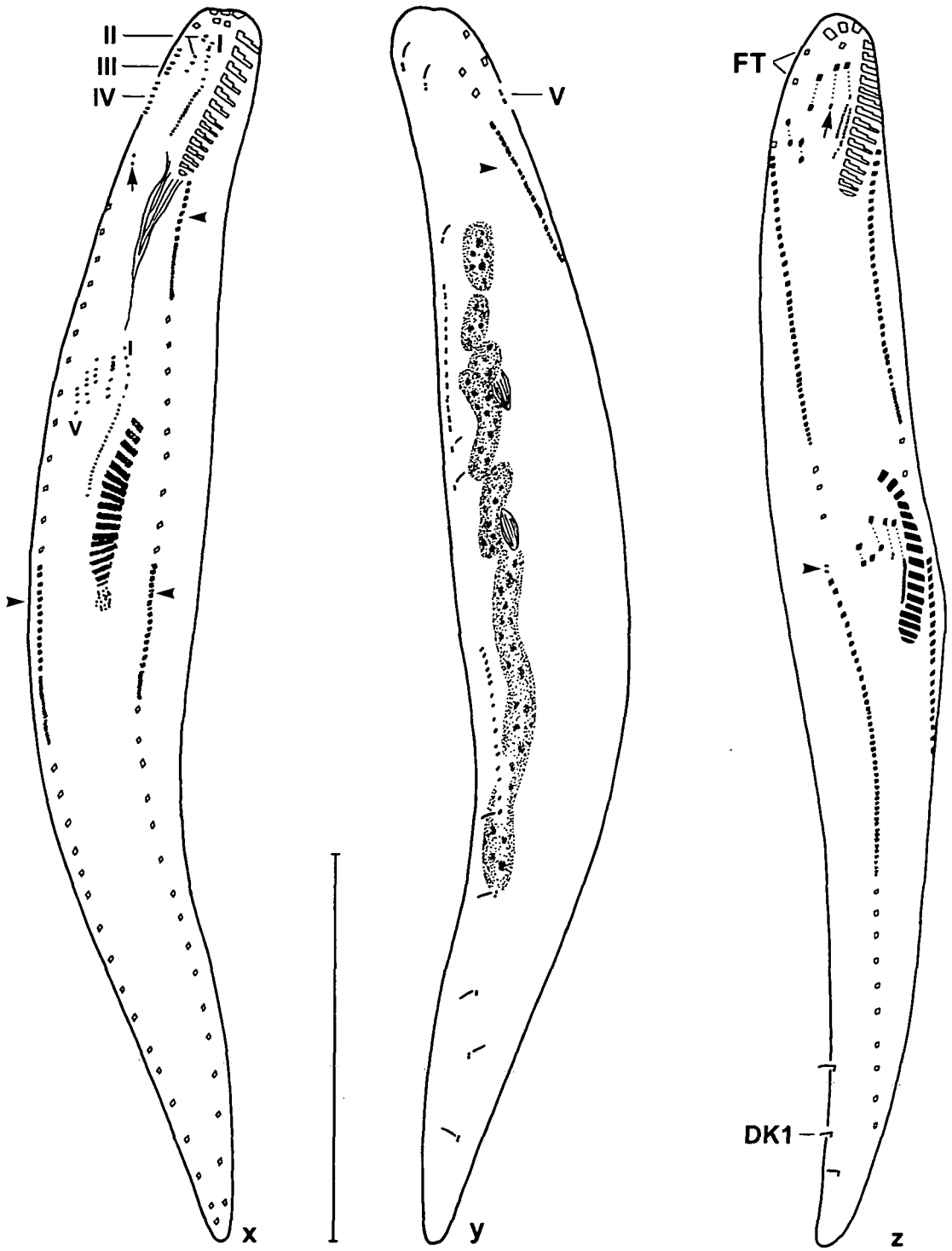


Fig. 164x–z. *Vermioxytricha arenicola*, a middle and a late divider after protargol impregnation. Parental structures shown by contour, newly formed shaded black. **x, y:** Ventral and dorsal side of a specimen with five anlagen each in proter and opisthe. Arrow marks some surplus basal bodies from the primary primordium (anlage V). Arrowheads denote anlagen within marginal rows. **z:** Late divider with nine new cirri in frontal field of proter and the usual set of eight cirri in the opisthe. Arrow denotes the new buccal cirrus. Arrowhead denotes new opisthe dorsal kinety 2. Dotted lines connect cirri originating from same anlage. DK1 – dorsal kinety 1, FT – parental frontoterminal cirri, I–V – cirral anlagen streaks. Scale bars 50 μm.

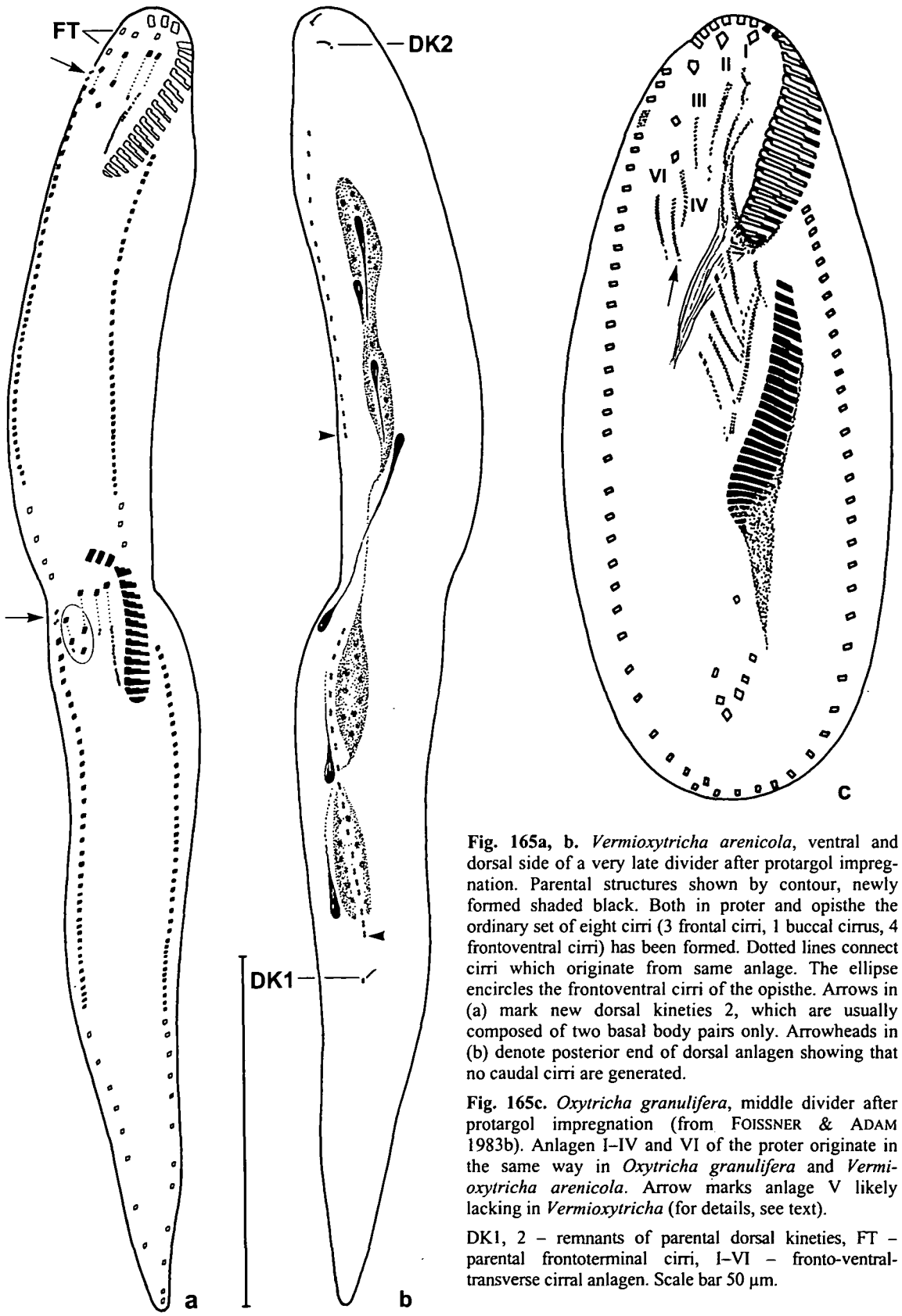


Fig. 165a, b. *Vermioxytricha arenicola*, ventral and dorsal side of a very late divider after protargol impregnation. Parental structures shown by contour, newly formed shaded black. Both in proter and opisthe the ordinary set of eight cirri (3 frontal cirri, 1 buccal cirrus, 4 frontoventral cirri) has been formed. Dotted lines connect cirri which originate from same anlage. The ellipse encircles the frontoventral cirri of the opisthe. Arrows in (a) mark new dorsal kineties 2, which are usually composed of two basal body pairs only. Arrowheads in (b) denote posterior end of dorsal anlagen showing that no caudal cirri are generated.

Fig. 165c. *Oxytricha granulifera*, middle divider after protargol impregnation (from FOISSNER & ADAM 1983b). Anlagen I–IV and VI of the proter originate in the same way in *Oxytricha granulifera* and *Vermioxytricha arenicola*. Arrow marks anlage V likely lacking in *Vermioxytricha* (for details, see text).

DK1, 2 – remnants of parental dorsal kineties, FT – parental frontoterminal cirri, I–VI – fronto-ventral-transverse cirral anlagen. Scale bar 50 µm.

is formed by the anlagen I–V: 1, 2, 2, 1, 2. Nuclear division and ontogenesis of the remaining ventral ciliature occur in the usual manner (Fig. 164w–z, 165a, b; 397n).

Formation of the dorsal ciliature commences with the production of two anlagen within parental kinety 1 (Fig. 164w). Later, a very short dorsomarginal kinety (= kinety 2) develops at/near the anterior end of the right marginal cirral anlagen (Fig. 164z, 165a). No caudal cirri are generated (Fig. 165b).

Occurrence and ecology: Great numbers of *Vermioxytricha arenicola* developed in the non-flooded Petri dish cultures from type location and nearby (Table 4), indicating the presence of many resting cysts and optimal growth conditions. The Tunisian sample, kindly provided by Prof. Dr. Thomas PEER from Salzburg University, was an alkaline (pH 8.1), cyanobacteria-covered crust soil mixed with red sand and some litter from drifting sand of the eastern part of the Grand Erg, 33°N 09°E. *Vermioxytricha arenicola* is well adapted to the sandy habitat by its vermiform shape, and is thus rather common in the dunes of the Namib Desert (Table 4).

Comparison with related species: *Vermioxytricha arenicola* is likely the sister species of *V. muelleri* (FOISSNER, 1986), which also occurs in Namibia, differing only by the cortical granules, distinct organelles we use as a species feature. → *Hemisincirra rariseta*, which has the same size, shape, and nuclear apparatus, also lacks cortical granules, and is thus easily confused with *V. muelleri*. However, *Hemisincirra rariseta* has more cirri in the frontal field (12 vs. 8), likely lacks a buccal cirrus, has fewer marginal cirri (around 26 per row vs. around 40), and two bipolar dorsal kineties (vs. one bipolar and one strongly reduced kinety in *V. arenicola*). There are several other, rather similar species discussed under → *Hemisincirra rariseta*. In vivo, *Vermioxytricha arenicola* is recognizable by the vermiform shape, the strand-like nuclear figure, the cortical granules, and the two dorsal bristle rows, one of which is strongly reduced. However, identification should be checked in protargol preparations.

Apourosomoida nov. gen.

Diagnosis: Oxytrichidae EHRENBERG, 1838 with adoral zone formed like a question mark and interrupted by a minute gap at left anterior corner of body. Undulating membranes in *Gonostomum* pattern. Frontoventral cirri in V-shaped pattern; originate from five anlagen, of which the rightmost are primary primordia. Number of postoral cirri increased to a conspicuous row, originating from anlage IV. Single transverse cirrus produced by rightmost anlage V. 1 right and 1 left row of marginal cirri. 2 dorsal kineties, each with a caudal cirrus; proter kineties originate from ordinary anlagen, while opisthe's kinety 1 is generated by posterior fragmentation of kinety 2.

Type species: *Apourosomoida halophila* nov. spec.

Etymology: Composite of the Greek prefix *apo* (derived from) and the generic name *Urosomoida*. Feminine gender.

Species assignable: The genus is monotypic. However, *Urosomoida minima* HEMBERGER, 1985 (Fig. 171e) might belong to *Apourosomoida*, as indicated by the gap in the

adoral zone and the reduced dorsal infraciliature, unfortunately not shown in detail by HEMBERGER. *Cladotricha variabilis*, as redescribed by BORROR & EVANS (1979), also has features resembling *A. halophila*. However, it likely produces six fronto-ventral-transverse cirral anlagen and an additional short row of postoral cirri. Thus, it might be a new genus related to *Apourosomoida* (see also discussion of *Cladotricha* below). Unfortunately, the genesis of the dorsal infraciliature was insufficiently described. Data from *Uroleptus natronophilus* DIETZ, 1965 are also too meagre for a definite classification.

Comparison with related genera: The ontogenetic data indicate that *Apourosomoida* belongs to the Oxytrichidae, as defined by BERGER & FOISSNER (1997) and BERGER (1999). Likely, it is related to *Urosomoida* and → *Erimophrya*, but the unique genesis of the postoral cirral row and the dorsal infraciliature forbids excluding that *Apourosomoida* belongs to another family, or even that it is the representative of a new family. Actually, this species shows once more that hypotrich evolution is possibly too intricate to be unravelled, both with classical and modern methods. The family Oxytrichidae contains now almost 30 genera, an indefensible situation for cladistic phylogeneticists. The following comparison is confined to genera which might be confused with *Apourosomoida*; as concerns the oxytrichids, the major revision by BERGER (1999) should be consulted.

Apourosomoida differs, inter alia, from *Urosomoida* by the adoral zone (with vs. without gap separating frontal and ventral membranelles), the number of dorsal kineties (two vs. four), the number of cirral anlagen (five vs. six), and the ontogenesis of the postoral cirri (from single vs. two anlagen) and dorsal bristles (*Apourosomoida* vs. *Urosomoida* pattern).

At first glance, *Apourosomoida* looks similar to → *Erimophrya* because both have the same fronto-ventral-transverse cirral pattern and both generate it from only five anlagen. However, → *Erimophrya* has distinctly reduced postoral cirri and an urosomoidal ventral and dorsal ontogenesis. Accordingly, the great overall similarity of, especially, → *Erimophrya arenicola* is produced by homoplasy.

Apourosomoida has, like *Gonostomum*, *Urosoma*, and → *Hemiurosoma*, primary primordia, a distinct apomorphy uniting these genera to a clade in the phylogenetic system of the Oxytrichidae (BERGER & FOISSNER 1997, BERGER 1999). However, the primary primordia of *Apourosomoida* possibly evolved convergently because, inter alia, the arrangement of the frontoventral cirri (*Urosomoida* vs. *Urosoma* pattern) and the arrangement and genesis of the dorsal bristles are entirely different (*Apourosomoida* pattern with fragmentation of kinety 2 vs. *Urosomoida* pattern without fragmentation but with a dorsomarginal kinety).

Apourosomoida differs from *Cladotricha koltzowii* (Fig. 166n), type of the genus and redescribed by BORROR & EVANS (1979), by the transverse cirri (present vs. lacking), the postoral cirri (present vs. lacking), and the arrangement of the frontoventral cirri (*Urosomoida* vs. *Cladotricha* pattern). Furthermore, ontogenesis is obviously quite different in *C. koltzowii* and *C. halophila* (BORROR & EVANS 1979, WILBERT 1995). BORROR & EVANS (1979) also investigated *Cladotricha variabilis*, whose morphology and ontogenesis are quite different from that of *C. koltzowii* and *C. halophila*, but rather similar to that of *Apourosomoida*, except for the transverse cirri (lacking vs. present) and the number of fronto-ventral-transverse cirral anlagen (likely six vs. five). Thus, *C. variabilis* redescribed by BORROR & EVANS is neither congeneric with *C. koltzowii* nor *Apourosomoida halophila* (Fig. 166o–s).

Apourosomoida halophila nov. spec. (Fig. 166a–f, 167a–v; 398a–j; Table 147)

Diagnosis: Size about 100 × 20 µm in vivo; elongate ellipsoidal with pointed posterior end. 2 elongate ellipsoidal macronuclear nodules and 1 micronucleus. Adoral zone usually composed of 17 membranelles occupying 20% of body length. On average about 19 cirri each in right and left marginal row, 3 frontal cirri, 4 frontoventral cirri, 1 buccal and transverse cirrus each, 5 cirri in postoral row, and 2 caudal cirri. Dorsal kineties 1 and 2 composed of an average of 2, respectively, 8 bristles.

Type location: Highly saline, sandy soil from the Unjab river bed, northern Namib Desert, Namibia, 20°10'S 13°10'E.

Etymology: Composite of the Greek words *hal* (salt) and *phil* (to like), referring to the saline environment the species prefers.

Description: Size 60–130 × 15–25 µm in vivo, usually near 100 × 20 µm, considerably shrunken and stouter in protargol and SEM preparations, viz., 71 × 21 µm, as also indicated by the high variation coefficient (25%; Table 147). Shape rather constant, elongate ellipsoidal to bluntly cylindroidal with anterior end narrowly rounded and posterior rather abruptly pointed; rarely slipper-shaped or curved specimens occur. Slightly to distinctly twisted along main body axis and flattened up to 2:1 dorsoventrally in oral area (Fig. 166a–c, e; 398a, c–e). Macronuclear nodules in middle third of cell left of midline, usually close together and connected by a fine thread, ellipsoidal to cylindroidal (7:1), on average elongate ellipsoidal (3:1); contain many small, globular nucleoli. Micronucleus lacking or not impregnated in about 30% of specimens, others have 1 or 2 micronuclei attached to the macronuclear nodules at variable position. No contractile vacuole recognizable. Cortex very flexible, lacks specific granules. Cytoplasm colourless, contains up to 7 µm-sized food vacuoles with bacterial remnants, some 3–5 µm long, ordinary crystals, and pale lipid droplets up to 3 µm across mainly in posterior body half. Glides and swims slowly on microscope slide.

Cirral pattern and number of cirri of usual variability, except for frontoventral cirri, which vary from 3–6 (Fig. 166a, e, f, 167a, n; 398d–f; Table 147). Cirri usually composed of 4–6 cilia, rarely of 2 (last cirrus of left marginal row) or 9 (frontal cirri, right caudal cirrus). Marginal cirral rows obliquely arranged due to body torsion, right row commences subapically on dorsal side and extends onto ventral margin in mid-body to end far subterminally, left row curves onto dorsal margin in mid-body and extends onto pointed end of cell; cirri decrease in size and become more widely spaced in posterior third, especially in left row. Frontal and frontoventral cirri in *Urosomoida* pattern, right frontoventral cirri form short row in flat furrow at right body margin. Postoral cirri conspicuous because forming a straight or slightly oblique row in body midline underneath adoral zone. Transverse cirrus at rear body end, forms rather conspicuous tuft together with caudal cirri and last cirri of left marginal row.

Adoral zone occupies about 20% of body length in vivo, while 26% in protargol preparations, likely due to increased shrinkage of postoral body portion; composed of an average of 3 minute frontal and 14 ordinary ventral membranelles separated by a distinct gap at left anterior corner of cell. Buccal field very narrow and flat, covered by an angularly projecting, hyaline lip bearing paroral membrane. Paroral and endoral membrane staggering side by side,

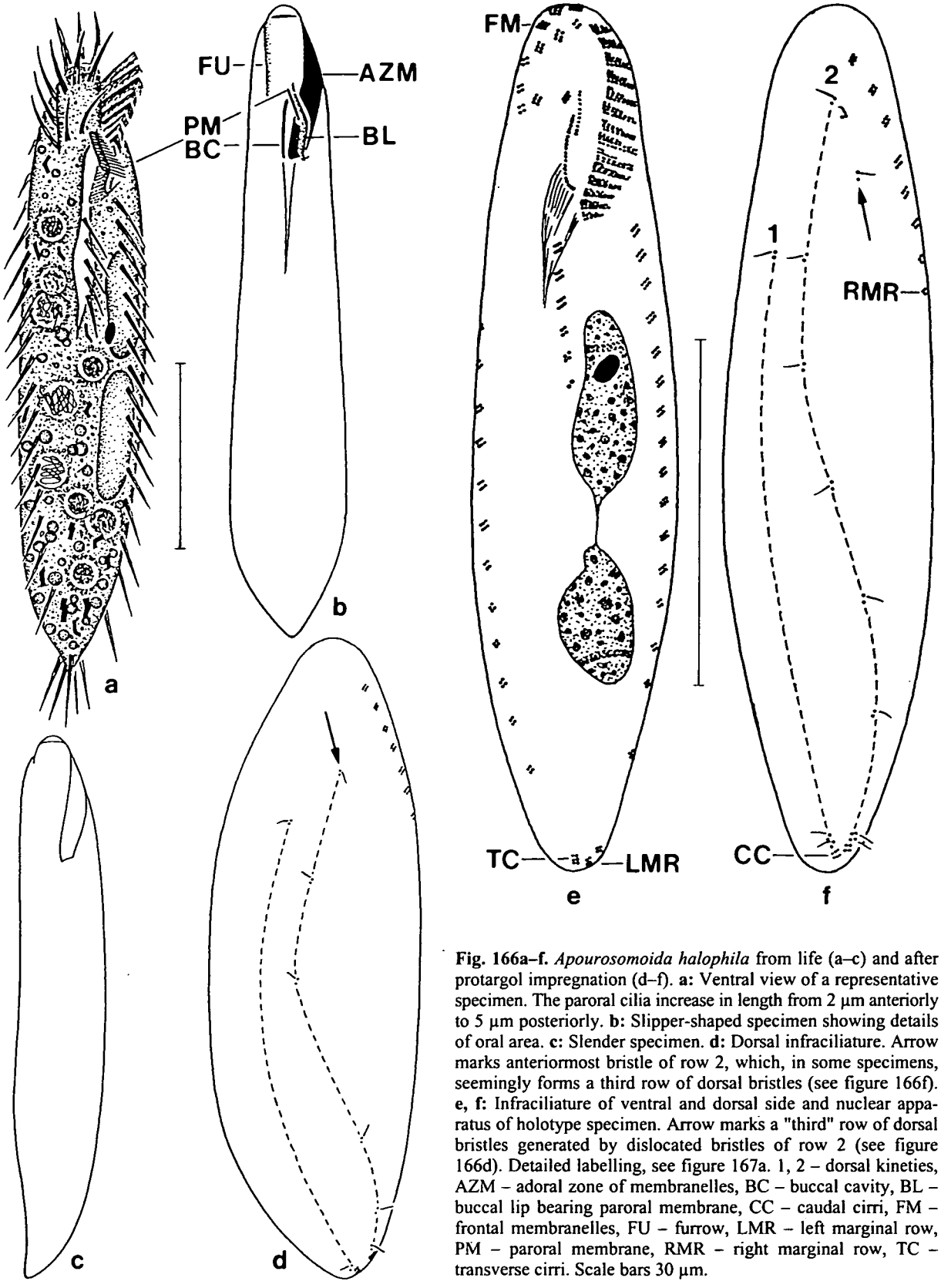


Fig. 166a–f. *Apourosomoida halophila* from life (a–c) and after protargol impregnation (d–f). **a:** Ventral view of a representative specimen. The paroral cilia increase in length from 2 µm anteriorly to 5 µm posteriorly. **b:** Slipper-shaped specimen showing details of oral area. **c:** Slender specimen. **d:** Dorsal infraciliature. Arrow marks anteriormost bristle of row 2, which, in some specimens, seemingly forms a third row of dorsal bristles (see figure 166f). **e, f:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrow marks a "third" row of dorsal bristles generated by dislocated bristles of row 2 (see figure 166d). Detailed labelling, see figure 167a. 1, 2 – dorsal kineties, AZM – adoral zone of membranelles, BC – buccal cavity, BL – buccal lip bearing paroral membrane, CC – caudal cirri, FM – frontal membranelles, FU – furrow, LMR – left marginal row, PM – paroral membrane, RMR – right marginal row, TC – transverse cirri. Scale bars 30 µm.

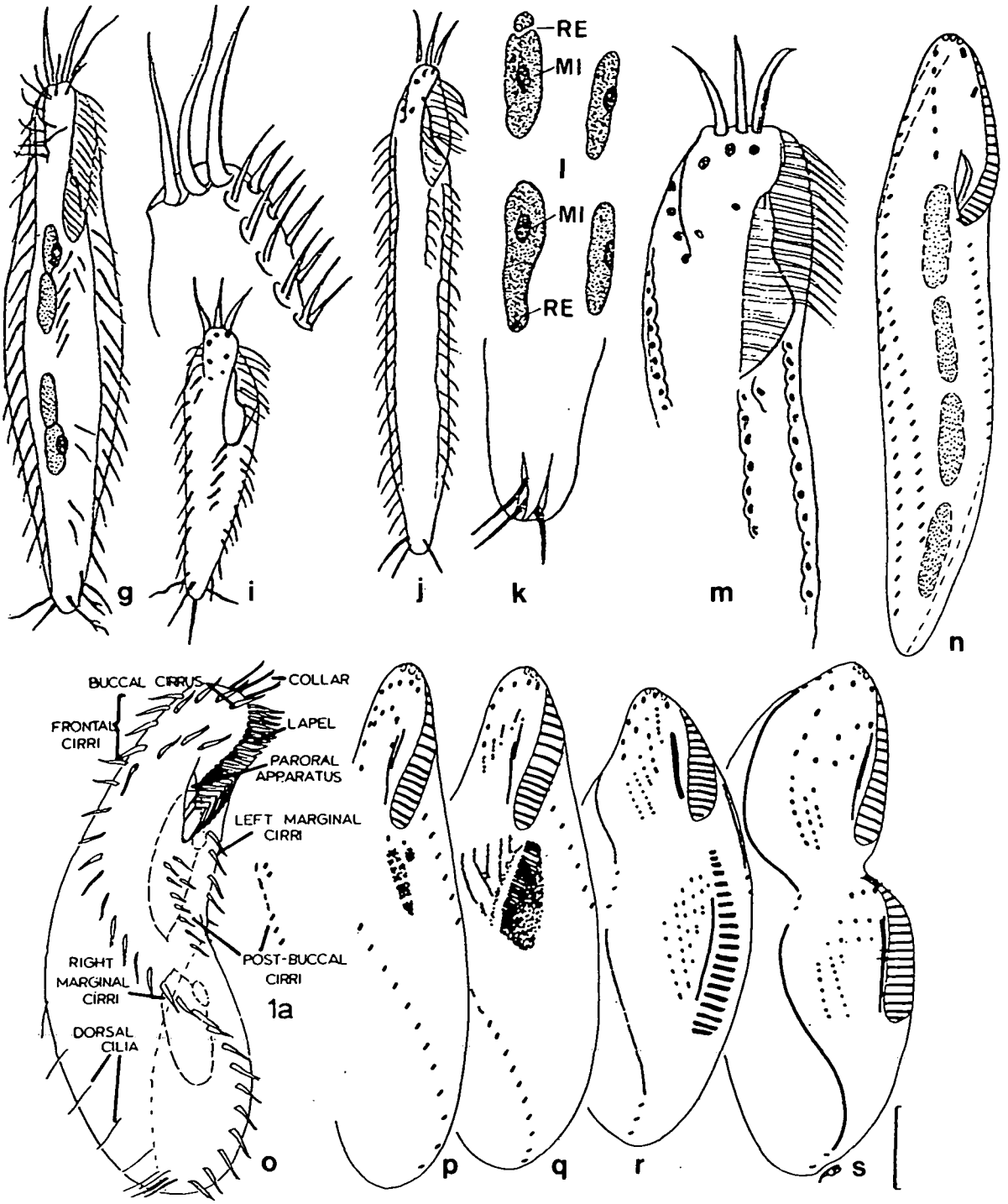


Fig. 166g–m. *Cladotricha variabilis* from life (from RUINEN 1938). **g, j:** Ventral views of a representative and an unusual specimen. **h, m:** Dorsal and ventral anterior region. **i:** Degenerated specimen. **k:** Dorsal view showing the insertion of the three caudal cirri; RUINEN emphasizes the lack of transverse cirri. **l:** Nuclear apparatus of two specimens. In our opinion, RUINEN mixed at least two species (see discussion). MI – micronuclei, RE – reorganization band.

Fig. 166n. *Cladotricha koltzowii*, ventral view after protargol impregnation, length 90 µm (from BORROR & EVANS 1979).

Fig. 166o–s. *Cladotricha variabilis*, morphostatic (o) and dividing (p–s) specimens, scale bar 20 µm (from BORROR & EVANS 1979). Note lack of transverse cirri and the different terminology.

each composed of a single row of cilia; paroral cilia gradually increase in length from about 2 µm anteriorly to 5 µm posteriorly; endoral cilia extend into pharynx supported by fibres of ordinary length and direction (Fig. 166a, b, e, 167a; 398a–d, f, g, j; Table 147).

Two rows of loosely spaced dorsal bristles (Fig. 166d, f, 167n; 398e; Table 147). Left row usually composed of a single anterior bristle at level of proximal end of adoral zone and one, rarely two bristles close to left caudal cirrus; rarely an additional bristle occurs in mid-body. Right row composed of an average of seven bristles forming sigmoidal row in body midline, one or two bristles close to right caudal cirrus, one to three anterior bristles more or less distinctly dislocated, seemingly forming third kinety along anterior portion of right marginal row (see ontogenesis).

Table 147. Morphometric data on *Apourosomoida halophila*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	70.9	65.0	17.8	3.9	25.1	52.0	118.0	21
Body, width	20.7	20.0	2.9	0.6	13.8	15.0	25.0	21
Body length:width, ratio	3.4	3.3	0.7	0.1	20.1	2.4	5.1	21
Anterior body end to proximal end of adoral zone, distance	18.3	18.0	1.4	0.3	7.4	15.0	20.0	21
Body length:length of adoral zone, ratio	3.8	3.6	0.8	0.2	21.4	2.9	5.9	21
Anterior body end to paroral membrane, distance	6.2	6.0	1.2	0.3	19.7	3.0	8.0	21
Paroral membrane, length	4.3	4.0	0.7	0.2	17.3	3.0	6.0	21
Anterior body end to endoral membrane, distance	8.6	8.5	1.4	0.3	16.7	5.0	10.5	21
Endoral membrane, length	6.7	7.0	0.8	0.2	11.7	5.0	8.0	21
Anterior body end to buccal cirrus, distance	6.2	6.0	1.1	0.3	18.4	3.0	8.0	21
Anterior body end to last frontoventral cirrus, distance	10.3	10.0	1.3	0.3	12.4	7.0	13.0	21
Anterior body end to postoral cirral row, distance	19.1	19.0	1.7	0.4	8.9	16.0	22.0	21
Anterior body end to end of postoral cirral row, distance	29.1	29.0	3.6	0.8	12.4	22.0	36.0	21
Anterior body end to right marginal row, distance	4.1	4.0	1.0	0.2	25.3	2.0	6.0	21
Posterior body end to right marginal row, distance	7.4	8.0	2.4	0.5	32.3	4.0	13.0	21
Posterior body end to left marginal row, distance	0.2	0.0	–	–	–	0.0	2.0	21
Posterior body end to transverse cirrus, distance	0.9	1.0	–	–	–	0.0	2.0	21
Anterior body end to first macronuclear nodule, distance	17.6	17.0	3.3	0.7	18.7	12.0	27.0	21
Nuclear figure, length	35.8	33.0	12.6	2.8	35.4	20.0	68.0	21
Macronuclear nodules, distance in between	2.0	2.0	1.7	0.4	83.7	0.0	5.0	21
Anterior macronuclear nodule, length	16.6	16.0	5.0	1.1	30.4	10.0	29.0	21
Anterior macronuclear nodule, width	5.0	5.0	0.8	0.2	15.5	4.0	6.0	21
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Micronuclei, length	3.3	3.0	0.6	0.1	18.9	2.0	4.5	21
Micronuclei, width	2.1	2.0	0.5	0.1	24.5	1.0	3.0	21
Micronuclei, number	0.8	1.0	–	–	–	0.0	2.0	21
Frontal adoral membranelles, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Ventral adoral membranelles, number	14.1	14.0	0.7	0.2	4.8	12.0	15.0	21
Adoral membranelles, total number	17.1	17.0	0.7	0.2	3.9	15.0	18.0	21
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Frontoventral cirri, number	4.3	4.0	0.6	0.1	15.0	3.0	6.0	21
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Postoral cirri, number	4.9	5.0	1.0	0.2	19.8	3.0	6.0	21
Transverse cirri, number [c]	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Caudal cirri, number [d]	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Right marginal cirri, number	19.9	20.0	1.9	0.4	9.5	16.0	25.0	21
Left marginal cirri, number	17.7	18.0	1.7	0.4	9.7	15.0	22.0	21
Dorsal kineties, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Dorsal kinety 1, number of bristles	2.1	2.0	–	–	–	2.0	3.0	21
Dorsal kinety 2, number of bristles	6.5	7.0	0.9	0.2	14.3	5.0	8.0	21
Dorsal kinety "3", number of bristles [b]	1.6	1.0	0.7	0.2	46.7	1.0	3.0	21
Dorsal kineties 2 + "3", number of bristles	8.1	8.0	1.3	0.3	15.8	6.0	10.0	21
Dorsal kinety 1, number of bristles in proter dividers	4.3	4.0	0.7	0.1	15.3	4.0	6.0	21
Dorsal kinety 2, number of bristles in proter dividers	10.3	10.0	0.8	0.2	8.2	8.0	12.0	21

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Kinety "3" is a slightly set off part of kinety 2 (see description).

[c] Rarely specimens with two transverse cirri occur.

[d] Rarely specimens with only one caudal cirrus occur.

Ontogenesis: The genesis of the infraciliature basically occurs as in oxytrichid hypotrichs (for a review, see BERGER 1999). Accordingly, it will be described briefly, emphasizing new, apomorphic features. Likewise, nuclear and cell division occur in the ordinary manner. All parental cirri and dorsal bristles not involved in anlagen formation are resorbed in late dividers and post-dividers. The parental buccal field and undulating membranes are completely reorganized, while the adoral zone is only partially renewed, that is, the short (leftmost) ciliary row of the membranelles disappears for a short period in late dividers (Fig. 167i).

Division commences with the formation of an oral primordium along the postoral cirral row, which is soon incorporated into the growing, obtriangular primordium, producing adoral membranelles very early (Fig. 167b, c). Some scattered dikinetids remain at the anterior margin of the growing membranellar ribbon and organize to long cirral streaks (primary primordia) extending into the parental frontal field. Concomitantly, cirrus III/2 and the buccal cirrus modify to anlagen proliferating basal bodies posteriorly; eventually, streak III/2 touches opisthe's anlage III. Thus, three long cirral anlagen streaks, so-called primary primordia, are recognizable in early dividers (Fig. 167c, d; 398h). Next the primary primordia divide transversely, providing each proter and opisthe with three anlagen (Fig. 167e). Five cirral anlagen streaks are recognizable in early-middle dividers (Fig. 167e, f; 398i). The proter anlagen originate as follows: anlage I is produced by the reorganizing undulating membranes; anlage II originates from the buccal cirrus; anlage III from cirrus III/2 and opisthe anlage III; and the anlagen IV and V originate from primary primordia generated by the opisthe. All opisthe anlagen originate from the oral primordium, which incorporates the postoral cirral row.

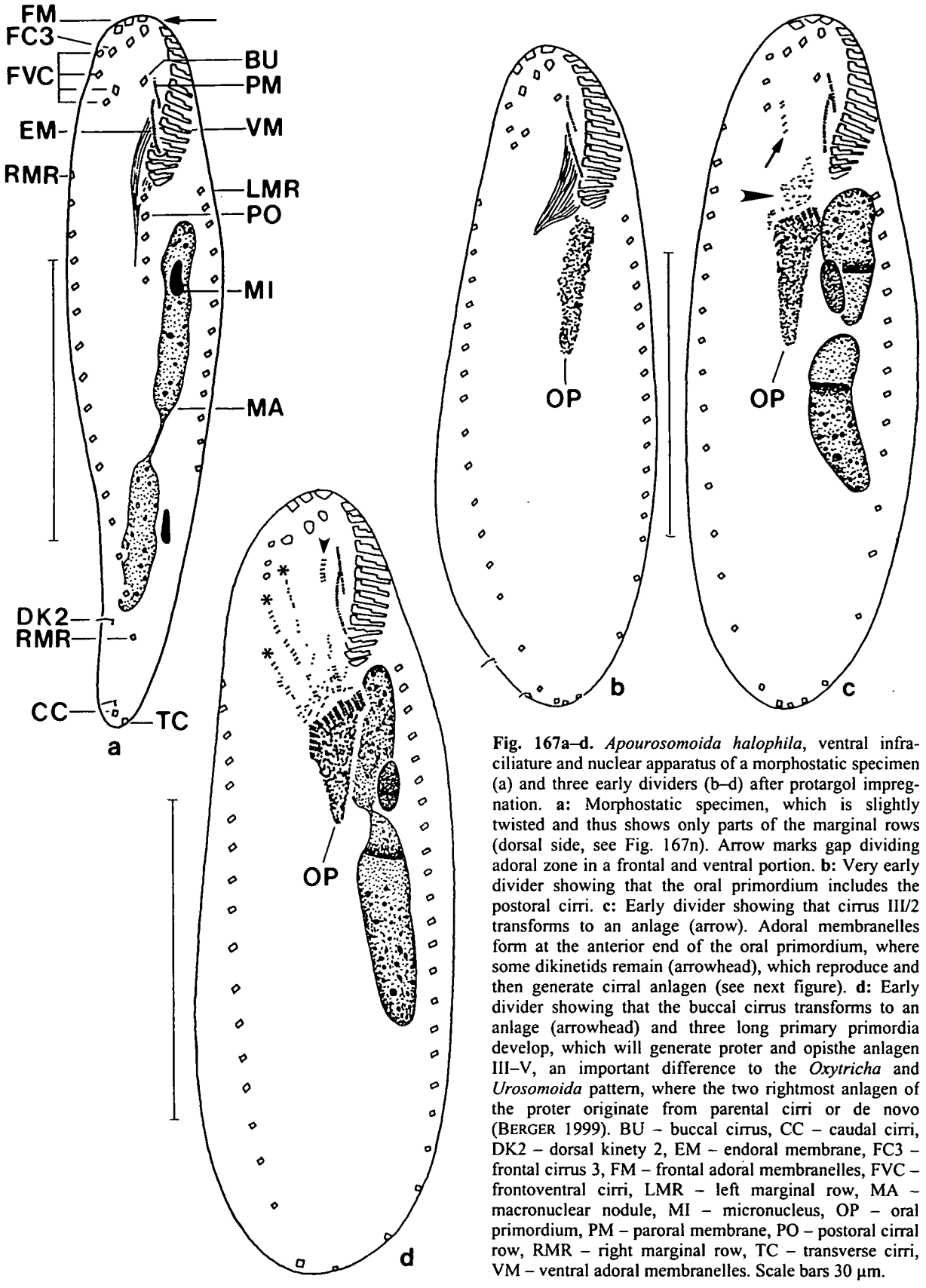


Fig. 167a–d. *Apourosomoida halophila*, ventral infraciliature and nuclear apparatus of a morphostatic specimen (a) and three early dividers (b–d) after protargol impregnation. **a:** Morphostatic specimen, which is slightly twisted and thus shows only parts of the marginal rows (dorsal side, see Fig. 167n). Arrow marks gap dividing adoral zone in a frontal and ventral portion. **b:** Very early divider showing that the oral primordium includes the postoral cirri. **c:** Early divider showing that cirrus III/2 transforms to an anlage (arrow). Adoral membranelles form at the anterior end of the oral primordium, where some dikinetids remain (arrowhead), which reproduce and then generate cirral anlagen (see next figure). **d:** Early divider showing that the buccal cirrus transforms to an anlage (arrowhead) and three long primary primordia develop, which will generate proter and opisthe anlagen III–V, an important difference to the *Oxytricha* and *Urosomoida* pattern, where the two rightmost anlagen of the proter originate from parental cirri or de novo (BERGER 1999). BU – buccal cirrus, CC – caudal cirri, DK2 – dorsal kinety 2, EM – endoral membrane, FC3 – frontal cirrus 3, FM – frontal adoral membranelles, FVC – frontoventral cirri, LMR – left marginal row, MA – macronuclear nodule, MI – micronucleus, OP – oral primordium, PM – paroral membrane, PO – postoral cirral row, RMR – right marginal row, TC – transverse cirri, VM – ventral adoral membranelles. Scale bars 30 µm.

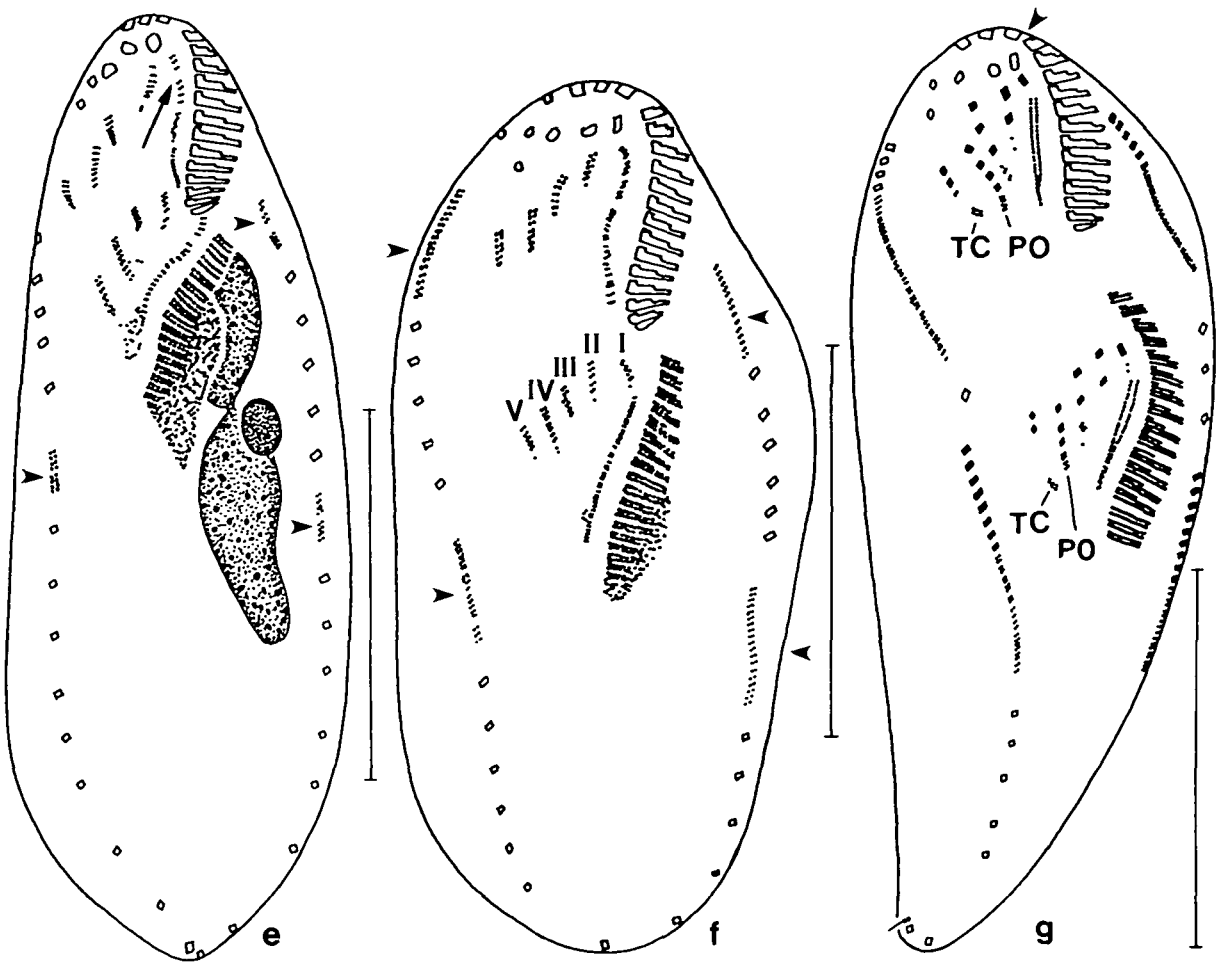


Fig. 167e–g. *Apourosomoida halophila*, ventral views of dividers after protargol impregnation. Parental structures shown by contour, newly formed shaded black. **e, f:** An early-middle and middle divider showing that the parental undulating membranes disorganize and form cirral anlage I (arrow). The three primary primordia (cp. figure 167d) split transversely. Thus, five cirral anlagen streaks (I–IV) are now recognizable both in proter and opisthe; in contrast, most oxytrichids have six streaks (BERGER 1999), but see several other oxytrichid genera described in this book, which also have only five anlagen streaks. Arrowheads mark marginal anlagen, which develop as is usual. **g:** A middle-late divider showing cirral segregation within the anlagen as well as beginning migration of the single transverse cirrus and anlage IV, which will form the postoral cirral row. The oral structures of the opisthe are almost finished. Note that the gap between frontal and ventral adoral membranelles disappeared (arrowhead). PO – migrating postoral cirral row (= anlage IV), TC – migrating transverse cirrus. Scale bars 30 μm.

Cirral segregation occurs in middle dividers and usually produces some supernumerary cirri, which are later resorbed, as in most oxytrichids. Cirral migration commences in middle-late dividers, while the final positioning occurs in early and late post-dividers. The entire anlage IV migrates to the buccal vertex, where it becomes the "postoral cirral row", while the last cirrus (rarely the last two cirri) of anlage V migrates to the rear to become the transverse cirrus (Fig. 167g–m).

Dorsal ontogenesis commences when the long primary primordia has been formed, that is, in early dividers. The anterior bristle of row 1 produces an anlage in the proter. The second, third, and likely the forth bristle of row 2 generate an anlage each in proter and opisthe (Fig. 167n–p).

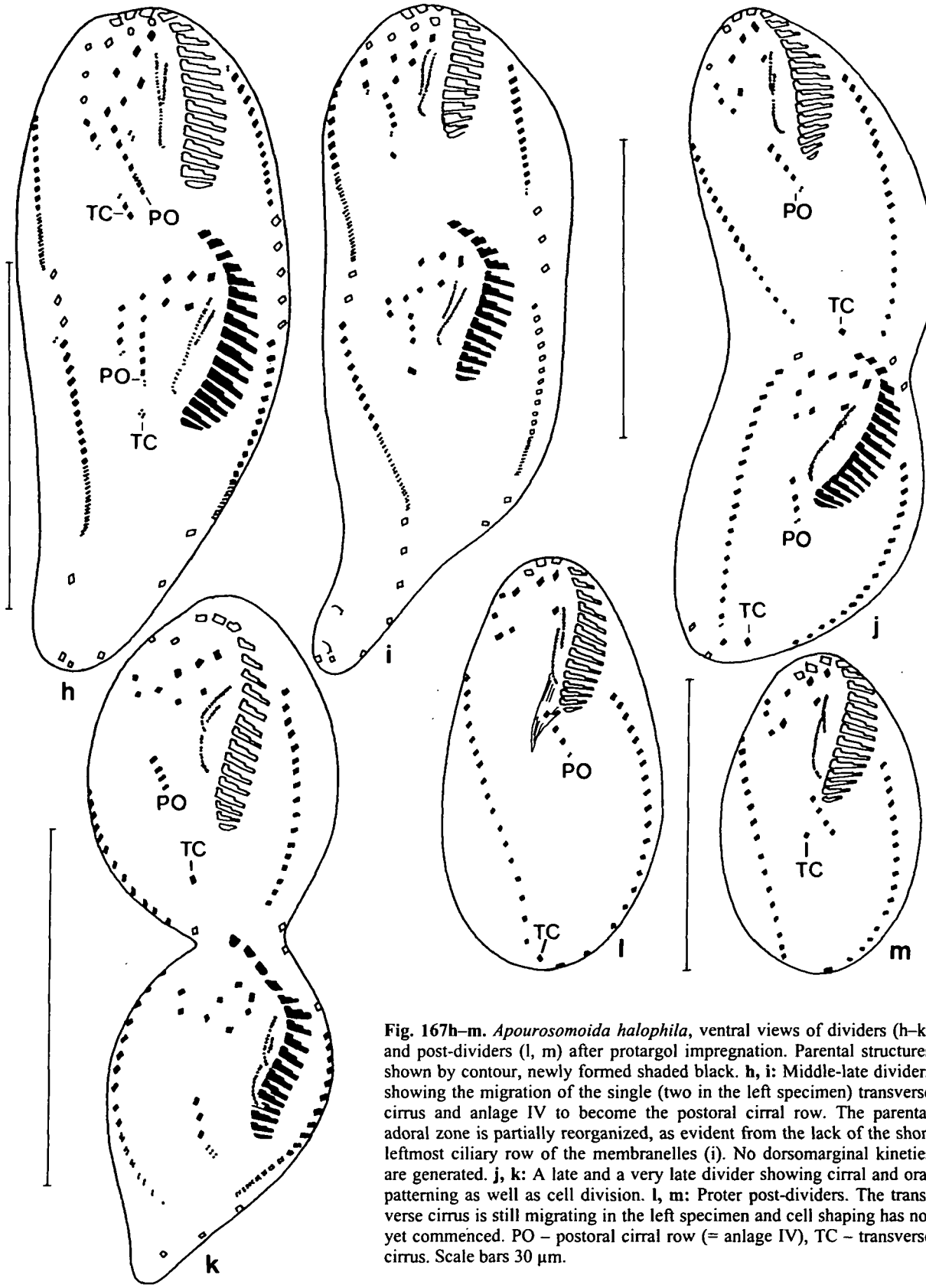


Fig. 167h–m. *Apourosomoida halophila*, ventral views of dividers (h–k) and post-dividers (l, m) after protargol impregnation. Parental structures shown by contour, newly formed shaded black. **h, i:** Middle-late dividers showing the migration of the single (two in the left specimen) transverse cirrus and anlage IV to become the postoral cirral row. The parental adoral zone is partially reorganized, as evident from the lack of the short leftmost ciliary row of the membranelles (i). No dorsomarginal kineties are generated. **j, k:** A late and a very late divider showing cirral and oral patterning as well as cell division. **l, m:** Proter post-dividers. The transverse cirrus is still migrating in the left specimen and cell shaping has not yet commenced. PO – postoral cirral row (= anlage IV), TC – transverse cirrus. Scale bars 30 µm.

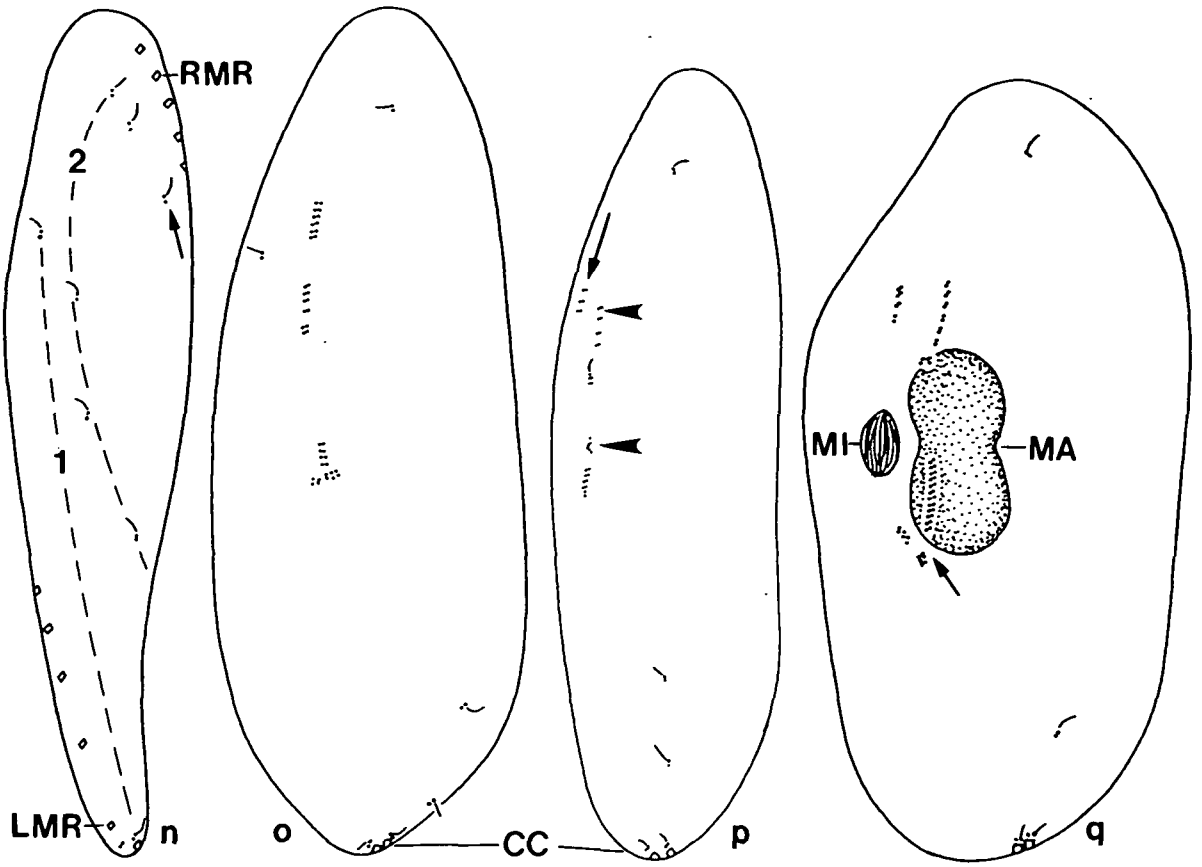
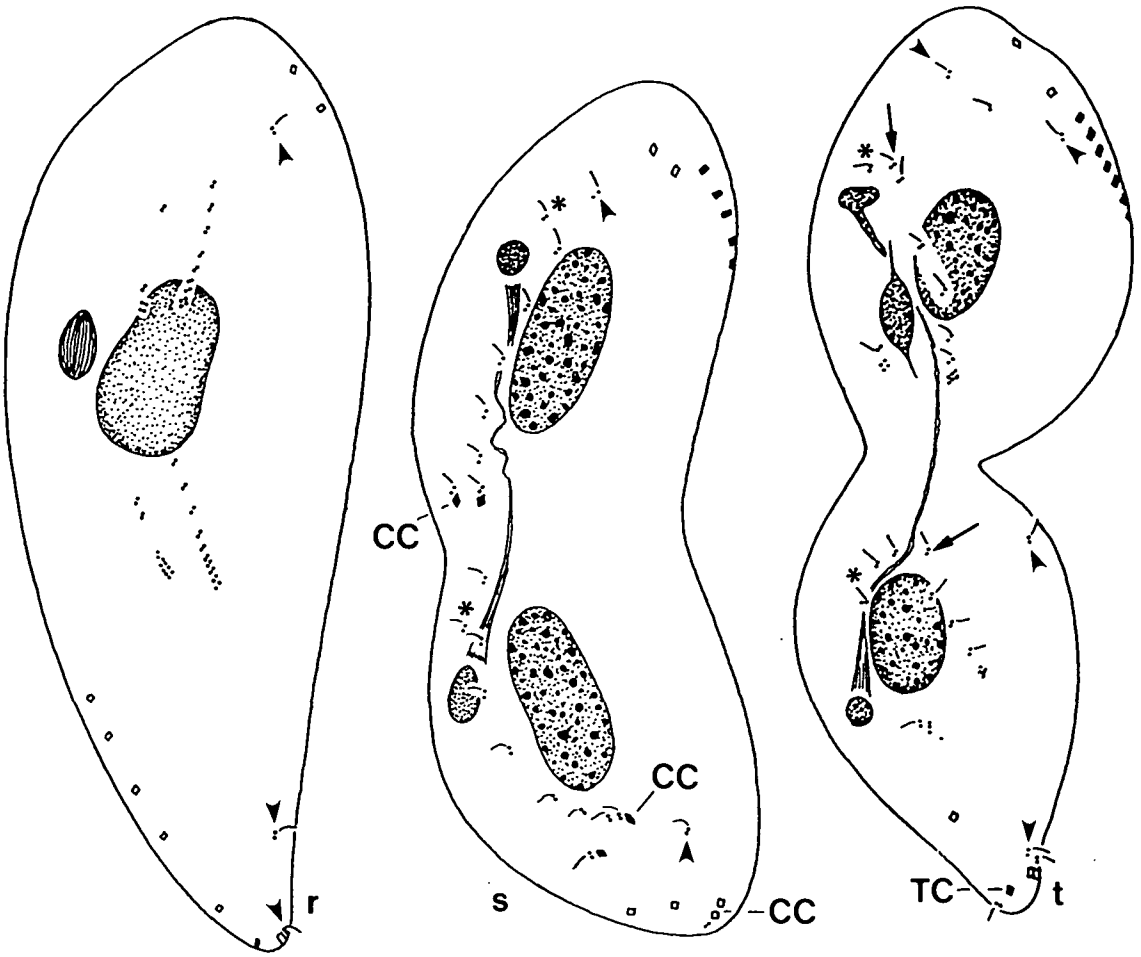


Fig. 167n–q. *Apourosomoida halophila*, dorsal views of a morphostatic specimen (n) and three dividers (o–q) after protargol impregnation. Corresponding ventral views, see figures 167a, e, none, f; length 76 µm, 78 µm, 83 µm, 68 µm, **n:** Dorsal kinety 1 consists of two bristles only, one in anterior body half and another close to the left caudal cirrus. Dorsal kinety 2 is composed of an average of seven bristles, of which one to three anterior bristles are more or less distinctly dislocated to the right, seemingly forming a third dorsal kinety along the anterior portion of the right marginal row (arrow); see also figures 166d, f. **o, p:** Early dividers showing that the anterior bristle of row 1 forms an anlage (arrow), while two anlagen are generated in kinety 2 (arrowheads), one for the proter and another for the opisthe. **q:** A middle divider showing that the new opisthe kinety 1 is generated by fragmentation and migration to the left of the anlage in kinety 2 (arrow). This unique mode is the main generic feature. The macronuclear nodules fuse and the micronucleus commences division. CC – caudal cirri, LMR – left marginal row, MA – macronucleus, MI – micronucleus, RMR – right marginal row.

While growing, the posterior portion of the opisthe anlage splits off and migrates left to become dorsal kinety 1 of the opisthe, an extraordinary process and the main generic feature. Thus, two dorsal anlagen each in proter and opisthe are recognizable in middle dividers (Fig. 167q, r). In late and very late dividers, when a caudal cirrus each has been formed at the posterior end of the anlagen and cell furrowing is in progress, one to three bristles at the anterior end of row 2 migrate more or less distinctly rightward (or are possibly displaced by cell shaping), producing a third row of dorsal bristles in the right anterior quadrant of the cell. We carefully checked that this row does not originate dorsomarginally, as in many oxytrichids; actually, it is the anterior part of row 2, as evident from bristle counts in interphase specimens and proter dividers (Fig. 167s–v; Table 147).



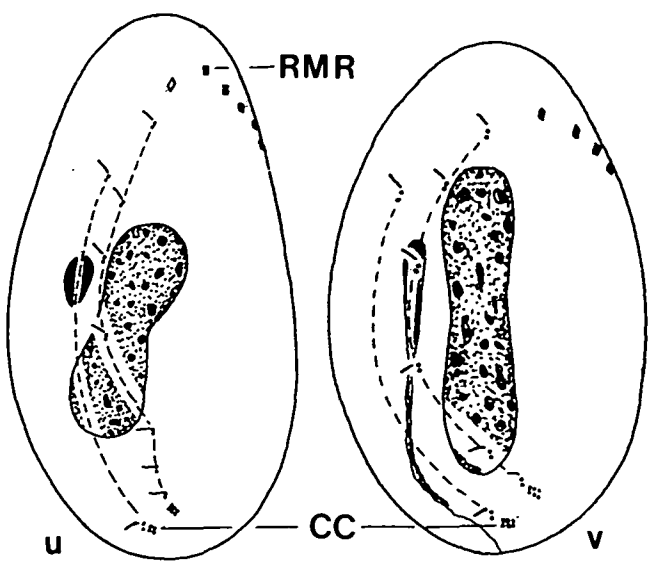


Fig. 167r–v. *Apourosomoida halophila*, dorsal views of dividers (r–t) and post-dividers (u, v) after protargol impregnation. Corresponding ventral views, see figures 167q, j, k, l, m; length 74 µm, 68 µm, 58 µm, 42 µm, 33 µm. Parental structures shown by contour, newly formed shaded black. **r–t:** A middle, late, and very late divider showing patterning of dorsal kineties and production of a caudal cirrus each at the posterior end. Arrowheads mark parental bristles; arrows denote more or less distinctly dislocated bristles at anterior end of row 2; asterisks mark anterior bristle of row 1. **u, v:** Proter post-dividers showing the two new rows of dorsal bristles and the dividing macronucleus. CC – caudal cirri, RMR – right marginal row, TC – transverse cirrus.

Occurrence and ecology: Rare at site (61), that is, in a highly saline soil from the margin of the Etosha Pan. Fortunately, an abundant population developed in a sample collected in 2001 in the area where the Unjab river crosses the main road to the village of Terrace Bay, about 150 m NE of the road. Here, the river bed is a swampy area grown with grasses, *Cyperus*, *Phragmites*, and shrubs. Up to 1 m high sand hills accumulate around the grass *Odyssea paucinervis* (brakweed). The sample was taken from such a sand hill, which contained so much organic debris that the sand was dark in colour. In the laboratory, no ciliates developed within three days because the sample had a salinity of 180‰. Thus, we washed it three times with tap water, decreasing salinity to 150‰. After a few days, *Apourosomoida halophila* appeared and reproduced rapidly. With time, the ciliate could be adapted to ordinary sea water (35‰), but did not grow as well as between 100‰ and 150‰, indicating that it prefers very high salinities.

Comparison with related species: *Apourosomoida halophila* has a clear identity due to the postoral cirral row. There are only two species with the same feature, viz., *Cladotricha variabilis* RUINEN, 1938 and *Uroleptus natronophilus* DIETZ, 1965. The specimen shown by RUINEN in figure 8c (here reproduced as Fig. 166j) highly resembles *A. halophila*, but lacks the single transverse cirrus so typical for that species. However, RUINEN might have mixed transverse and caudal cirri (Fig. 166j, k). On the other hand, BORROR & EVANS (1979), who reinvestigated a very similar species, confirmed the absence of transverse cirri by ontogenetic data (Fig. 166n, o). Later, this was sustained by an ontogenetic study of *Cladotricha halophila* WILBERT, 1995. Thus, the Namibian population cannot be conspecific with the Australian *C. variabilis*. Furthermore, RUINEN (1938) likely mixed at least two species, as indicated by the different nuclear and postoral cirral pattern (Fig. 166g–m). We fix the unnumbered, leftmost specimen shown in RUINEN's figure 8 as type of *Cladotricha variabilis* (here reproduced as Fig. 166g). It differs from *Apourosomoida halophila* by the number of macronuclear nodules (four vs. two) and a second, short row of postoral cirri. *Cladotricha variabilis* redescribed by BORROR & EVANS (1979) from New Hampshire, USA, has only two macronuclear nodules and many more frontoventral cirri, suggesting that it is another, new species (Fig. 166o, p).

Uroleptus natronophilus DIETZ, 1965 has a similar cirral pattern as *A. halophila*, but is only 35-50 x 9-11 µm in size and has a conspicuous, sail-like undulating membrane. Further, the macronuclear nodules are small and close together in the left anterior half of the cell. Likely, it lacks a buccal cirrus.

Urosomoida reticulata nov. spec. (Fig. 168a–e, i–l; 381m–o; Tables 148, 149)

Diagnosis: Size about 140 × 40 µm in vivo; elongate ellipsoidal to oblanceolate. 2 macronuclear nodules with a micronucleus each. On average 37 adoral membranelles, 29 right marginal cirri, 25 left marginal cirri, 3 postoral cirri, 3 pretransverse and transverse cirri, and 2 caudal cirri. Buccal cavity deep and of usual width; paroral commences close to left frontal cirrus.

Type location: Litter of *Combretum imberbe* (leadwood tree) at foot of the Brandberg, an island mountain at the east margin of the central Namib Desert, Namibia, 21°S 14°35'E (site 48 in figure 2 and chapter 2.1.2).

Etymology: Composite of the Latin noun *reticulum* (small web), the suffix *-at*, and the inflectional ending *-a*, referring to the web-like, cortical pattern usually present.

Description of type population: Three populations were studied, namely from Namibian site (48; type population), from Costa Rica, and from Venezuela (only in vivo). They agree very well in the main features so that conspecificity is beyond reasonable doubt. However, data are kept separate and the diagnosis and description contain only the type population because some features indicate that the South American populations might be a distinct subspecies.

Size 110–200 × 35–60 µm in vivo, usually about 140 × 40 µm, average length:width ratio 3.4:1 both in vivo and in protargol preparations (Table 148), only slightly flattened dorsoventrally, ventral side flat, dorsal often distinctly vaulted in mid-body. Shape highly variable, that is, elongate ellipsoidal to oblanceolate and sigmoidal due to the gradually narrowed and curved posterior body portion; about 20% of specimens with prominent and about 40% with moderately distinct furrow along dorsal kinety 4 (Fig. 168a–c); body acontractile but very flexible. Macronuclear nodules in middle third of body left of midline, each nodule with small to medium-sized nucleoli, and, on average, two micronuclei attached at various positions; anterior nodule invariably shorter but wider than posterior (Table 148), usually ellipsoidal (2:1); posterior nodule on average elongate ellipsoidal (3:1). Contractile vacuole slightly above mid-body at left cell margin. Cortex with web-like pattern produced by many bright, about 0.5 µm-sized globules arranged in single, paired, or rarely triplicate short rows; web nodes frequently contain an about 1 µm-sized crystal sparkling under interference contrast illumination. Larger, 2–4 µm-sized crystals of ordinary shape scattered underneath cortex and, more rarely, in cytoplasm (Fig. 168c; 381m–o). Globule and crystal pattern pronounced only in cells from well-growing cultures, while almost lacking in young, just excysted specimens. Cytoplasm colourless, often packed with fat globules 2–4 µm across and some crystals as described above. Feeds on fungal spores (*Fusarium*), testate amoebae (*Euglypha* sp.), and ciliates (*Gonostomum* sp.) digested in 15–40 µm sized vacuoles. Moves moderately fast, sometimes jerkily on microscope slide and between soil particles, showing great flexibility.

Cirral pattern and number rather constant, except for postoral cirri, which vary from two to four (Fig. 168d; Table 148). Marginal cirri about 15 µm long in vivo, right row commences at level of frontoventral cirri and terminates, like left row, at rear end, leaving blank small area occupied by caudal cirri on dorsal side. Frontal cirri distinctly enlarged. Buccal cirrus on average 5 µm (range 2–7 µm) behind anterior end of paroral. Frontoventral cirri in hook-shaped pattern. Postoral cirri rather close to buccal vertex. Near posterior end usually one, rarely two pretransverse cirri ahead of two slightly enlarged, about 23 µm long transverse cirri.

Dorsal bristles 3–4 µm long in vivo, arranged in four rows, as in most congeners (Fig. 168e; Table 148). Row 1 distinctly shortened anteriorly; rows 2 and 3 bipolar; row 4 extends beside a distinct furrow and terminates near mid-body. Usually one about 23 µm long and thus prominent caudal cirrus at end of dorsal kineties 1 and 2; rarely two cirri attached to kinety 1 and one to kinety 2.

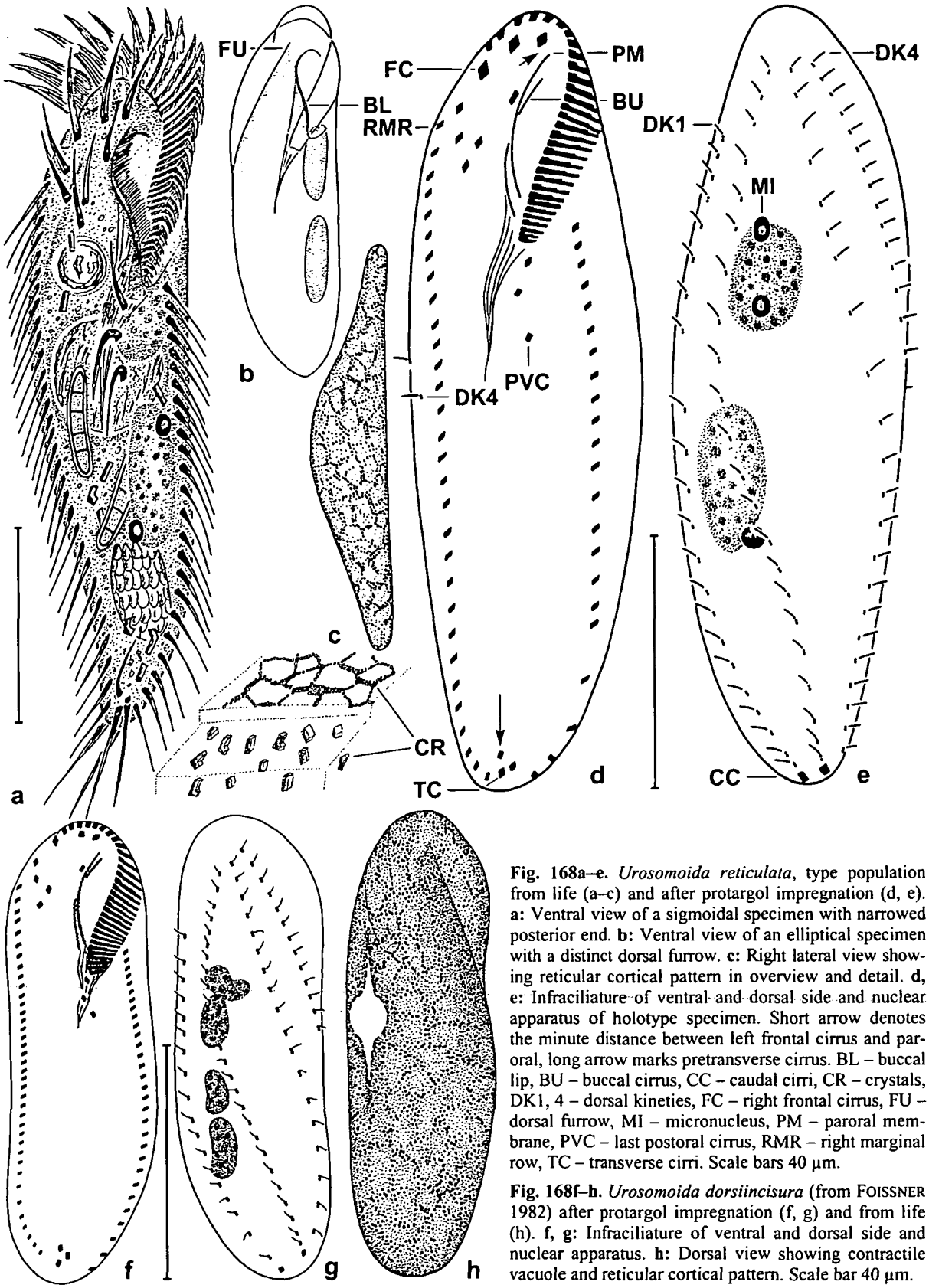


Fig. 168a–e. *Urosomoida reticulata*, type population from life (a–c) and after protargol impregnation (d, e). **a:** Ventral view of a sigmoidal specimen with narrowed posterior end. **b:** Ventral view of an elliptical specimen with a distinct dorsal furrow. **c:** Right lateral view showing reticular cortical pattern in overview and detail. **d, e:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Short arrow denotes the minute distance between left frontal cirrus and paroral, long arrow marks pretransverse cirrus. BL – buccal lip, BU – buccal cirrus, CC – caudal cirri, CR – crystals, DK1, 4 – dorsal kineties, FC – right frontal cirrus, FU – dorsal furrow, MI – micronucleus, PM – paroral membrane, PVC – last postoral cirrus, RMR – right marginal row, TC – transverse cirri. Scale bars 40 µm.

Fig. 168f–h. *Urosomoida dorsiincisura* (from FOISSNER 1982) after protargol impregnation (f, g) and from life (h). **f, g:** Infraciliature of ventral and dorsal side and nuclear apparatus. **h:** Dorsal view showing contractile vacuole and reticular cortical pattern. Scale bar 40 µm.

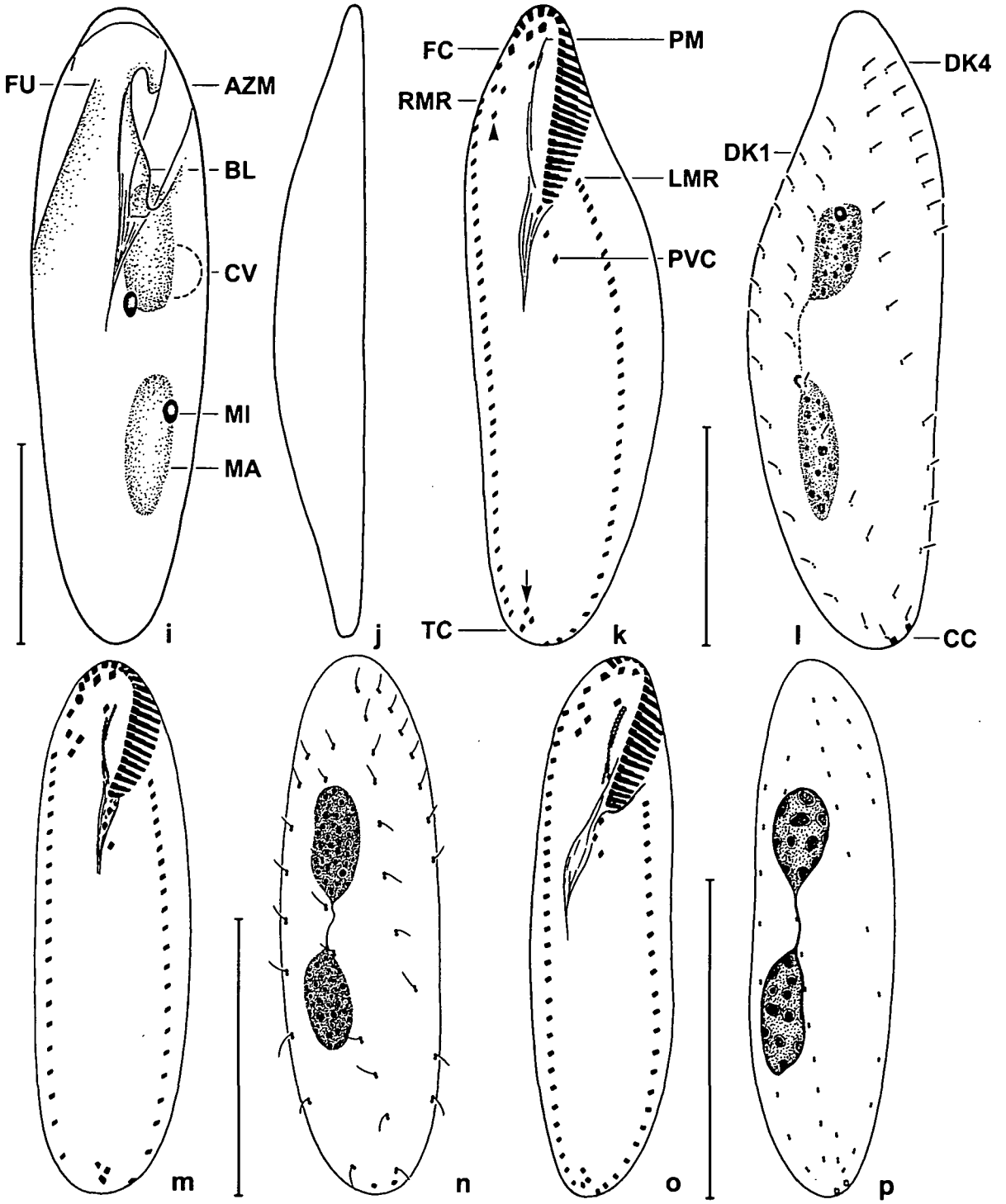


Fig. 168i–p. *Urosomoida reticulata* (i–l, Costa Rican population) and *U. agiliformis* (m–p; from FOISSNER 1982 and FOISSNER & ADAM 1983a) from life (i, j) and after protargol impregnation (k–p). **i, j:** Ventral and lateral view. **k–p:** Infraciliature of ventral and dorsal side. Arrowhead in (k) marks last frontoventral cirrus, arrow denotes pretransverse cirrus. Note the very similar dorsal ciliary pattern in the Costa Rican *U. reticulata* and the European *U. agiliformis* populations. AZM – adoral zone of membranelles, BL – buccal lip, CC – caudal cirri, CV – contractile vacuole, DK1, 4 – dorsal kineties, FC – right frontal cirrus, FU – dorsal furrow, LMR – left marginal row, MA – macronuclear nodule, MI – micronucleus, PM – paroral membrane, PVC – last postoral cirrus, RMR – right marginal row, TC – transverse cirri. Scale bars 40 µm.

Adoral zone occupies 26–38%, usually 33% of body length, composed of an average of 37 membranelles of ordinary shape and structure (Fig. 168a, d; Table 148); bases of largest membranelles about 10 µm wide in vivo, in the largest specimens up to 15 µm. Buccal cavity deep but rather narrow, anterior margin semicircular as in *Cyrtohymena*, right (buccal lip) conspicuously curved bearing paroral in distinct slit and covering proximal portion of adoral zone. Undulating membranes in *Oxytricha* pattern, that is, distinctly curved and optically intersecting slightly behind buccal cirrus; paroral uniquely commencing close to left frontal cirrus, likely composed of zigzagging, about 10 µm long cilia; endoral cilia about 15 µm long. Pharyngeal fibres clearly recognizable in vivo and after protargol impregnation, extend obliquely backwards.

Observations on other populations: We found *Urosomoida reticulata* also in Costa Rica and Venezuela. A detailed morphometric analysis of the Costa Rican population revealed some conspicuous differences to the type population, indicating subspecies status. However, at the present state of knowledge it seems more appropriate to describe them as populations (Fig. 168i–l; Table 148): Size 110–150 × 25–45 µm, usually around 130 × 35 µm in vivo; no reticulate cortical pattern, but this feature was probably not recognized or weakly developed, as described in the Venezuelan population; on average two micronuclei, usually one attached to each macronuclear nodule in various positions. Feeds on bacteria up to 15 µm long and heterotrophic flagellates. Number of buccal cirri, frontoventral, and postoral cirri rather variable. Buccal cirrus on average 2 µm (range 0–6 µm) behind anterior end of paroral; a quarter of the specimens analyzed has a second buccal cirrus at 13% of body length. Dorsal kinety 2 distinctly shortened anteriorly, kinety 4 terminates at 37% of body length on average. Adoral zone of membranelles occupies 22–36%, on average 29% of body length, bases of largest membranelles about 7 µm wide in vivo.

Venezuelan population (only data from life): Size 135 × 45 µm (n = 8, range 120–160 × 35–60 µm); specimens analyzed three days after rewetting the sample without reticular cortical pattern; however, after a week, when many specimens were present, all had the same cortical pattern as described in the type population. Also in the Venezuelan specimens it is highly conspicuous that the paroral almost touches the first frontal cirrus.

Occurrence and ecology: In Africa as yet found only at type location, where it became abundant three weeks after rewetting the sample. The Costa Rican population occurred in a mud sample (pH 3.9) from the tanks of bromelias at the bank of the Rio Sarapiquí, Selva Verde National Park, 10°28'N 84°W. The Venezuelan population was found in a slightly saline (10 ‰) soil taken near the coastal village of Choroni in the Henry Pittier National Park. These data indicate that *U. reticulata* has a broad ecological range and an at least Gondwanan distribution.

Generic classification and comparison with related species: This oxytrichid ciliate is unusual because it has a reduced number of cirri, in spite of its considerable size and deep, *Cyrtohymena*-like buccal cavity. However, the hook-like arranged frontoventral cirri, the reduced number of pretransverse, transverse (three instead of seven) and caudal cirri (two instead of three), the four dorsal kineties, and the undulating membranes in *Oxytricha* pattern classify it unequivocally in *Urosomoida* HEMBERGER in FOISSNER, 1982.

However, the most outstanding feature of *U. reticulata* is the paroral membrane which extends almost to the left frontal cirrus (Fig. 168d, k), similarly as in *Tachysoma pellionellum* sensu PÄTSCH (1974; possibly a preparation artifact) and the **quadrinucleate** *Urosomoida*

dorsiincisura FOISSNER, 1982 (Fig. 168f–h). The latter species has not only this feature in common with *U. reticulata*, but also the reticular cortical pattern (Fig. 168c, h) and, only with the Namibian population, the specific dorsal infraciliature (Fig. 168e, g): both have an anteriorly unshortened dorsal kinety 2, a long (about 50% of body length) kinety 4, and a rather high number of bristles within each row. By contrast, the dorsal ciliary pattern of the Costa Rican specimens agrees with that of *Urosomoida agiliformis* FOISSNER, 1982 (cp. figure 168 l with figures 168n, p) in that kinety 2 is distinctly shortened anteriorly, kinety 4 is rather short (< 40% of body length), and the bristles within each row are widely spaced. However, *Urosomoida agiliformis* differs from all populations of *U. reticulata* in size (length below 100 µm vs. above 100 µm), distance between left frontal cirrus and paroral (large vs. small), shape of buccal cavity (flat vs. *Cyrtohymena*-like), location of buccal cirrus (at anterior end of paroral vs. distinctly behind), and some main morphometrics (Table 149). In vivo, *Urosomoida reticulata* is easily confused with certain *Oxytricha*, *Notohymena*, and *Cyrtohymena* species (usually five transverse and two pretransverse cirri; for a review, see BERGER 1999).

We exclude that the Namibian population is composed mainly of macrostome individuals of *Urosomoida* spp. because the relative length of the adoral zone of membranelles (33%) is very near to that found in *U. dorsiincisura* (31%) and of flexible oxytrichids in general (< 40%). In vivo, *Urosomoida reticulata* is recognizable by the considerable size (> 100 µm), the *Cyrtohymena*-like buccal cavity, the paroral membrane extending to the first frontal cirrus, the reduced number of pretransverse and transverse cirri, the two macronuclear nodules, and the reticulate cortical crystal pattern.

Table 148. Morphometric data on *Urosomoida reticulata* from Costa Rica (upper line) and Namibian type location (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length in vivo	–	–	–	–	–	120.0	130.0	2
	141.5	132.5	27.1	8.6	19.1	110.0	200.0	10
Body, width in vivo	–	–	–	–	–	40.0	50.0	2
	42.0	40.0	11.6	3.7	27.6	25.0	60.0	10
Body, length	118.1	117.0	9.9	2.5	8.4	106.0	142.0	16
	125.9	124.0	12.6	3.1	10.0	108.0	156.0	17
Body, width	32.9	33.0	5.3	1.3	16.0	22.0	46.0	16
	38.9	39.0	5.4	1.3	13.9	28.0	49.0	17
Body length:width, ratio	3.6	3.6	0.4	0.1	11.5	3.1	4.9	16
	3.3	3.3	0.3	0.1	10.0	2.6	4.0	17
Anterior body end to proximal end of adoral zone,	34.7	33.5	5.4	1.4	15.6	28.0	50.0	16
distance	41.4	41.0	4.5	1.1	10.9	34.0	50.0	17
Body length:length of adoral zone, ratio	3.5	3.4	0.4	0.1	10.9	2.8	4.4	16
	3.1	3.0	0.3	0.1	9.8	2.7	3.8	17
Anterior body end to first frontoventral cirrus, distance	9.6	10.0	1.6	0.4	16.5	6.0	12.0	16
	12.1	12.0	1.7	0.4	13.6	9.0	14.0	17
Anterior body end to last frontoventral cirrus, distance	19.6	19.5	3.0	0.7	15.1	14.0	25.0	16
	25.0	25.0	2.2	0.5	8.6	22.0	29.0	17
Anterior body end to buccal cirrus, distance	8.6	9.0	1.4	0.3	15.8	7.0	12.0	16

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	11.2	12.0	1.2	0.3	11.1	9.0	13.0	17
Anterior body end to right marginal row, distance	15.9	16.0	3.4	0.9	21.7	11.0	23.0	16
	18.9	18.0	3.6	0.9	18.8	14.0	28.0	17
Anterior body end to first postoral cirrus, distance	34.1	33.0	5.3	1.3	15.4	28.0	48.0	16
	43.0	43.0	5.0	1.2	11.7	36.0	56.0	17
Anterior body end to last postoral cirrus, distance	45.4	44.5	8.7	2.3	19.1	34.0	69.0	14
	58.2	56.0	9.2	2.2	15.9	47.0	81.0	17
Anterior body end to last postoral cirrus:body length,	39.0	38.0	5.0	1.0	14.2	29.0	49.0	14
ratio (in %)	46.0	46.0	7.0	2.0	14.4	40.0	69.0	15
Posterior body end to rear transverse cirrus, distance	2.3	2.3	1.0	0.2	43.4	1.0	5.0	16
	2.3	2.4	0.9	0.2	40.4	1.0	4.0	17
Posterior body end to anteriormost pretransverse cirrus,	6.1	6.0	1.4	0.4	23.7	3.0	9.0	16
distance	6.5	6.0	1.9	0.5	29.5	3.0	10.0	17
Posterior body end to anteriormost pretransverse cirrus:	5.0	5.0	1.0	0.0	21.6	3.0	7.0	16
body length, ratio (in %)	5.0	5.0	1.0	0.0	26.2	3.0	8.0	17
Posterior body end to right marginal row, distance	4.6	5.0	1.3	0.3	28.2	1.6	6.0	16
	2.9	2.5	2.1	0.5	73.9	0.0	7.0	16
Posterior body end to left marginal row, distance	1.7	1.5	1.2	0.3	75.0	0.0	4.0	16
	1.5	1.0	2.3	0.6	148.7	0.0	9.0	16
Anterior body end to paroral membrane, distance	6.1	6.0	0.9	0.2	14.2	4.0	7.0	13
	5.9	6.0	1.0	0.2	17.3	4.0	8.0	17
Paroral membrane, length	18.1	16.0	4.3	1.4	24.0	14.0	28.0	9
	24.9	25.5	2.0	0.6	8.1	22.0	28.0	10
Proximal margin of left (first) frontal cirrus to paroral	1.0	0.7	–	–	–	0.0	3.5	25
membrane, distance	0.8	1.0	–	–	–	0.0	2.5	25
Anterior body end to endoral membrane, distance	8.2	8.0	1.3	0.4	15.5	6.0	10.0	12
	8.2	8.0	1.1	0.3	13.9	6.0	10.0	17
Endoral membrane, length	19.9	19.5	5.5	1.7	27.6	14.0	33.0	10
	27.8	28.0	2.7	0.8	9.5	24.0	34.0	12
Anterior body end to first macronuclear nodule,	30.8	30.5	4.8	1.2	15.6	22.0	42.0	16
distance	34.8	34.0	3.7	0.9	10.7	28.0	40.0	17
Nuclear figure, length	60.2	60.5	6.3	1.6	10.5	52.0	76.0	16
	59.3	58.0	6.8	1.6	11.4	50.0	74.0	17
Nuclear figure length:body length, ratio (in %)	51.0	51.0	3.0	1.0	6.6	45.0	57.0	16
	47.0	47.0	4.0	1.0	7.8	41.0	55.0	17
Macronuclear nodules, distance in between	13.1	13.5	2.2	0.6	16.9	8.0	16.0	16
	8.4	8.0	2.9	0.7	34.9	4.0	16.0	17
Anterior macronuclear nodule, length	20.4	19.0	3.8	1.0	18.8	15.0	29.0	16
	23.0	22.0	3.0	0.7	13.1	16.0	28.0	17
Anterior macronuclear nodule, width	8.3	8.0	1.5	0.4	18.0	6.0	11.0	16
	11.6	12.0	1.9	0.5	16.0	8.0	15.0	17
Posterior macronuclear nodule, length	27.1	27.0	4.2	1.1	15.6	21.0	36.0	16
	29.1	29.0	5.6	1.4	19.2	20.0	46.0	17
Posterior macronuclear nodule, width	7.2	7.0	1.1	0.3	15.4	5.0	10.0	16
	9.9	10.0	1.6	0.4	16.1	6.0	12.0	17
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	16
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	17
Anterior micronucleus, length	2.7	3.0	–	–	–	2.0	3.0	16

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	3.4	3.0	–	–	–	2.5	5.0	17
Anterior micronucleus, width	1.7	1.5	–	–	–	1.5	2.0	16
	3.0	3.0	–	–	–	2.5	4.0	17
Micronuclei attached to anterior macronuclear nodule,	0.9	1.0	–	–	–	0.0	2.0	15
number	1.8	2.0	–	–	–	1.0	3.0	17
Micronuclei attached to posterior macronuclear nodule,	1.1	1.0	–	–	–	1.0	2.0	16
number	1.7	2.0	–	–	–	0.0	4.0	17
Micronuclei, total number	1.9	2.0	0.9	0.2	47.2	1.0	4.0	16
	3.5	4.0	1.2	0.3	33.4	2.0	6.0	17
Adoral membranelles, number	29.3	28.5	4.1	1.0	14.1	25.0	42.0	16
	36.8	37.0	5.3	1.3	14.4	28.0	46.0	17
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	16
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	17
Frontoventral cirri, number	4.0	4.0	–	–	–	3.0	5.0	16
	4.1	4.0	–	–	–	4.0	5.0	17
Buccal cirri, number	1.3	1.0	–	–	–	1.0	2.0	16
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	17
Postoral cirri, number	3.3	3.0	0.9	0.2	27.0	2.0	5.0	15
	3.0	3.0	–	–	–	2.0	4.0	17
Pretransverse cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	16
	1.2	1.0	–	–	–	1.0	2.0	17
Transverse cirri, number	2.1	2.0	–	–	–	2.0	3.0	16
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	17
Pretransverse and transverse cirri, number	3.1	3.0	–	–	–	3.0	4.0	16
	3.2	3.0	–	–	–	3.0	4.0	17
Right marginal cirri, number	34.3	34.0	3.8	1.0	11.2	31.0	46.0	16
	29.4	29.0	2.2	0.5	7.4	26.0	33.0	17
Left marginal cirri, number	32.5	32.0	4.7	1.2	14.5	23.0	42.0	16
	25.1	25.0	3.2	0.8	12.6	20.0	31.0	17
Caudal cirri, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	16
	2.1	2.0	–	–	–	2.0	3.0	17
Dorsal kineties, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	9
	4.0	4.0	0.0	0.0	0.0	4.0	4.0	15
Anterior body end to dorsal kinety 1, distance	25.4	24.5	5.1	1.8	20.0	19.0	34.0	8
	19.9	20.0	3.3	1.0	16.5	16.0	24.0	10
Anterior body end to dorsal kinety 2, distance	20.5	20.5	3.4	1.4	16.8	16.0	26.0	6
	10.4	10.0	2.0	0.7	19.2	7.0	14.0	9
Anterior body end to dorsal kinety 3, distance	8.7	8.0	3.4	1.3	39.0	6.0	16.0	7
	8.1	8.0	1.6	0.5	20.3	6.0	10.0	11
Anterior body end to dorsal kinety 4, distance	8.9	9.0	1.6	0.5	18.2	6.0	12.0	9
	10.1	9.5	2.4	0.6	23.5	7.0	14.0	14
Anterior body end to end of dorsal kinety 4, distance	45.9	40.0	13.4	4.7	29.2	33.0	69.0	8
	63.6	64.0	8.1	2.1	12.7	52.0	86.0	15
Anterior body end to end of dorsal kinety 4:body	37.0	35.0	8.0	3.0	21.0	29.0	49.0	8
length, ratio (in %)	50.0	49.0	6.0	1.0	11.0	40.0	59.0	15
Dorsal kinety 1, number of bristles	17.3	16.5	2.6	1.1	14.9	15.0	21.0	6
	26.0	26.5	4.2	1.5	16.1	20.0	32.0	8
Dorsal kinety 2, number of bristles	21.0	21.0	3.7	1.8	17.4	17.0	25.0	4

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
	24.8	26.0	3.3	1.5	13.5	19.0	27.0	5
Dorsal kinety 3, number of bristles	21.5	21.5	1.3	0.6	6.0	20.0	23.0	4
	25.6	25.0	4.4	2.0	17.2	20.0	30.0	5
Dorsal kinety 4, number of bristles	9.0	8.5	2.1	0.7	23.0	7.0	13.0	8
	15.3	15.5	2.4	0.6	15.5	11.0	19.0	14

[a] Data based, if not otherwise stated, on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Table 149. Comparison of main morphometrics in several *Urosomoida* species and populations.

Characteristics [a]	Pop [b]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	A1	70.4	71.5	4.0	1.1	5.6	64.0	77.0	12
	A2	69.5	70.0	7.2	1.5	10.4	55.0	87.0	25
	R1	118.1	117.0	9.9	2.5	8.4	106.0	142.0	16
	R2	125.9	124.0	12.6	3.1	10.0	108.0	156.0	17
	DO	81.3	80.5	8.5	2.7	10.4	70.0	98.0	10
Body, width	A1	20.6	20.5	2.2	0.6	10.8	17.0	24.0	12
	A2	21.7	21.0	3.2	0.6	14.9	16.0	28.0	25
	R1	32.9	33.0	5.3	1.3	16.0	22.0	46.0	16
	R2	38.9	39.0	5.4	1.3	13.9	28.0	49.0	17
	DO	24.0	24.0	2.0	0.6	8.3	20.0	27.0	10
Anterior body end to proximal end of adoral zone, distance	A1	18.6	18.5	1.3	0.4	7.1	17.0	21.0	12
	A2	21.0	21.0	1.6	0.3	7.6	18.0	24.0	25
	R1	34.7	33.5	5.4	1.4	15.6	28.0	50.0	16
	R2	41.4	41.0	4.5	1.1	10.9	34.0	50.0	17
	DO	25.6	25.0	3.3	1.0	13.0	20.0	33.0	10
Body length:length of adoral zone, ratio	A1	3.8	–	–	–	–	–	–	12
	A2	3.3	–	–	–	–	–	–	25
	R1	3.5	3.4	0.4	0.1	10.9	2.8	4.4	16
	R2	3.1	3.0	0.3	0.1	9.8	2.7	3.8	17
	DO	3.2	–	–	–	–	–	–	10
Adoral membranelles, number	A1	21.7	22.0	0.8	0.2	3.9	20.0	23.0	12
	A2	22.2	22.0	1.3	0.3	6.0	20.0	26.0	25
	R1	29.3	28.5	4.1	1.0	14.1	25.0	42.0	16
	R2	36.8	37.0	5.3	1.3	14.4	28.0	46.0	17
	DO	31.6	31.5	2.2	0.7	7.0	28.0	36.0	10
Right marginal cirri, number	A1	20.1	20.0	1.0	0.3	4.7	19.0	22.0	12
	A2	24.1	24.0	2.3	0.5	9.7	20.0	29.0	25
	R1	34.3	34.0	3.8	1.0	11.2	31.0	46.0	16
	R2	29.4	29.0	2.2	0.5	7.4	26.0	33.0	17

(continued)

Characteristics[a]	Pop[b]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Left marginal cirri, number	DO	34.1	34.0	1.9	0.6	5.6	32.0	39.0	10
	A1	19.6	20.0	1.6	0.5	8.2	16.0	22.0	12
	A2	21.6	22.0	2.0	0.4	9.2	18.0	25.0	25
	R1	32.5	32.0	4.7	1.2	14.5	23.0	42.0	16
	R2	25.1	25.0	3.2	0.8	12.6	20.0	31.0	17
	DO	29.7	29.5	2.4	0.8	8.1	26.0	34.0	10

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] A1, A2 – *Urosomoida agiliformis* from FOISSNER (1982) and FOISSNER & ADAM (1983a); R1, R2 – *Urosomoida reticulata* from Costa Rica and Namibian type location (from Table 148); DO – *Urosomoida dorsiincisura* from FOISSNER (1982).

Urosomoida namibiensis nov. spec. (Fig. 169a, b; Table 150)

Diagnosis: Size about 115 × 35 µm in vivo; outline elongate elliptical. 4 macronuclear nodules in series. Cortical granules in longitudinal rows, ellipsoidal (1.5 × 0.8 µm), colourless. On average 22 adoral membranelles, 26 cirri each in right and left marginal row, 1 buccal cirrus, 3 postoral cirri, 3 transverse cirri, 3 caudal cirri, and 4 dorsal kineties.

Type location: Mud and soil from road puddles in the Bambatsi Guest Farm, Namibia, 20°10'S 15°25'E (site 49 in figure 2 and chapter 2.1.2).

Etymology: Named after the country discovered.

Description: The overall appearance, size, and the cortical granulation of this species are very similar to the binucleate *Oxytricha longigranulosa* BERGER & FOISSNER, 1989a. Thus, we refer to this species as concerns the in vivo aspect.

Size about 100–140 × 25–45 µm in vivo, length:width ratio on average 3.2:1 in protargol preparations (Table 150). Centre of nuclear figure slightly ahead of body centre, left of midline. Macronuclear nodules in series, rarely in fairly distinct pairs, ellipsoidal to globular, with some large (3 µm) and small nucleoli. Most specimens with two or three slightly ellipsoidal, compact micronuclei usually attached or close to first, third and fourth macronuclear nodule. Cortical granules in closely spaced rows, individual granules colourless, ellipsoidal (about 1.5 × 0.8 µm), do not impregnate with the protargol method used.

Cirral pattern constant, number of cirri rather variable (Fig. 169a; Table 150). Right marginal row begins at level of first frontoventral cirrus and ends slightly subterminally, left row usually ends in midline of rear end; bases of cirri in posterior body half often distinctly smaller than those in anterior. Frontal cirri slightly enlarged, in usual pattern. Buccal cirrus right of anterior end of paroral membrane. Frontoventral cirri in V-shaped pattern with left

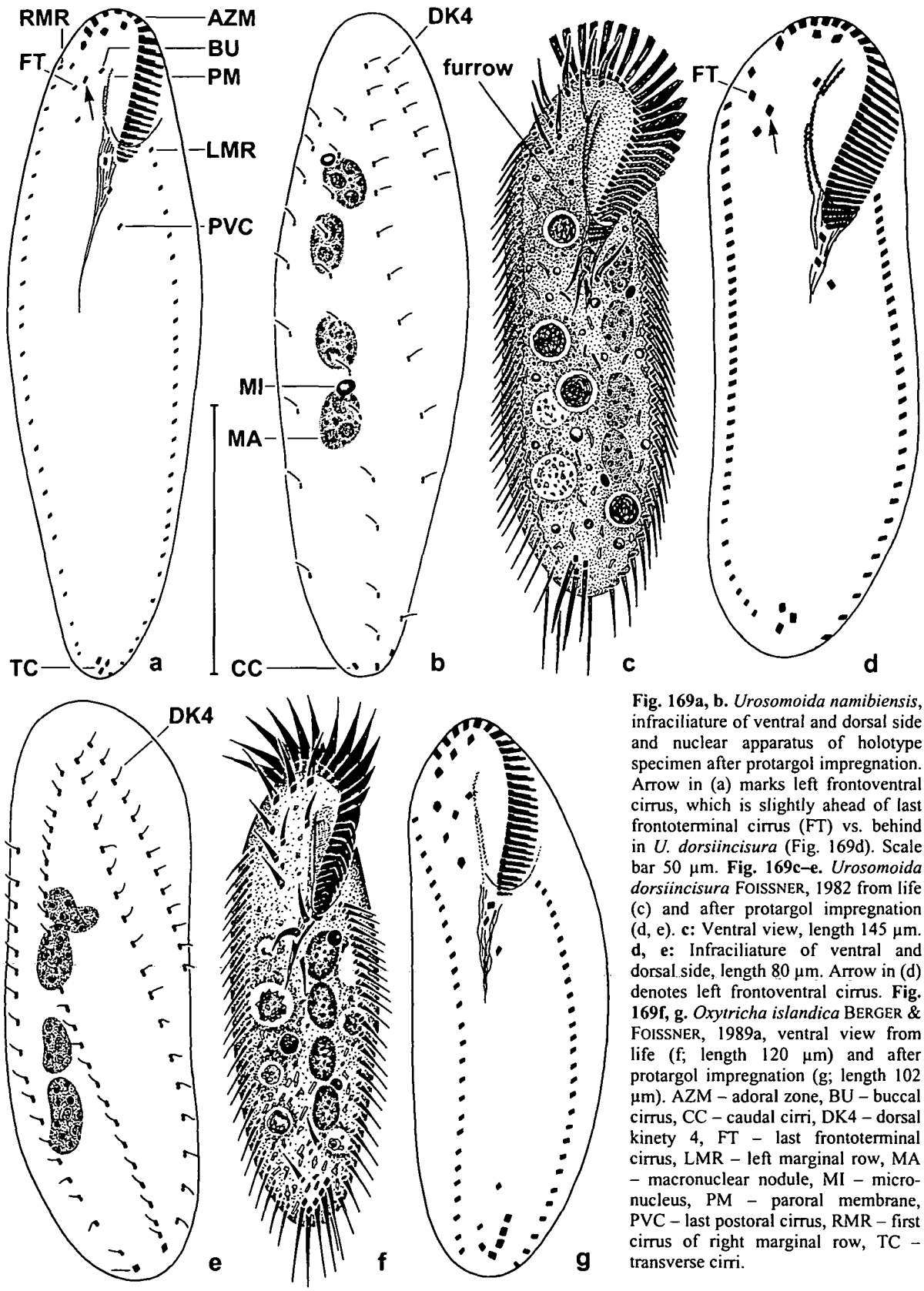


Fig. 169a, b. *Urosomoida namibiensis*, infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen after protargol impregnation. Arrow in (a) marks left frontoventral cirrus, which is slightly ahead of last frontoterminal cirrus (FT) vs. behind in *U. dorsiincisura* (Fig. 169d). Scale bar 50 µm. **Fig. 169c–e.** *Urosomoida dorsiincisura* FOISSNER, 1982 from life (c) and after protargol impregnation (d, e). **c:** Ventral view, length 145 µm. **d, e:** Infraciliature of ventral and dorsal side, length 80 µm. Arrow in (d) denotes left frontoventral cirrus. **Fig. 169f, g.** *Oxytricha islandica* BERGER & FOISSNER, 1989a, ventral view from life (f; length 120 µm) and after protargol impregnation (g; length 102 µm). AZM – adoral zone, BU – buccal cirrus, CC – caudal cirri, DK4 – dorsal kinety 4, FT – last frontoterminal cirrus, LMR – left marginal row, MA – macronuclear nodule, MI – micronucleus, PM – paroral membrane, PVC – last postoral cirrus, RMR – first cirrus of right marginal row, TC – transverse cirri.

cirrus (= cirrus III/2; arrow in Fig. 169a) slightly above level of last frontoterminal cirrus. Usually three postoral cirri in series with first cirrus very near to oral vertex. Frequently three, rarely two, four or five transverse cirri (including pretransverse cirri possibly present close to transverse cirri) at rear end and thus distinctly projecting from body proper, about of same size as most marginal cirri.

Dorsal bristles about 3 µm long, arranged in four rows (Fig. 169b; Table 150): row 1 begins about at 20% of body length, composed of only eight bristles on average, distances between individual bristles increase from anterior to posterior; row 2 also distinctly shortened anteriorly, slightly sigmoidal, composed of 14 bristles on average; row 3 only slightly shortened anteriorly, composed of 12 bristles on average; row 4 begins at about 9% and terminates at 26% of body length, composed of only five bristles on average. Usually one inconspicuous caudal cirrus each associated with bristle rows 1, 2 and 3.

Adoral zone occupies 19–30%, on average 25% of body length, composed of an average of 22 membranelles, of usual shape and structure (Fig. 169a; Table 150); bases of largest membranelles about 6 µm wide in protargol preparations. Undulating membranes straight to slightly curved, side by side, paroral 9 µm long, begins 2–3 µm ahead of 10 µm long endoral at level of buccal cirrus; both membranes likely composed of dikinetids. Pharyngeal fibres distinct after protargol impregnation, of ordinary length and structure.

Table 150. Morphometric data on *Urosomoida namibiensis*.

Characteristics[a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	106.8	105.0	10.6	2.1	9.9	91.0	133.0	25
Body, width	34.3	34.0	4.5	0.9	13.1	25.0	44.0	25
Body length:width, ratio	3.2	3.1	0.4	0.1	13.0	2.5	3.9	25
Anterior body end to proximal end of adoral zone, distance	26.7	28.0	2.4	0.5	9.1	22.0	32.0	25
Body length:length of adoral zone, ratio	4.0	3.9	0.5	0.1	11.7	3.4	5.2	25
Anterior body end to paroral membrane, distance	10.0	10.0	1.6	0.3	15.9	6.0	13.0	25
Paroral membrane, length	9.2	9.0	1.4	0.3	15.7	7.0	13.0	24
Anterior body end to endoral membrane, distance	12.6	13.0	1.7	0.4	13.3	9.0	14.0	22
Endoral membrane, length	9.5	10.0	1.2	0.3	12.8	8.0	13.0	21
Anterior body end to first frontoventral cirrus, distance	10.4	10.0	2.0	0.4	18.9	6.0	14.0	25
Anterior body end to last frontoventral cirrus, distance	20.4	21.0	2.1	0.4	10.1	15.0	23.0	25
Anterior body end to buccal cirrus, distance	10.0	10.0	1.7	0.3	16.6	6.0	13.0	25
Anterior body end to right marginal row, distance	10.2	10.0	2.3	0.5	22.6	6.0	14.0	25
Anterior body end to first postoral cirrus, distance	25.9	26.0	2.1	0.4	8.1	21.0	30.0	25
Anterior body end to last postoral cirrus, distance	36.8	36.0	3.8	0.8	10.4	29.0	44.0	23
Anterior body end to dorsal kinety 1, distance	20.9	21.0	4.1	0.8	19.5	13.0	28.0	25
Anterior body end to dorsal kinety 4, distance	9.7	10.0	2.5	0.5	25.7	5.0	16.0	23
Anterior body end to end of dorsal kinety 4, distance	27.7	28.0	4.2	0.9	15.0	20.0	34.0	24
Anterior body end to first macronuclear nodule, distance	24.0	24.0	2.7	0.5	11.2	18.0	30.0	25
Nuclear figure, length	48.0	48.0	7.6	1.5	15.7	28.0	60.0	25
Macronuclear nodules 2 and 3, distance in between	5.6	5.0	2.8	0.6	50.9	0.0	12.0	25
Anterior macronuclear nodule, length	10.7	10.0	2.4	0.5	22.6	7.0	18.0	25
Anterior macronuclear nodule, width	7.3	7.0	1.3	0.3	18.0	6.0	10.0	25
Macronuclear nodules, number[b]	4.0	4.0	0.0	0.0	0.0	4.0	4.0	25

(continued)

Characteristics[a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Anterior micronucleus, length	2.8	3.0	–	–	–	2.5	4.0	25
Anterior micronucleus, width	2.6	3.0	–	–	–	2.5	4.0	25
Micronuclei, number	2.5	2.0	0.7	0.1	26.3	1.0	4.0	25
Posterior body end to last transverse cirrus, distance	3.1	2.8	1.2	0.2	38.7	1.5	6.0	24
Posterior body end to first transverse cirrus, distance	6.4	6.0	1.4	0.3	21.1	4.0	9.0	25
Posterior body end to right marginal row, distance	6.5	6.0	2.7	0.6	41.8	3.0	15.0	23
Posterior body end to left marginal row, distance	1.5	1.0	–	–	–	0.0	5.0	23
Adoral membranelles, number	22.4	23.0	2.2	0.4	9.9	17.0	27.0	25
Frontal cirri, number[c]	3.0	3.0	0.0	0.0	0.0	3.0	3.0	25
Frontoventral cirri, number[d]	4.0	4.0	0.0	0.0	0.0	4.0	4.0	25
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	25
Postoral cirri, number[e]	2.9	3.0	0.6	0.1	20.8	1.0	4.0	25
Transverse cirri, number[f]	3.0	3.0	0.6	0.1	20.5	2.0	5.0	24
Right marginal cirri, number	25.5	26.0	3.5	0.7	13.9	19.0	33.0	25
Left marginal cirri, number	26.1	26.0	3.9	0.8	15.0	18.0	34.0	25
Caudal cirri, number[g]	3.0	3.0	0.0	0.0	0.0	3.0	3.0	25
Dorsal kineties, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	25
Dorsal kinety 1, number of bristles	7.5	7.5	1.5	0.3	20.2	5.0	11.0	24
Dorsal kinety 2, number of bristles	13.9	14.0	2.3	0.5	16.7	7.0	17.0	25
Dorsal kinety 3, number of bristles	11.7	12.0	1.9	0.4	16.1	7.0	15.0	24
Dorsal kinety 4, number of bristles	5.1	5.0	1.8	0.4	34.2	2.0	9.0	24

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Specimens with three nodules occur very rarely.

[c] Specimens with only two frontal cirri occur very rarely.

[d] Specimens with five frontoventral cirri occur very rarely.

[e] Of 25 specimens analyzed, two have only one postoral cirrus, and one has four.

[f] Including pretransverse ventral cirri possibly present close to transverse cirri.

[g] Specimens with five caudal cirri occur very rarely.

Occurrence and ecology: To date found only at type location, where it was fairly rare.

Generic classification and comparison with related species: In the absence of ontogenetic data, we classify this species in *Urosomoida* because it has only three transverse cirri (including pretransverse cirri possibly present close to transverse cirri) and four dorsal kineties. *Oxytricha* species usually have seven transverse cirri (including pretransverse cirri) and five or six dorsal kineties (for a review, see BERGER 1999).

Urosomoida namibiensis differs from *Urosomoida dorsiincisura* FOISSNER, 1982 (Fig. 169c–d), the sole quadrinucleate congener, by several features: distinct dorsal furrow absent vs. present; cortical granules ellipsoidal (1.5 × 0.8 µm) and in longitudinal rows vs. 0.5 µm

across and in reticular pattern; undulating membranes rather short and almost straight vs. rather long and curved; buccal cirrus at anterior end of paroral vs. behind; left frontoventral cirrus (arrows in Fig. 169a, d) in front of level of rear frontoterminal cirrus vs. behind; on average 22 vs. 32 adoral membranelles; three caudal cirri vs. usually two; lower number of bristles in dorsal kineties 1–4, namely on average 8, 14, 12, 5 vs. 18, 26, 18, 14 (values from type specimen; Fig. 169e). *Oxytricha islandica* BERGER & FOISSNER, 1989a, another quadrinucleate species, lacks cortical granules and invariably has seven transverse cirri including two pretransverse ventral cirri (Fig. 169f, g). In vivo, *Urosomoida namibiensis* is characterized by the following combination of features: four macronuclear nodules; ellipsoidal cortical granules in longitudinal rows; usually three transverse cirri.

Urosomoida monostyla nov. spec. (Fig. 170a–d; Table 151)

Diagnosis: Size about 45 × 12 µm in vivo; outline elongate elliptical. 2 ellipsoidal macronuclear nodules with a single micronucleus in between. On average 15 adoral membranelles, 14 cirri each in right and left marginal row, 1 postoral cirrus, 3 transverse and 2 pretransverse cirri, 2 caudal cirri, and 4 dorsal kineties.

Type location: Highly saline soil from margin of Etosha Pan, lookout site "Pan", Namibia, 19°10'S 15°55'E (site 57 in figures 2, 3 and chapter 2.1.2).

Etymology: Composite of Greek adjective *mono* (single) and the Greek noun *styla* (rod ~ cirrus), referring to the single postoral cirrus, a main feature of this minute ciliate.

Description: Size 35–65 × 10–15 µm in vivo, usually about 45 × 12 µm, length:width ratio on average 3.5:1 in protargol preparations (Table 151). Outline elongate elliptical or, in the broader specimens, almost rectangular (Fig. 170a, b); dorsoventrally flattened up to 2:1, acontractile. Nuclear apparatus in body centre left of midline, invariably consists of two ellipsoidal, almost abutting macronuclear nodules and a single, compact micronucleus in between (Fig. 170a, d). Contractile vacuole near mid-body at left margin. Cortex flexible and thin, without specific granules. Cytoplasm colourless, contains some small fat globules and food vacuoles with remnants of bacteria and heterotrophic flagellates. Ontogenesis commences with the formation of an oral primordium underneath the postoral cirrus.

Cirral pattern and number of cirri of usual variability (Fig. 170a, c; Table 151). Cirri thick compared to body size, marginal and frontoventral cirri 7–8 µm long, transverse and caudal cirri about 12 µm. Right marginal row commences slightly above level of last frontoventral cirrus and ends subterminally, left row extends to body midline posteriorly; distances between individual marginal cirri increase slightly from anterior to posterior in both rows. Frontal cirri about of same size as other cirri. Buccal cirrus right of anterior end of paroral membrane. Four frontoventral cirri, three of which forming conspicuous bow with frontal cirri. A single postoral cirrus behind buccal vertex. Number and pattern of transverse and pretransverse cirri very constant: transverse cirri close together, right of body midline near rear end and thus distinctly projecting from body proper; pretransverse cirri between transverse cirri and last cirrus of right marginal row.

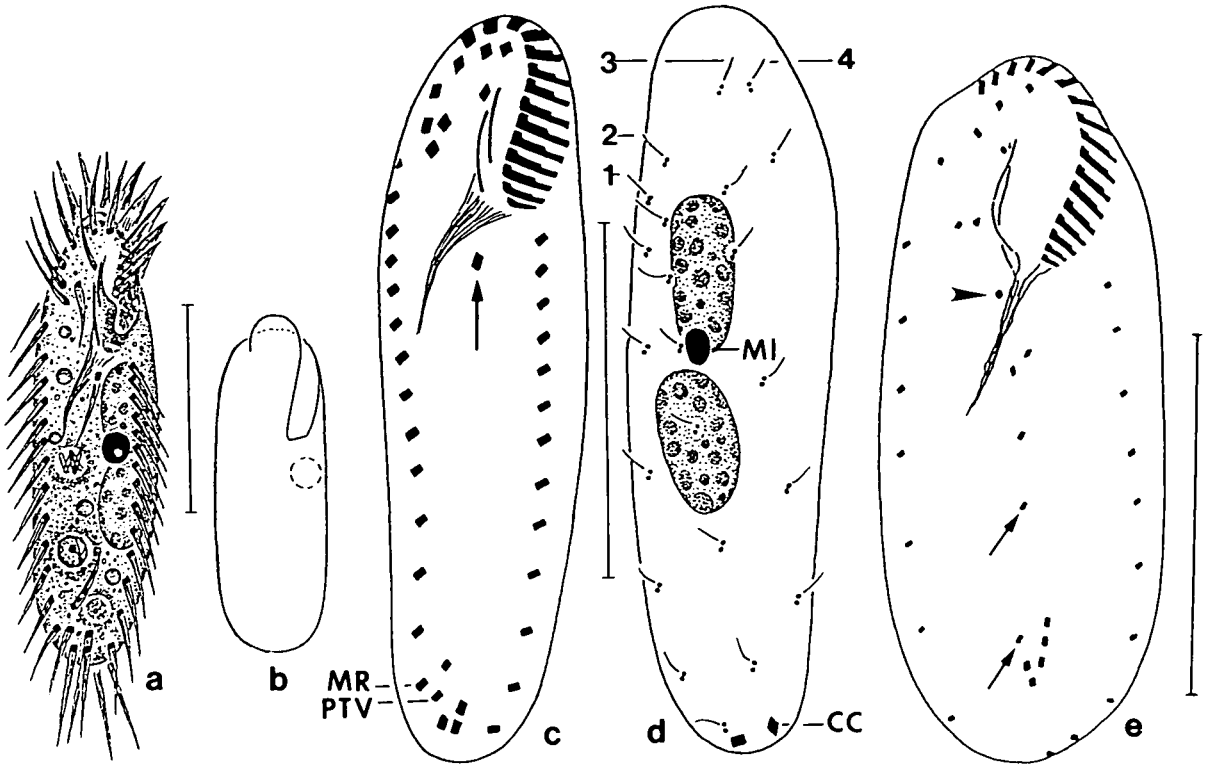


Fig. 170a–d. *Urosomoida monostyla* from life (a, b) and after protargol impregnation (c, d). **a:** Ventral view of a representative specimen. **b:** Rectangular shape variant. **c, d:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrow marks the single postoral cirrus, a main feature of the species. Numbers denote dorsal bristle rows. CC – caudal cirri, MI – micronucleus, MR – last cirrus of right marginal row, PTV – pretransverse cirrus. Scale bars 20 µm.

Fig. 170e. *Oxytricha elegans*, infraciliature of ventral side after protargol impregnation (from FOISSNER 1999b). Arrows mark pretransverse cirri; arrowhead denotes the posteriormost frontoventral cirrus. Scale bar 30 µm.

Dorsal bristles about 3 µm long, arranged in four rows (Fig. 170d; Table 151): rows 1 and 2 commence subapically, row 1 composed of an average of only six bristles, distances between individual bristles increase slightly from anterior to posterior; row 3 commences near anterior end in body midline and ends subterminally at right margin of cell; row 4 consists of only two to three bristles near left anterior body end. Invariably two conspicuous caudal cirri associated with dorsal kineties 1 and 2, as shown by a late divider.

Adoral zone occupies 21–40%, on average 30% of body length, composed of an average of 15 membranelles of usual shape and structure; bases of largest membranelles about 3 µm wide in protargol preparations (Fig. 170a, c; Table 151). Buccal cavity narrow and flat; buccal lip angularly projecting, covers proximal portion of adoral zone and bears paroral membrane. Undulating membranes slightly curved and staggering side by side, further details not recognizable. Pharyngeal fibres distinct, of ordinary length and structure, extend rightwards and then posteriorly (Fig. 170a, c; Table 151).

Occurrence and ecology: To date found only at type location, where it developed in a culture of artificial sea water, some crushed wheat grains, and a few millilitres of the

percolate from the non-flooded Petri dish culture. Abundance was low. *Urosomoida monostyla* is well adapted to the soil habitat by its minute and flexible body.

Generic classification and comparison with related species: Possibly, this species belongs to the genus → *Erimophrya*, as indicated by the reduced number of postoral cirri. However, in the absence of detailed ontogenetic data, we classify it conservatively in the genus *Urosomoida*.

Urosomoida monostyla has a clear identity, making it easily recognizable both in vivo and protargol preparations: small size (≤ 50 µm); only one postoral cirrus; and a reduced number

Table 151. Morphometric data on *Urosomoida monostyla*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	39.5	40.0	6.5	1.5	16.4	30.0	57.0	19
Body, width	11.4	11.0	1.5	0.3	13.2	9.0	14.0	19
Body length:width, ratio	3.5	3.3	0.8	0.2	22.7	2.7	5.7	19
Anterior body end to proximal end of adoral zone, distance	12.0	12.0	0.7	0.2	5.9	10.0	13.0	19
Body length:length of adoral zone, ratio	3.3	3.3	0.5	0.1	15.4	2.5	4.8	19
Anterior body end to last frontoventral cirrus, distance	7.8	8.0	0.7	0.2	9.2	7.0	9.0	19
Anterior body end to buccal cirrus, distance	3.9	4.0	–	–	–	3.0	4.0	19
Anterior body end to right marginal row, distance	7.3	7.0	1.1	0.3	15.1	5.0	9.0	19
Macronuclear nodules, distance in between	0.8	1.0	0.8	0.2	99.7	0.0	2.0	19
Anterior macronuclear nodule, length	8.3	8.0	1.7	0.4	20.5	6.0	13.0	19
Anterior macronuclear nodule, width	4.5	5.0	0.6	0.1	14.0	3.5	5.0	19
Macronuclear nodules, number	2.1	2.0	–	–	–	2.0	3.0	19
Anterior micronucleus, length	2.8	3.0	–	–	–	2.3	3.5	19
Anterior micronucleus, width	2.0	2.0	–	–	–	2.0	2.3	19
Micronuclei, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
Adoral membranelles, number	14.6	15.0	0.6	0.1	4.1	13.0	15.0	19
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
Frontoventral cirri, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	19
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
Transverse cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
Pretransverse cirri, number	2.0	2.0	–	–	–	1.0	2.0	19
Postoral cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
Right marginal cirri, number	13.8	14.0	1.1	0.2	7.7	12.0	16.0	19
Left marginal cirri, number	13.4	14.0	1.1	0.3	8.4	11.0	15.0	19
Caudal cirri, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
Dorsal kineties, number [b]	4.0	4.0	0.0	0.0	0.0	4.0	4.0	19
Dorsal kinety 1, number of bristles	5.6	6.0	0.6	0.1	10.6	5.0	7.0	19

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Three kineties in one out of thirty specimens.

(3 vs. 5) of transverse cirri. There is only one congener with the same nuclear pattern, viz., *Urosomoida perthensis*, which has a size of 50–70 × 20–30 µm and the usual three oxytrichid postoral cirri (for a review of the genus, see BERGER 1999). *Lamtostyla perisincirra* (HEMBERGER, 1985) BERGER & FOISSNER, 1988a, which has a similar size (50–90 × 20–30 µm) and the same nuclear pattern, lacks the postoral cirrus and the short dorsal kinety 4.

Inexperienced workers might confuse *U. monostyla* with several *Oxytricha* species, especially *O. elegans* FOISSNER, 1999b, which occurs in the same geographic region and has the same nuclear pattern. However, *O. elegans* is larger (70 × 25 vs. 45 × 12 µm in vivo), has five transverse cirri (vs. three), and the cirri are extraordinarily long (17–25 µm vs. 7–12 µm) and fine (Fig. 170e).

Urosomoida deserticola nov. spec. (Fig. 171a–d; Table 152)

Diagnosis: Size about 65 × 10 µm in vivo. 2 ellipsoidal macronuclear nodules with a micronucleus each. Both marginal cirral rows anteriorly and posteriorly shortened by an average of at least 15%. Transverse and caudal cirri form conspicuous tuft at posterior body end. On average 13 adoral membranelles, about 10 right and left marginal cirri each, 2 postoral cirri, 3 transverse and 2 pretransverse cirri, 2 caudal cirri, and 4 dorsal kineties.

Type location: Dune soil (sand) in the Central Namib Escarpment, north of the village of Solitaire, Namibia, 23°50'S 16°E (site 33 in figure 2 and chapter 2.1.2).

Etymology: Composite of the Latin words *deserta* (desert) and *colere* (inhabiting), referring to the habitat the species was discovered.

Description: Size 45–85 × 8-12 µm in vivo, usually near 65 × 10 µm, length:width ratio 4.6–6.7:1, on average 5.7:1 in protargol preparations (Table 152). Outline elongate fusiform with both ends narrowly rounded, rarely elliptical (Fig. 171a, b); dorsoventrally flattened up to 2:1, acontractile. Nuclear apparatus in middle body third left of midline, invariably consists of two ellipsoidal, rather closely spaced macronuclear nodules each associated with an ellipsoidal micronucleus at various positions. Contractile vacuole slightly above mid-body at left margin. Cortex flexible, thin, without specific granules. Cytoplasm colourless, contains some small fat globules and up to 8 µm-sized food vacuoles with remnants of bacteria and heterotrophic flagellates. Glides rather rapidly on microscope slide. Ontogenesis commences with the production of an oral primordium left of the postoral cirri.

Cirral pattern and number of cirri of usual variability, pattern almost unique within genus (Fig. 171a, b; Table 152). Cirri fine, consist of four (frontal, frontoventral, postoral, pretransverse, and caudal cirri) to six (marginal and transverse cirri) cilia only. Marginal cirri about 8 µm long in vivo, form a row each at right and left ventral margin of cell, both rows distinctly (≥ 15% on average; Table 152) shortened anteriorly and posteriorly, distances between individual cirri increase from anterior to posterior in both rows. Frontal cirri not enlarged, arranged in oblique row. Frontoventral cirri about 10 µm long in vivo, form two short, staggering rows each composed of two cirri right of buccal cavity; buccal cirrus at right anterior end of paroral membrane, that is, far subapical. Postoral cirri in series close underneath buccal vertex, indicating that the third cirrus has been lost. Pretransverse, transverse,

and caudal cirri about 12 µm long in vivo, number and pattern very constant, form conspicuous tuft at posterior body end: transverse cirri at left posterior margin of cell, pretransverse cirri subterminal in body midline, caudal cirri at right posterior end of cell.

Dorsal bristles about 3 µm long in vivo, arranged in four slightly oblique, sparsely ciliated rows (Fig. 171c, d; Table 152). Rows 1 and 2 distinctly shortened anteriorly, that is, commence at level of oral vertex; row 1 shortened also posteriorly, consists of three to four bristles only. Row 3 slightly shortened anteriorly, where it commences in body midline, and

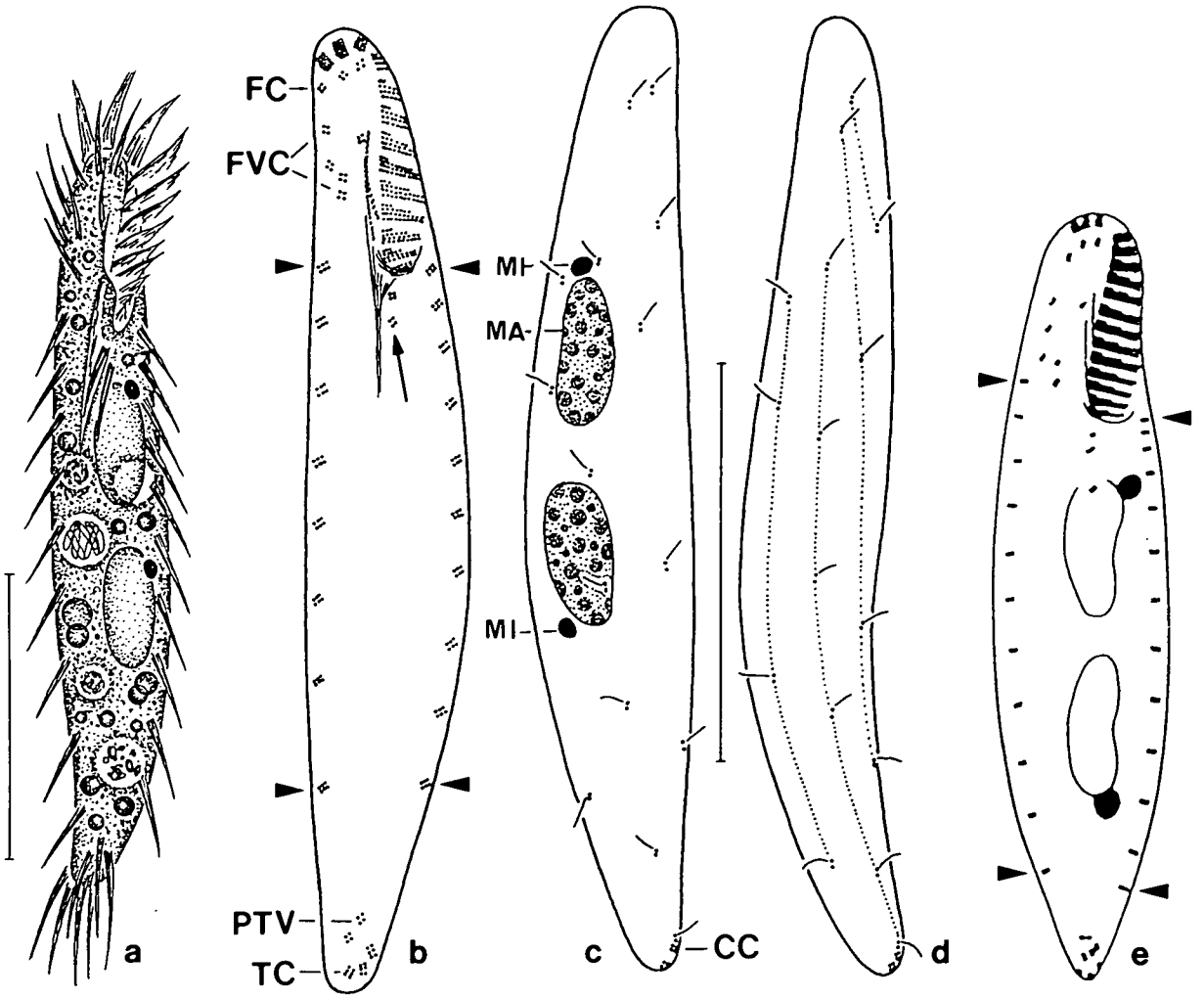


Fig. 171a–d. *Urosomoida deserticola* from life (a) and after protargol impregnation (b–d). **a:** Ventral view of a representative specimen showing the conspicuous tuft produced by the pretransverse, transverse, and caudal cirri at posterior body end. **b, c:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrowheads mark beginning and end of marginal rows, which are distinctly shortened anteriorly and posteriorly, a main feature of *U. deserticola*, like the two postoral cirri (arrow). **d:** Dorsal bristle pattern of another specimen, with the very widely spaced bristles connected by dotted lines. CC – two caudal cirri, FC – three frontal cirri, FVC – five (with buccal cirrus) frontoventral cirri, MA – two macronuclear nodules, MI – micronuclei, PTV – two pretransverse cirri, TC – three transverse cirri. Scale bars 25 µm.

Fig. 171e. *Urosomoida minima*, infraciliature of ventral side and nuclear apparatus after protargol impregnation, length 80 µm (from HEMBERGER 1985). This species has, like *U. deserticola*, distinctly shortened marginal rows (arrowheads), but possesses six frontoventral (vs. five), three postoral (vs. two), and three caudal cirri (vs. two).

distinctly so posteriorly, where it ends at right margin of cell. Row 4 in right anterior corner of cell, invariably consists of two bristles only. Two caudal cirri at right posterior margin of cell associated with dorsal kineties 1 and 2, one bristle invariably close to upper caudal cirrus.

Table 152. Morphometric data on *Urosomoida deserticola*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	57.1	60.0	7.5	1.7	13.2	43.0	72.0	19
Body, width	10.1	10.0	0.9	0.2	8.4	9.0	12.0	19
Body length:width, ratio	5.7	5.5	0.6	0.1	11.0	4.6	6.7	19
Anterior body end to proximal end of adoral zone, distance	14.4	15.0	1.0	0.2	7.0	13.0	16.0	19
Body length:length of adoral zone, ratio	4.0	4.0	0.4	0.1	9.6	3.3	4.8	19
Anterior body end to last frontoventral cirrus, distance	9.6	9.0	1.4	0.3	14.1	8.0	14.0	19
Anterior body end to buccal cirrus, distance	5.9	6.0	0.6	0.1	10.0	5.0	7.0	19
Anterior body end to right marginal row, distance	13.5	14.0	1.3	0.3	9.7	11.0	16.0	19
Posterior body end to right marginal row, distance	8.7	9.0	2.5	0.6	28.0	5.0	14.0	19
Posterior body end to left marginal row, distance	9.3	9.0	2.7	0.6	28.8	6.0	16.0	19
Anterior body end to paroral membrane, distance	5.1	5.0	0.6	0.1	11.4	4.0	6.0	19
Paroral membrane, length	5.0	5.0	0.5	0.1	9.4	4.0	6.0	19
Anterior body end to proximal end of endoral membrane, distance	12.0	12.0	1.5	0.3	12.3	7.0	14.0	19
Endoral membrane, length	4.3	4.0	0.5	0.1	11.9	3.5	5.0	19
Anterior body end to anterior macronuclear nodule, distance	15.0	15.0	1.8	0.4	12.2	11.0	19.0	19
Nuclear figure, length	23.2	23.0	3.7	0.8	15.9	18.0	32.0	19
Macronuclear nodules, distance in between	2.7	3.0	1.1	0.3	40.1	0.0	4.0	19
Anterior macronuclear nodule, length	9.6	9.0	1.4	0.3	14.9	8.0	13.0	19
Anterior macronuclear nodule, width	4.2	4.0	0.8	0.2	18.3	3.0	6.0	19
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
Anterior micronucleus, length	2.0	2.0	–	–	–	1.8	2.5	18
Anterior micronucleus, width	1.3	1.3	–	–	–	1.0	2.0	18
Micronuclei, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	18
Adoral membranelles, number	12.7	13.0	0.6	0.1	4.6	11.0	13.0	19
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
Frontoventral cirri, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	19
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
Transverse cirri, number	2.8	3.0	–	–	–	2.0	3.0	19
Pretransverse cirri, number	2.0	2.0	–	–	–	1.0	2.0	19
Postoral cirri, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
Right marginal cirri, number	9.3	9.0	0.7	0.2	7.9	8.0	11.0	19
Left marginal cirri, number	10.1	10.0	0.8	0.2	8.0	8.0	12.0	19
Caudal cirri, number	1.9	2.0	0.5	0.1	24.2	0.0	2.0	19
Dorsal kineties, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	19
Dorsal kinety 1, number of bristles	3.6	4.0	–	–	–	3.0	4.0	19
Dorsal kinety 4, number of bristles	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Adoral zone inconspicuous because occupying only 23–28%, on average 25% of body length, composed of an average of 13 membranelles of usual shape and structure; bases of largest membranelles about 3 µm wide in protargol preparations (Fig. 171a, b; Table 152). Buccal cavity narrow and flat; buccal lip angularly projecting, covers proximal portion of adoral zone and bears paroral membrane. Undulating membranes slightly curved and staggering side by side frequently slightly overlapping in anterior third. Pharyngeal fibres of ordinary length and structure.

Occurrence and ecology: To date found only at type location, once more emphasizing the highly clumped distribution of ciliate species in the Namib Desert. *Urosomoida deserticola* is well adapted to sand life by its slender, flexible, small body. Abundance was moderate in the non-flooded Petri dish culture.

Generic assignment and comparison with related species: The generic home of *U. deserticola* is uncertain because no appropriate dividers were found. The two postoral cirri indicate that it could belong to → *Erimophrya*.

Urosomoida deserticola has several outstanding features, especially the distinctly shortened marginal rows and the tuft formed by the pretransverse, transverse, and caudal cirri at posterior body end. There is only one congener with the same combination of features, viz., *Urosomoida minima* HEMBERGER, 1985 (Fig. 171e). However, this species, which was discovered in garden soil near Bonn, Germany, has only three dorsal kineties, but possesses six frontoventral, three postoral, and three caudal cirri. Furthermore, frontal and ventral adoral membranelles are separated by a wide gap. Thus, these are distinct species.

The general appearance of *U. deserticola* is very near to other small members of the genera → *Urosomoida*, → *Erimophrya*, and → *Oxytricha* (for a review, see BERGER 1999). Thus, identification should be checked by protargol impregnation.

Urosomoida agiliformis FOISSNER, 1982

This species is frequent in Namibia and in soils globally. The knowledge available was reviewed by BERGER (1999). Several "typical" populations occur in Namibia. However, at site (27) rather unusual specimens were discovered, casting doubts on, especially, the taxonomic value of the number of postoral cirri, which is highly variable. Likewise, the number of transverse and pretransverse cirri is between that of the Austrian type population (3) and of classical *Oxytricha* species (7), namely 4 to 5. Possibly, the Namibian site (27) population is a distinct subspecies, as indicated by the increased number of transverse and pretransverse cirri.

Among 30 specimens investigated, 7 have only one postoral cirrus, 1 has two, and 22 have the usual three; 6 have two transverse cirri and 24 have three; all have two pretransverse cirri.

Erimophrya nov. gen.

Diagnosis: Oxytrichidae with oral apparatus in *Oxytricha* pattern and V-like arranged frontoventral cirri. Number of postoral and transverse cirri distinctly reduced. 1 right and 1 left row of marginal cirri. 3 or 4 dorsal kineties. Caudal cirri present. Ontogenesis in *Urosomoida* pattern, but with only 5 fronto-ventral-transverse cirral anlagen streaks.

Type species: *Erimophrya glatzeli* nov. spec.

Etymology: Composite of the Greek nouns *erimos* (desert) and *ophrya* (eyebrow ~ cilia ~ ciliate), meaning a ciliate type occurring in deserts. Feminine gender.

Comparison with related genera: This new genus is established for two *Urosomoida*-like hypotrichs as yet found only in the dunes of the Namib Desert. The genus is founded with the arguments discussed under → *Hemiurosoma*, that is, mainly based on the reduced number (5 vs. 6) of fronto-ventral-transverse cirral anlagen, a feature possibly caused by the reduced number of transverse and postoral cirri. The general and especially the frontoventral cirral pattern is quite similar to that of *Urosomoida*, from which this type of hypotrichs likely evolved. Thus, it cannot be confused with *Hemisincirra*. *Urosomoida antarctica* FOISSNER, 1996a also lacks one postoral cirrus, but has a full set of transverse cirri and thus likely does not belong to *Erimophrya*. The generic home of → *U. monostyla*, which lacks even two of the three postoral cirri, also requires ontogenetic data.

Erimophrya glatzeli nov. spec. (Fig. 172a–g; Table 153)

Diagnosis: Size about 110 × 25 µm in vivo; elongate elliptical. On average 2 widely separated, elongate ellipsoidal macronuclear nodules, 21 adoral membranelles, 20 cirri each in right and left marginal row, 2 postoral cirri, 1 transverse cirrus, 2 caudal cirri, and 4 dorsal kineties.

Type location: Humous sand under *Acacia erioloba* in the Sossus Vlei of the Namib Desert, 24°50'S 15°20'E (site 24 in figure 2 and chapter 2.1.2).

Dedication: Wilhelm FOISSNER dedicates this new species to Prof. Dr. Gerhard GLATZEL, famous forest ecologist at the University of Vienna, for his friendship over many years.

Description: Size 80–150 × 20–30 µm in vivo, usually near 110 × 25 µm, length:width ratio highly variable, that is, 3.3–6.6:1, on average 4.7:1 both in vivo and protargol preparations (Table 153); flexible but acontractile, dorsoventrally flattened up to 2:1 with rather distinct furrow along dorsal kinety 4. Body outline usually very elongate elliptical with a small concavity at oral vertex; posterior portion more distinctly narrowed than anterior, occasionally with bluntly pointed end or rather broad, highly resembling → *Urosomoida agiliformis* (Fig. 172a–c, e–g). Macronuclear nodules in middle body third left of midline, posterior nodule usually closer to body margin than anterior one, invariably connected by a fine, granulated thread, broadly (1.5:1) to very elongate (5:1) ellipsoidal, on average 2.6:1 and widely separated; nucleoli highly variable, often some large and many small ones. A globular

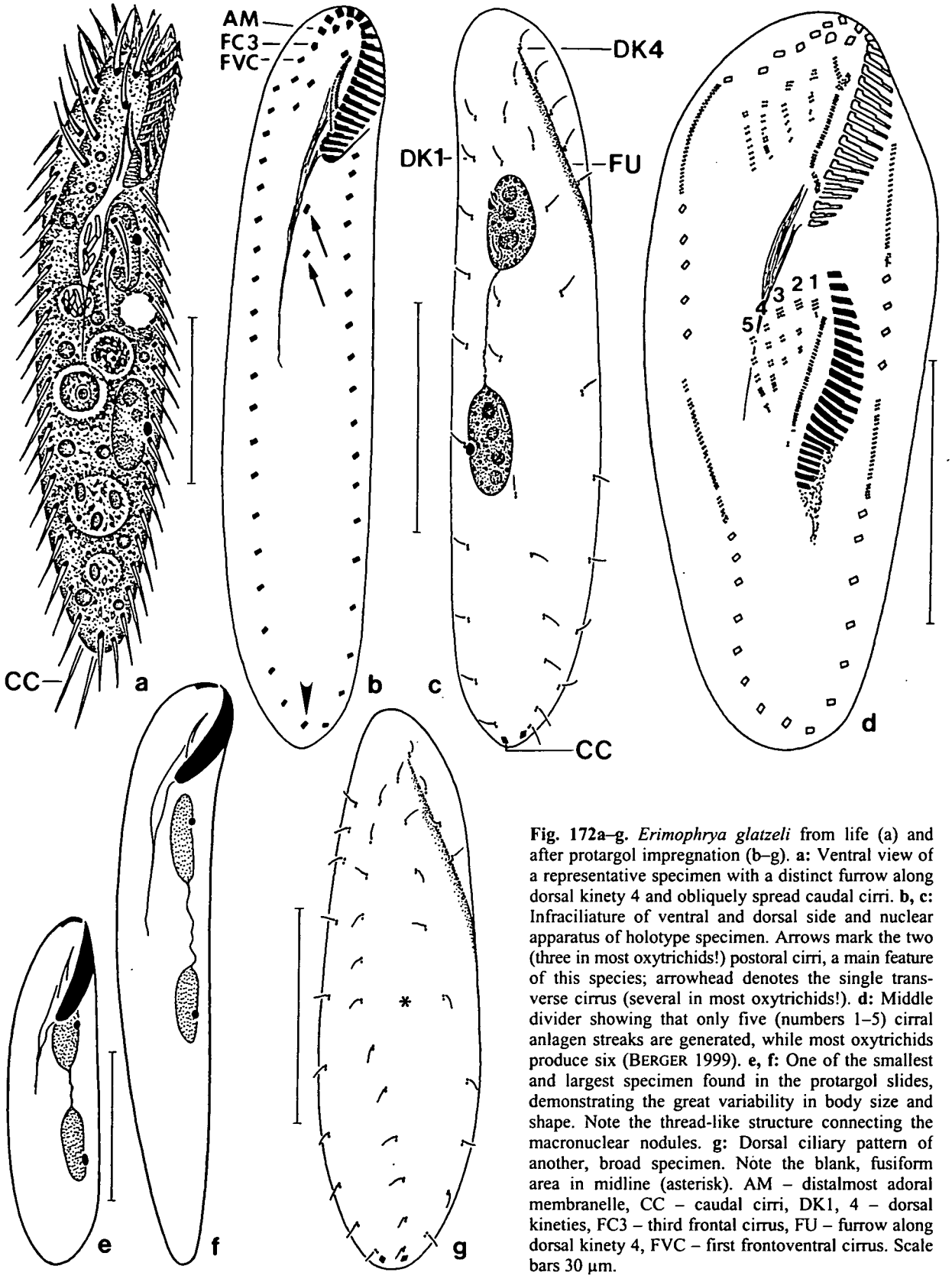


Fig. 172a–g. *Erimophrya glatzeli* from life (a) and after protargol impregnation (b–g). **a:** Ventral view of a representative specimen with a distinct furrow along dorsal kinety 4 and obliquely spread caudal cirri. **b, c:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrows mark the two (three in most oxytrichids!) postoral cirri, a main feature of this species; arrowhead denotes the single transverse cirrus (several in most oxytrichids!). **d:** Middle divider showing that only five (numbers 1–5) cirral anlagen streaks are generated, while most oxytrichids produce six (BERGER 1999). **e, f:** One of the smallest and largest specimen found in the protargol slides, demonstrating the great variability in body size and shape. Note the thread-like structure connecting the macronuclear nodules. **g:** Dorsal ciliary pattern of another, broad specimen. Note the blank, fusiform area in midline (asterisk). AM – distalmost adoral membranelle, CC – caudal cirri, DK1, 4 – dorsal kineties, FC3 – third frontal cirrus, FU – furrow along dorsal kinety 4, FVC – first frontoventral cirrus. Scale bars 30 μm.

to ellipsoidal micronucleus each attached to left side of macronuclear nodules, about 2.5 µm across and thus inconspicuous. Contractile vacuole slightly to distinctly above mid-body at left cell margin. Cytopyge subterminal dorsal. No specific cortical granules. Cytoplasm colourless, contains some lipid droplets and 5–15 µm-sized food vacuoles with heterotrophic flagellates and bacteria. Swims and glides rather rapidly.

Cirral pattern very constant, number of cirri of usual variability (Fig. 172a, b; Table 153). Most cirri in vivo 10 µm long, caudal cirri elongated to about 15 µm and obliquely spread. Right marginal row commences at level of middle frontoventral cirrus and ends subterminally, while the left ends at level of transverse cirrus, that is, almost at posterior body end; distances between individual cirri increase slightly from anterior to posterior in both right and left row, while cirral size hardly changes. Frontal cirri slightly enlarged. Buccal cirrus right of anterior end of paroral membrane. Invariably four frontoventral cirri in V-like pattern, three of which form a conspicuous bow with the frontal cirri. Usually two, rarely one or three postoral cirri distinctly behind buccal vertex, indicating that the first of the three cirri has been reduced. Usually one, rarely two transverse cirri between last cirrus of marginal rows, that is, in body midline near posterior end, producing seemingly confluent marginal cirral rows.

Dorsal bristles 3–4 µm long in vivo, arranged in four rows forming very constant pattern (Fig. 172c, g; Table 153). Rows 1 and 2 slightly shortened anteriorly, each composed of about 10 bristles and associated with a caudal cirrus; row 3 slightly shortened anteriorly, extends to rear body end, convex, leaving blank a fusiform field in body midline because row 2 is concave; row 4 originates dorsomarginally and is composed of only three to six bristles extending along a rather distinct furrow in anterior quarter of cell.

Adoral zone occupies 18–30%, on average 22% of body length, of usual shape and structure, consists of an average of 20 membranelles; bases of largest membranelles about 6 µm wide in vivo. Buccal cavity narrow and flat; buccal lip angularly projecting and thus prominent, covers posterior portion of adoral zone of membranelles and bears paroral membrane. Both undulating membranes curved and almost side by side, optically intersecting slightly in anterior quarter; paroral commences a few micrometers ahead of endoral, which is longer posteriorly, likely consists of closely spaced dikinetids. Pharyngeal fibres distinct in vivo and protargol preparations, extend to at least mid-body right of midline (Fig. 172a, b; Table 153).

Ontogenesis not studied in detail, commences with the formation of an anarchic field of basal bodies each left of the posterior postoral cirrus and the single transverse cirrus, quite similarly to *Urosomoida agiliformis* (for a review, see BERGER 1999). Proter and opisthe cirral anlagen streaks develop independently and produce supernumerary cirri that are reduced during cirral patterning, indicating that the *Erimophrya* pattern is apomorphic. Four middle dividers invariably show that only five cirral anlagen streaks develop (Fig. 172d), that is, one less than in most oxytrichids (BERGER 1999).

Occurrence and ecology: To date found at type location and surroundings, where it occurred in great numbers, indicating that many cysts were present.

Comparison with related species: *Erimophrya glatzeli* differs from → *E. arenicola* by body shape (elongate elliptical vs. distinctly narrowed posteriorly), nuclear pattern (macronuclear nodules widely separated and connected by a thread-like structure vs. almost abutting and not connected), the number of postoral cirri (two vs. one), the dorsal

infraciliature (four vs. three rows and row 1 complete vs. distinctly reduced), and ontogenesis (*E. arenicola* lacks the anarchic field of basal bodies left of the transverse cirrus). Thus, both species are very distinct and easily distinguished even in vivo.

However, in vivo *E. glatzeli* is easily confused with several medium-sized hypotrichs, especially *Urosomoida agiliformis*. Thus, check the number of postoral cirri (two vs. three), which are easily recognized.

Table 153. Morphometric data on *Erimophrya glatzeli* (upper line) and *Erimophrya arenicola* (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	103.2	102.0	16.6	3.6	16.0	76.0	133.0	21
	85.0	85.0	6.6	1.4	7.8	74.0	100.0	23
Body, width	21.8	21.0	2.1	0.5	9.9	20.0	29.0	21
	12.4	12.0	1.5	0.3	11.9	10.0	15.0	23
Body length:width, ratio	4.8	4.7	0.9	0.2	18.6	3.3	6.6	21
	6.9	6.7	0.8	0.2	11.7	6.0	9.0	23
Anterior body end to proximal end of adoral zone, distance	22.4	22.0	0.9	0.2	3.9	21.0	24.0	21
	18.1	18.0	1.1	0.2	6.2	16.0	21.0	23
Body length:length of adoral zone, ratio	4.6	4.6	0.7	0.2	15.0	3.3	5.7	21
	4.7	4.8	0.4	0.1	8.9	3.9	5.3	23
Anterior body end to paroral membrane, distance	6.1	6.0	0.8	0.2	12.9	5.0	8.0	21
				not measured				
Paroral membrane, length	8.3	9.0	1.3	0.3	15.3	7.0	12.0	21
				not measured				
Anterior body end to endoral membrane, distance	8.2	8.0	0.7	0.2	8.5	7.0	10.0	21
				not measured				
Endoral membrane, length	9.5	9.0	0.9	0.2	9.2	8.0	11.0	21
				not measured				
Anterior body end to first frontoventral cirrus, distance	6.0	6.0	1.1	0.3	19.0	4.0	8.0	21
				not measured				
Anterior body end to last frontoventral cirrus, distance	13.9	14.0	1.5	0.3	10.7	12.0	17.0	21
	10.3	10.0	0.8	0.2	7.5	9.0	12.0	22
Anterior body end to buccal cirrus, distance	6.1	6.0	0.8	0.2	12.6	5.0	8.0	21
	6.5	6.0	0.8	0.2	12.2	5.0	8.0	23
Anterior body end to right marginal row, distance	11.0	11.0	1.9	0.4	17.5	8.0	14.0	21
	12.3	12.5	1.6	0.3	13.1	10.0	15.0	22
Anterior body end to first postoral cirrus, distance	26.9	27.0	2.4	0.5	8.8	23.0	32.0	21
	21.5	22.0	1.3	0.3	5.9	19.0	24.0	23
Anterior body end to second postoral cirrus, distance	32.8	33.0	3.0	0.7	9.2	27.0	39.0	21
				lacking				
Anterior body end to dorsal kinety 1, distance	16.7	17.0	2.8	0.6	16.6	10.0	22.0	21
				not measured				
Anterior body end to dorsal kinety 4, distance	5.8	6.0	1.0	0.2	16.9	4.0	8.0	21
				not measured				
Anterior body end to end of dorsal kinety 4, distance	22.1	22.0	3.1	0.7	14.2	16.0	27.0	21
				not measured				

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Anterior body end to first macronuclear nodule, distance	23.6	23.0	3.0	0.7	12.8	17.0	29.0	21
	20.7	21.0	2.1	0.4	10.1	18.0	25.0	23
Nuclear figure, length	47.6	49.0	8.8	1.9	18.6	32.0	64.0	21
	33.3	32.0	5.7	1.2	17.0	22.0	44.0	23
Macronuclear nodules, distance in between	14.2	15.0	4.3	0.9	30.0	7.0	22.0	21
	3.3	3.0	1.9	0.4	58.4	0.0	8.0	28
Anterior macronuclear nodule, length	16.6	17.0	3.5	0.8	21.3	12.0	24.0	21
	15.0	14.0	3.2	0.7	21.2	6.0	23.0	23
Anterior macronuclear nodule, width	6.3	6.0	1.1	0.2	17.5	5.9	9.0	21
	4.2	4.0	1.9	0.4	44.3	3.0	12.0	23
Macronuclear nodules, number (specimens with three or four nodules occur very rarely)	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	23
Anterior micronucleus, length	2.2	2.2	–	–	–	1.9	2.5	21
	2.8	2.5	0.6	0.1	20.6	1.5	4.0	22
Anterior micronucleus, width	2.0	2.0	–	–	–	1.5	2.2	21
	1.7	1.5	–	–	–	1.5	2.5	22
Micronuclei, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	1.7	2.0	0.6	0.1	36.5	1.0	3.0	22
Posterior body end to transverse cirrus, distance	2.0	2.0	0.5	0.1	24.3	1.0	3.0	21
			not measured					
Posterior body end to right marginal row, distance	5.5	5.0	2.6	0.6	46.8	2.0	14.0	21
			not measured					
Posterior body end to left marginal row, distance	2.2	2.0	1.3	0.3	60.6	1.0	5.0	21
			not measured					
Adoral membranelles, number	20.5	20.0	0.8	0.2	3.7	19.0	22.0	21
	15.0	15.0	0.9	0.2	5.8	13.0	17.0	22
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	22
Frontoventral cirri, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21
	4.0	4.0	0.4	0.1	9.5	3.0	5.0	22
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	23
Postoral cirri, number (specimens with one or three cirri occur very rarely in *E. glatzeli*)	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	23
Transverse cirri, number (from late dividers in *E. arenicola*)	1.1	1.0	–	–	–	1.0	2.0	21
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	5
Right marginal cirri, number	21.2	22.0	1.7	0.4	8.1	17.0	24.0	21
	18.6	19.0	2.4	0.5	12.9	14.0	24.0	22
Left marginal cirri, number	19.8	20.0	1.7	0.4	8.5	18.0	24.0	21
	19.3	19.0	3.4	0.7	17.9	14.0	27.0	23
Caudal cirri, number (only one caudal cirrus occurs very rarely in *E. glatzeli*)	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	22
Dorsal kineties, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	22
Dorsal kinety 1, number of bristles	9.3	9.0	0.7	0.2	7.8	8.0	11.0	21
	3.0	3.0	1.5	0.4	49.4	2.0	7.0	11
Dorsal kinety 2, number of bristles	12.1	12.0	1.1	0.2	8.8	10.0	15.0	21
	9.7	10.0	1.4	0.4	14.6	7.0	12.0	11

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Dorsal kinety 3, number of bristles	9.3	9.0	1.2	0.3	12.4	7.0	12.0	21
	3.3	3.0	0.6	0.2	19.1	2.0	4.0	12
Dorsal kinety 4, number of bristles	4.3	4.0	1.0	0.2	23.5	3.0	6.0	21
				lacking				

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Erimophrya arenicola nov. spec. (Fig. 173a–h; Table 153)

Diagnosis: Size about 90 × 13 µm in vivo; pisciform and slightly twisted about main body axis. On average 2 almost abutting, very elongate ellipsoidal macronuclear nodules, 15 adoral membranelles, 19 cirri each in right and left marginal row, 1 postoral cirrus, 1 transverse cirrus, 2 caudal cirri, and 3 dorsal kineties.

Type location: Sand with litter from *Nara* scrubs in the Sossus Vlei of the Namib Desert, 24°50'S 15°20'E (site 23 in figure 2 and chapter 2.1.2).

Etymology: The Latin *arenicola* (living in the sand) refers to the habitat the species was discovered.

Description: Size 70–110 × 10–20 µm in vivo, length:width ratio about 7:1 on average both in vivo and after protargol impregnation (Table 153); flexible but acontractile. Shape fairly constant, usually slenderly fusiform or pisciform, that is, anterior end narrowly rounded and posterior tail-like elongated (Fig. 173a, b, d–f); occasionally elongate ellipsoidal with both ends rounded or posterior end bluntly pointed (Fig. 173c); usually slightly twisted about main body axis and inconspicuously flattened dorsoventrally. Macronuclear nodules in middle body third left of midline, ellipsoidal (2:1) to very elongate ellipsoidal (4.5:1), on average 4:1 and close together; with many minute nucleoli. On average two ellipsoidal micronuclei, one attached to each macronuclear nodule in variable positions. Contractile vacuole slightly to distinctly above mid-body at left cell margin. No specific cortical granules. Cytoplasm colourless, with few to many lipid droplets 1–3 µm across and some ordinary cytoplasmic crystals mainly in posterior body portion, which may thus appear dark under low magnification. Feeds on the flagellate *Polytomella* and bacteria. Moves rather slowly and clumsily, possibly due to the tortuous body.

Cirral pattern rather constant, number of cirri of usual variability (Fig. 173a, e, f; Table 153). Most cirri about 8 µm long in vivo and rather fine; transverse cirrus and caudal cirri about 12 µm long. Right marginal row begins near level of last frontoventral cirrus, left extends onto dorsolateral surface posteriorly due to the body torsion; distances between individual marginal cirri increase distinctly from anterior to posterior in both right and left row. Frontal

cirri about same size as other cirri. Buccal cirrus right of anterior end of paroral membrane. Usually four frontoventral cirri, uppermost cirrus in, or almost in, line with frontal cirri. A single postoral cirrus behind the buccal vertex. Number of transverse cirri not recognizable in morphostatic specimens; ontogenesis shows that only a single transverse cirrus is formed (Fig. 173g, h); thus, one of the three cirri usually present at posterior end is a transverse cirrus (Fig. 173e, f; arrows).

Dorsal bristles about 2 µm long in vivo, arranged in three rows (Fig. 173f; Table 153): row 1 composed of 2–7 bristles only, one bristle invariably near corresponding caudal cirrus; row 2 slightly shortened anteriorly and also terminating with a caudal cirrus; row 3 originates dorsomarginally and is composed of only two to four bristles extending in anterior quarter of cell.

Adoral zone occupies 18–25%, on average 21% of body length, of usual shape and structure, consists of an average of 15 membranelles; bases of largest membranelles 6 µm wide in vivo; frontal three membranelles usually separated from ventral membranelles by a more or less distinct gap at left anterior body corner. Buccal cavity narrow and flat; buccal lip angularly projecting and thus prominent, covers posterior third of adoral zone of membranelles and bears paroral membrane. Both undulating membranes slightly curved and almost in parallel, endoral about 7–10 µm long, paroral 5–6 µm long, begins about 2 µm in front of endoral at level of buccal cirrus; exact structure of membranes not clearly recognizable. Pharyngeal fibres distinct in vivo and after protargol impregnation, of ordinary length and structure, extend obliquely backwards (Fig. 173a, e; Table 153).

Ontogenesis was not studied in detail, but is very similar to that of *Urosomoida* (for a review, see BERGER 1999). It commences with the formation of an oral primordium left of the single postoral cirrus. Then five cirral anlagen streaks each develop independently in proter and opisthe, that is, no primary primordia, as in → *Apourosomoida*, are generated. Anlage IV produces the single postoral cirrus, while anlage V generates the transverse cirrus (Fig. 173g, h). Two dorsal anlagen each are generated in proter and opisthe and produce a caudal cirrus each; the short kinety 3 originates dorsomarginally.

Occurrence and ecology: To date found only at type location, that is, the Namib Desert. Great numbers developed in the non-flooded Petri dish culture, indicating that many resting cysts were present. With its slender body, *Erimophrya arenicola* is perfectly adapted to the sandy biotope, like *Circinella arenicola* FOISSNER, 1994a, a very large (about 400 × 22 µm), vermiform species discovered in an inland sand dune of Utah, USA.

Comparison with related species: For distinguishing *Erimophrya arenicola* and → *E. glatzeli*, see that species. The most important features are the number of postoral cirri (one vs. two) and dorsal bristle rows (three vs. four). In vivo, *E. arenicola* is easily confused with *Urosomoida agilis* (three postoral cirri and yellow cortical granules) and → *Hemiurosoma similis* (FOISSNER, 1982), which, however, entirely lacks postoral cirri (Fig. 183k). In vivo, *E. arenicola* is identified by the following combination of features: very slender (7:1), two almost abutting macronuclear nodules, single postoral cirrus. Nevertheless, identifications should be checked by protargol impregnation.

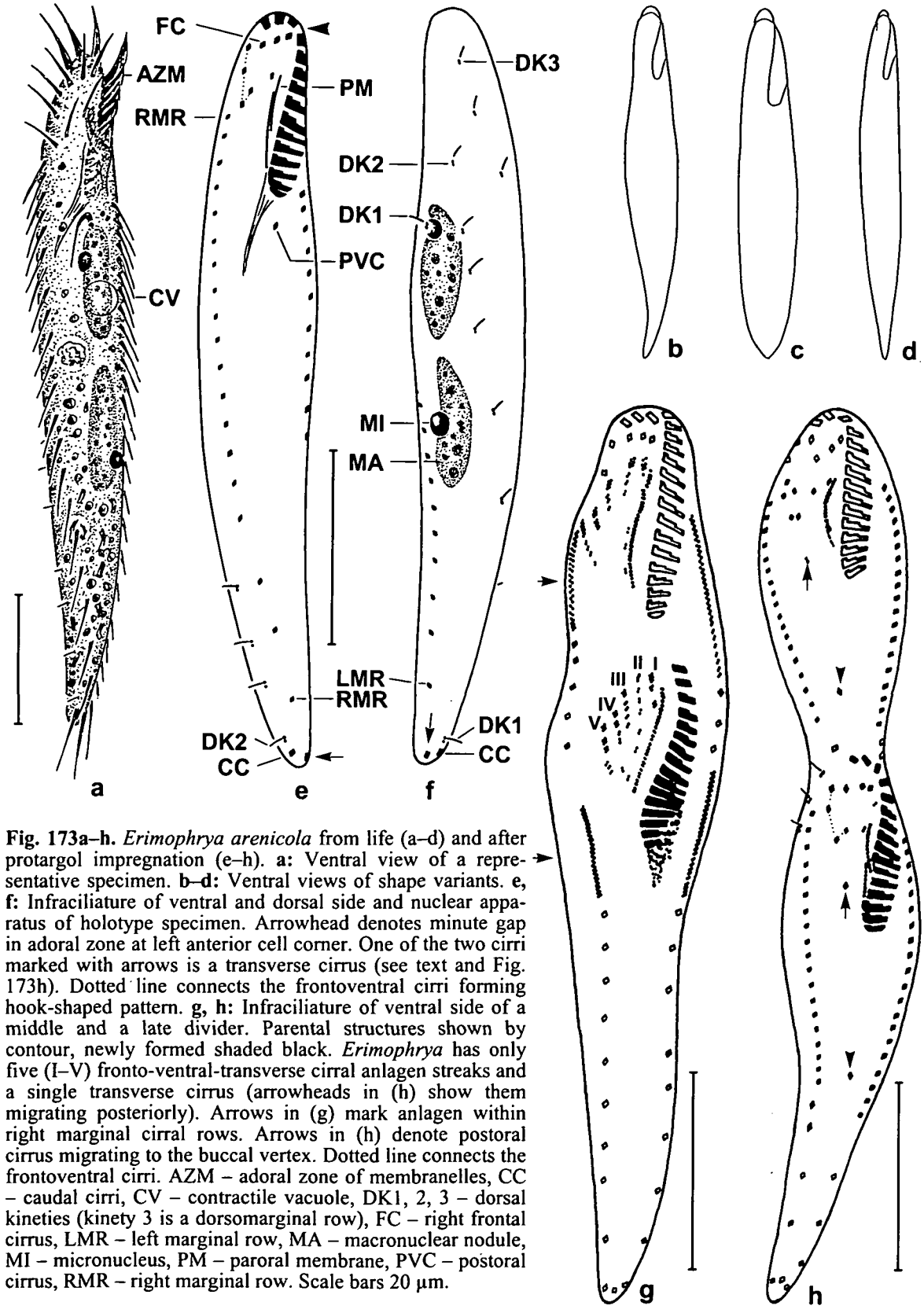


Fig. 173a–h. *Erimophrya arenicola* from life (a–d) and after protargol impregnation (e–h). **a:** Ventral view of a representative specimen. **b–d:** Ventral views of shape variants. **e, f:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrowhead denotes minute gap in adoral zone at left anterior cell corner. One of the two cirri marked with arrows is a transverse cirrus (see text and Fig. 173h). Dotted line connects the frontoventral cirri forming hook-shaped pattern. **g, h:** Infraciliature of ventral side of a middle and a late divider. Parental structures shown by contour, newly formed shaded black. *Erimophrya* has only five (I–V) fronto-ventral-transverse cirral anlagen streaks and a single transverse cirrus (arrowheads in (h) show them migrating posteriorly). Arrows in (g) mark anlagen within right marginal cirral rows. Arrows in (h) denote postoral cirrus migrating to the buccal vertex. Dotted line connects the frontoventral cirri. AZM – adoral zone of membranelles, CC – caudal cirri, CV – contractile vacuole, DK1, 2, 3 – dorsal kineties (kinety 3 is a dorsomarginal row), FC – right frontal cirrus, LMR – left marginal row, MA – macronuclear nodule, MI – micronucleus, PM – paroral membrane, PVC – postoral cirrus, RMR – right marginal row. Scale bars 20 μm.

Gonostomum algicola GELLÉRT, 1942 (Fig. 174a–t, w, 175a–t; 399a–g; Tables 154, 155)

Neotype material: Neotypified from Namibian site (62) population, according to reasons 1, 3, 4, 6 given in chapter 2.4.2.

Synonymy: FOISSNER (1998a) synonymized *Trachelostyla canadensis* BUITKAMP & WILBERT, 1974 with *Gonostomum algicola*, but considered the latter, like BERGER (1999), BUITKAMP (1977b) and HEMBERGER (1982), as a synonym of *G. affine*.

Improved diagnosis: Size about 80 × 22 µm in vivo; lanceolate. 2 macronuclear nodules. Cortical granules colourless and loosely spaced. Cirri conspicuously fine, most comprising only 4 cilia. On average 18 right marginal, 13 left marginal, 2 frontoterminal, 5 frontoventral, and 3 caudal cirri; 1 buccal cirrus slightly above paroral and 1 transverse cirrus near posterior end. Adoral zone of membranelles about one third of body length, composed of 20 membranelles on average. 3–6, usually 4 paroral kinetids.

Redescription: Size 60–110 × 15–30 µm in vivo, as calculated from measurements of live specimens and values shown in table 154, assuming a shrinkage of 10–20% due to the preparation procedures; length:width ratio also highly variable (2.6–5.9:1), usually 3.9:1 both in vivo and after protargol impregnation; very flexible but acontractile. Overall shape usually lanceolate, that is, distinctly tapering anteriorly and posteriorly, left margin almost straight, dorsal convex and with distinct furrow along anterior portion of right marginal row, which extends onto dorsal side; rarely elongate ellipsoidal or sigmoidal with bluntly pointed left anterior end (Fig. 174a, k, l–n); dorsoventrally flattened up to 1.5:1. Macronuclear nodules usually slightly diagonal in central body third, that is, anterior nodule in midline, posterior left of midline; elongate ellipsoidal, contain numerous globular nucleoli. Micronuclei near or attached to macronuclear beads, globular, rarely ellipsoidal. Contractile vacuole with two collecting canals extending anteriorly and posteriorly slightly above mid-body at left margin. Cortical granules 0.8 × 0.5 µm in vivo, although highly refractive difficult to recognize because colourless and loosely spaced in longitudinal rows (Fig. 174p), stain red with methyl green-pyronin; tightly underneath cortex ellipsoidal structures, possibly mitochondria (Fig. 174o). Cytoplasm without crystalline inclusions, with some colourless fat globules 2–3 µm across and about 5 µm-sized food vacuoles containing residues of bacteria and their spores. Movement rather rapidly, without peculiarities.

Cirral pattern very constant, cirral number of usual variability. Cirri conspicuously fine compared to congeners because composed of only 2–8, usually 4 basal bodies (Fig. 174b, c, q, r; 399a–e; Table 154). Marginal cirri about 10 µm long in vivo, arranged in two rows almost confluent posteriorly, gap occupied by transverse cirrus and caudal cirri; right row slightly shorter than left, extends onto dorsal side anteriorly. Eleven fronto-ventral-transverse cirri on average. Frontal cirri about 12 µm long in vivo, not distinctly enlarged, except slightly posteriorly dislocated cirrus I/1, which invariably consists of two fairly long ciliary rows. Buccal cirrus slightly right of and above paroral membrane. Frontoventral cirri in three short, staggered rows close together, thus forming a rather irregular pattern or line usually slightly shorter than, occasionally as long as adoral zone of membranelles. Frontoterminal cirri near or on right dorsolateral surface, form short, slightly oblique row. Transverse cirrus at or slightly right of midline near posterior end.

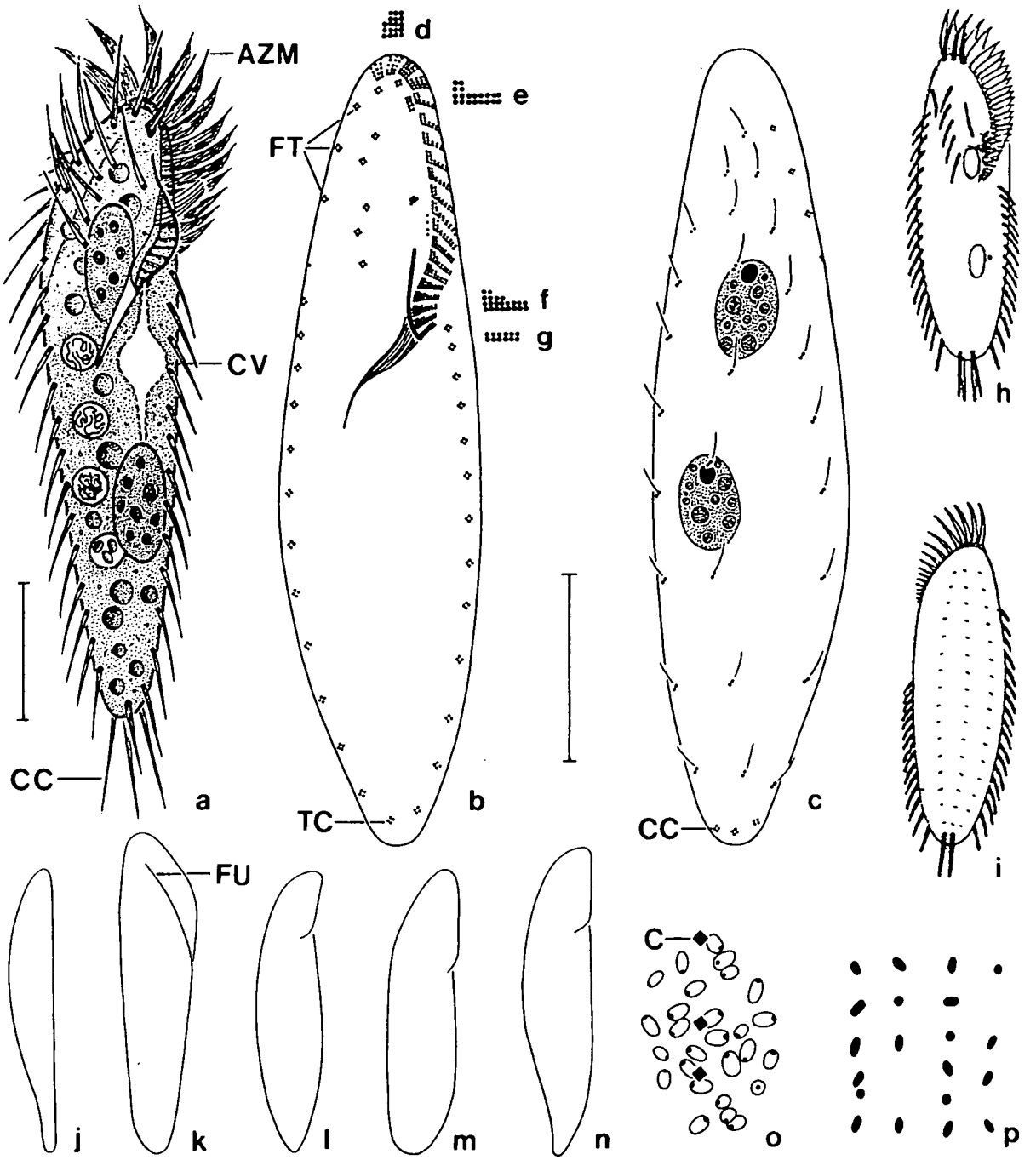


Fig. 174a–p. *Gonostomum algicola* from life (a, j–n, p; k–n redrawn from video records), after protargol impregnation (b, c, o), and opal blue preparation (h, i; from GELLÉRT 1942). **a:** Ventral view of a representative specimen from Namibian neotype population. **b, c:** Infraciliature of ventral and dorsal side of neotype specimen. Most cirri consist of only four cilia. For detailed labelling, see figures 174q, r. **d–g:** Structure of membranelles in frontal, middle, and buccal region of adoral zone, and of last membranelle. The same or a very similar pattern was found in an Australian population of *G. strenuum*. **h, i:** Ventral and dorsal view of specimens from Hungarian type population, which was discovered on tree bark; length 60–100 µm. **j:** Lateral view. **k:** Dorsal view of shape variant showing furrow along right marginal row. **l–n:** Ventral view of shape variants. **o:** Subcortical structures, possibly mitochondria. **p:** The cortical granules are highly refractive but difficult to recognize because small (0.8 × 0.5 µm), colourless, and loosely spaced. AZM – adoral zone of membranelles, C – cirrus, CC – caudal cirri, CV – contractile vacuole, FT – frontoterminal cirri, FU – furrow, TC – transverse cirrus. Scale bars 20 µm.

Dorsal bristles about 3 µm long in vivo, arranged in three rows (Fig. 174c, r). Row 1 extends along left cell margin, commences subapically at level of paroral membrane; row 2 extends in double curved line from left subapical end to midline (or right) of posterior end; row 3 curves from midline of anterior end to right posterior end. Caudal cirri about 15 µm long in vivo, one each attached to dorsal ciliary rows, right cirrus often on lateral surface near last marginal cirrus. Posterior marginal cirri, caudal cirri and transverse cirrus difficult to distinguish because of similar size and close together on narrowed body end (see ontogenesis).

Oral apparatus in *Gonostomum* pattern (Fig. 174a, b, q, v; Table 154). Adoral zone of membranelles occupies only about 37% of body length (50% in congeners), commences near midline of anterior body end and extends straight along left body margin, performing abrupt right bend and slight clockwise rotation to plunge into buccal cavity near left body margin. Largest membranelle bases 4–5 µm wide, membranelle structure depends on zone region (Fig. 174d–g): buccal membranelles composed of two long rows of basal bodies with, except

Table 154. Morphometric data on *Gonostomum algicola*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	71.2	70.0	10.7	2.5	15.0	52.0	95.0	19
Body, width	18.9	19.0	3.8	0.9	19.9	14.0	27.0	19
Body length:width, ratio	3.9	3.7	0.9	0.2	22.6	2.6	5.9	19
Anterior body end to proximal end of adoral zone, distance	26.6	26.0	2.1	0.5	7.8	24.0	31.0	19
Body length:length of adoral zone of membranelles, ratio	2.7	2.7	0.3	0.1	12.7	2.1	3.4	19
Anterior end to posteriormost frontoventral cirrus, distance	21.8	21.0	4.8	1.1	22.1	14.0	32.0	19
Anterior macronuclear nodule, length	12.1	12.0	2.4	0.5	19.6	7.0	16.0	19
Anterior macronuclear nodule, width	4.8	5.0	0.5	0.1	11.2	4.0	6.0	19
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
Micronuclei, length	1.1	1.0	–	–	–	1.0	2.0	19
Micronuclei, width	1.0	1.0	–	–	–	1.0	1.0	19
Micronuclei, number	1.6	2.0	–	–	–	1.0	3.0	19
Adoral membranelles, number	20.2	20.0	1.0	0.2	4.8	19.0	22.0	19
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
Frontoterminal cirri, number	2.4	2.0	–	–	–	2.0	3.0	19
Frontoventral cirri, number	4.8	5.0	1.0	0.2	19.8	4.0	8.0	19
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
Right marginal cirri, number	18.3	18.0	1.8	0.4	10.0	15.0	24.0	19
Left marginal cirri, number	12.9	13.0	1.8	0.4	13.5	10.0	16.0	19
Transverse cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
Caudal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
Dorsal kineties, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
Kinetids in middle dorsal kinety, number	9.1	9.0	1.2	0.3	13.1	7.0	11.0	19
Paroral kinetids, number	4.4	4.0	0.8	0.2	17.4	3.0	6.0	19
Paroral membrane, length	2.9	3.0	1.0	0.2	34.3	1.0	4.0	19
Endoral membrane, length	10.9	11.0	0.7	0.2	6.8	10.0	12.0	19

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

for last membranelle, two short rows of unequal length attached at right anterior end; membranelles in middle portion of zone consist of two long rows of basal bodies with two very short rows, each composed of two basal bodies, attached; frontal membranelles very likely composed of three to four fairly short rows of basal bodies. Proximal portion of adoral zone of membranelles and buccal cavity covered with curved, about 5 µm wide cortical process (lip). Buccal cavity narrow and flat, at right bordered by slightly curved endoral membrane composed of closely spaced basal bodies; paroral slightly above and left of endoral, consists of only three to six widely spaced, about 9 µm long cilia. Pharyngeal fibres clearly recognizable only after protargol impregnation, extend obliquely backwards.

Ontogenesis (Fig. 174s, t, w, 175a–t; 399f, g; Table 155): Terminology and interpretation of the anlagen follow figure 174u, that is, BERGER & FOISSNER (1997). Note that the cirral primordia of the proter and opisthe develop as single streaks (primary primordia), which separate (secondary primordia) only in middle dividers. Thus, a distinction between proter's and opisthe's anlagen is impossible in early dividers, except for anlage 1, which develops differently.

Stomatogenesis commences with the apokinetal proliferation of basal bodies underneath the buccal vertex, where a cuneate anarchic field develops (Fig. 174s, t). The differentiation of adoral membranelles commences at the left anterior end of the oral primordium (Fig. 175a). Membranelle formation proceeds posteriad, while the anlage for the opisthe's paroral and endoral separates as a streak of loosely arranged basal bodies at the right margin of the oral primordium (Fig. 175e, f, g; 399f). These basal bodies arrange to a straight line of dikinetids distinctly separate from the forming adoral zone of membranelles, which curves leftward (Fig. 175i, k; 399g). A rather wide buccal field is thus recognizable in this stage (Fig. 399k). Later, when the shaping of the oral apparatus commences, the paroral and endoral incline and move close to the posterior half of the adoral zone. Thus, the buccal field narrows. The further differentiation of the paroral and endoral anlage occurs as follows (Fig. 175m; 399g): the anterior portion of the dikinetidal line splits longitudinally, producing a long row of closely spaced basal bodies (the new endoral) to the left and, to the right, a short row of widely spaced basal bodies, the prospective paroral. Interestingly and typical for the *Gonostomum* group, the paroral locates left of the endoral when the buccal cavity is shaped, respectively, reorganized in the proter (Fig. 175g, i, o, q; BERGER & FOISSNER 1997). Possibly, this is caused by the growing buccal lip, which takes along the paroral. In the proter, both membranes reorganize after the formation of frontal cirrus I/1 (Fig. 175k, m), while the parental adoral zone of membranelles is retained; the pharyngeal fibres, however, disaggregate in middle dividers and are rebuilt in post-dividers.

The fronto-ventral-transverse cirri originate as follows: when the anarchic field of the oral primordium elongates, proter's anlage I originates at the anterior end of the paroral, and the buccal cirrus disorganizes and proliferates basal bodies anteriorly and posteriorly; furthermore, the posteriormost cirrus of frontoventral row 1 (Fig. 174q) disorganizes and proliferates basal bodies posteriorly, which become anlage III (Fig. 174t, w). Simultaneously, anlage VI is formed de novo right of and at large distance from the frontoterminal cirri (Fig. 174w, 175a, b). In the next series of events, basal bodies from the anterior end of the oral primordium migrate anteriad and form two streaks right of the parental endoral (Fig. 175c, d): the left streak, which becomes opisthe's anlage I, is slightly but clearly separate from anlage II, while the right streak touches proter's anlage III. Subsequently, anlagen IV and V, which are generated

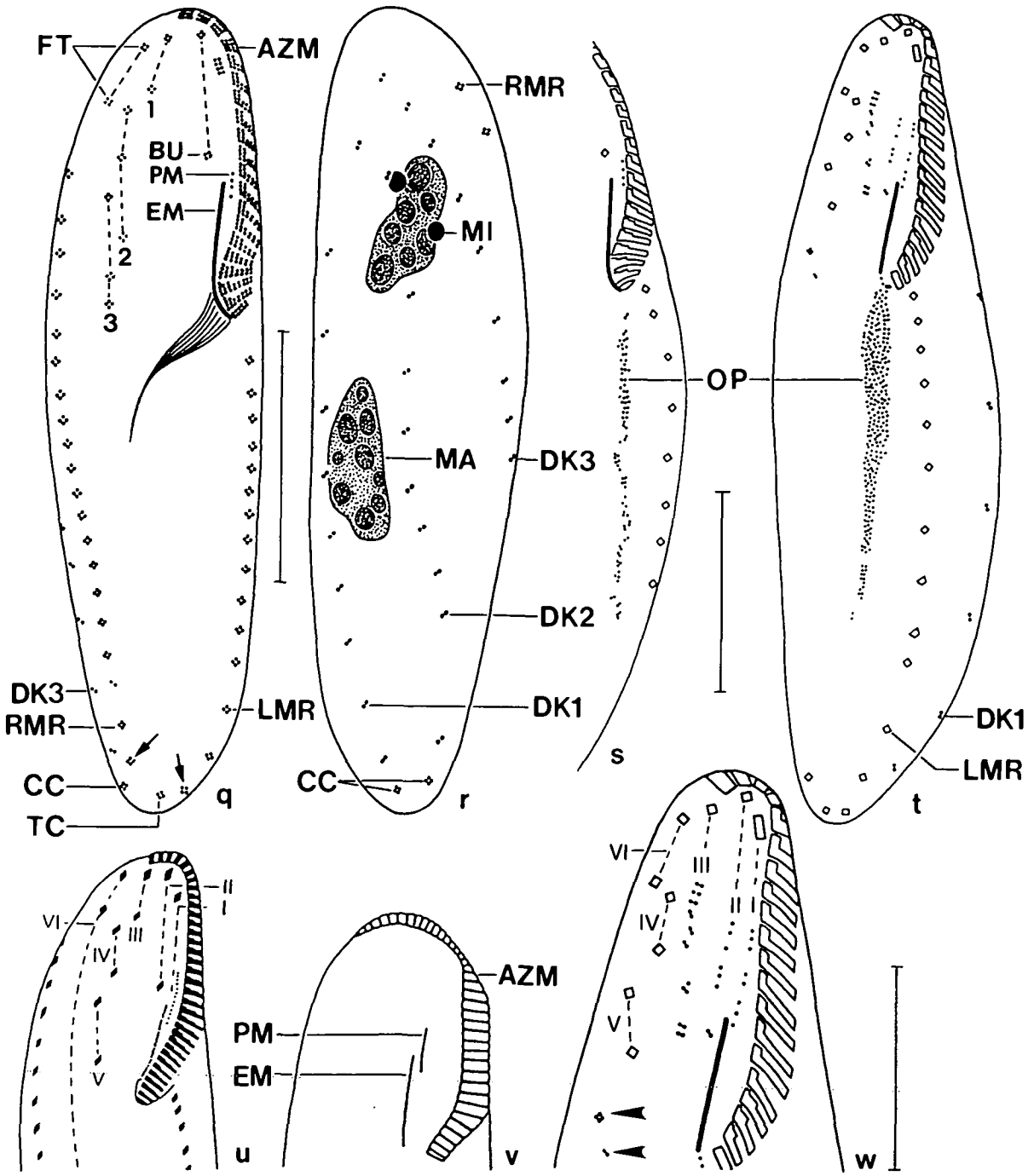
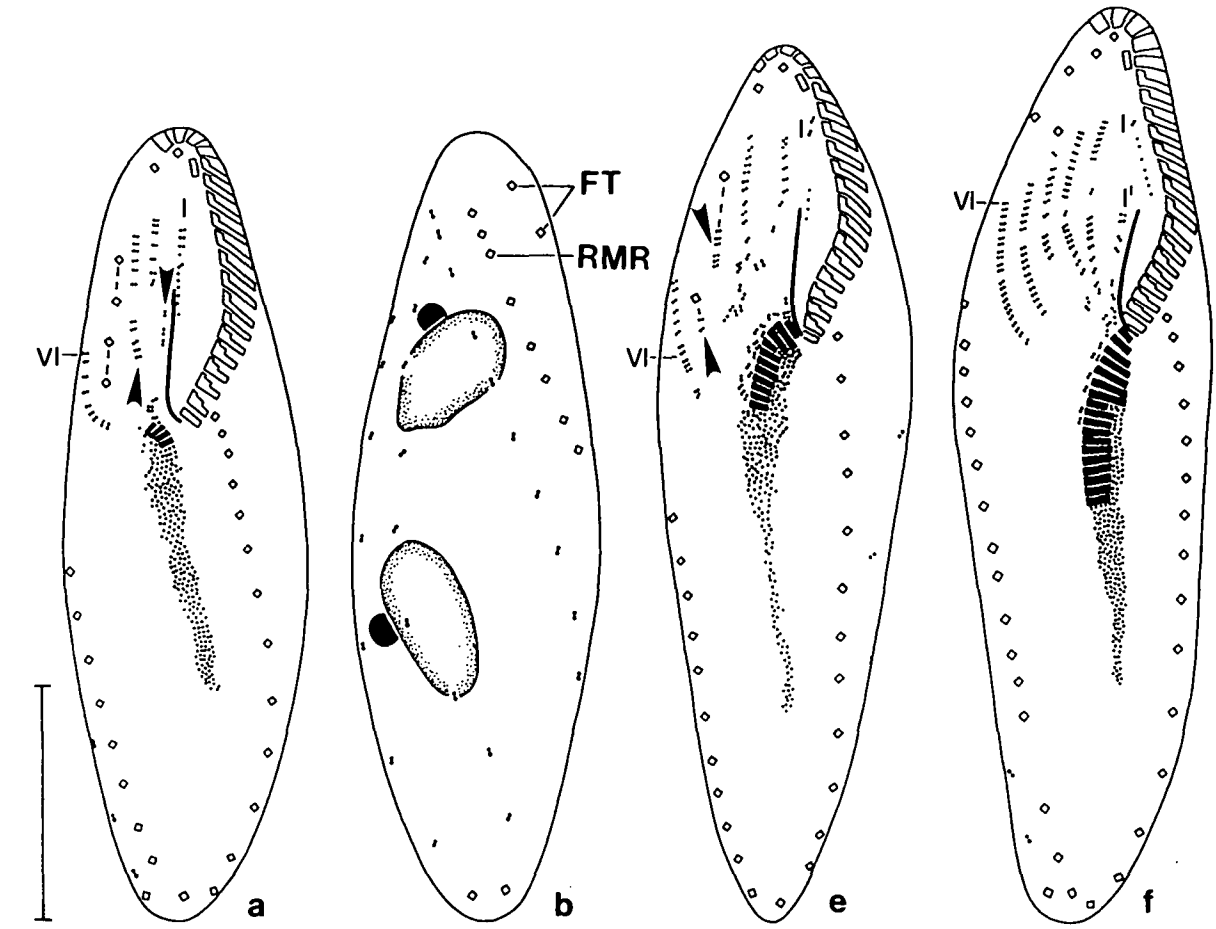


Fig. 174q–t, w. *Gonostomum algicola*, infraciliature of morphostatic (q, r) and dividing (s, t, w) specimens after protargol impregnation. **q, r:** Infraciliature of ventral and dorsal side. Marginal cirri (arrows), the single transverse cirrus, and the right caudal cirrus are close together and were thus misinterpreted in the original description. **s:** Ventral view of a very early divider showing apokinetal origin of oral primordium. **t, w:** Ventral view of an early divider showing origin of proter anlagen I–III from parental structures, whereas anlage VI (arrowheads) originates de novo.

Fig. 174u, v. Terminology of frontoventral cirri and anlagen in *Gonostomum*, and *Gonostomum* pattern of oral apparatus (from BERGER & FOISSNER 1997). AZM – adoral zone of membranelles, BU – buccal cirrus, CC – caudal cirri, DK1-3 – dorsal kineties, EM – endoral membrane, FT – frontoterminal cirri, LMR – left marginal row, MA – macronucleus, MI – micronucleus, OP – oral primordium, PM – paroral membrane, RMR – right marginal row, TC – transverse cirrus, 1-3 – ventral cirral rows, I-VI – cirral anlagen. Scale bars 20 µm (q–t) and 10 µm (w).



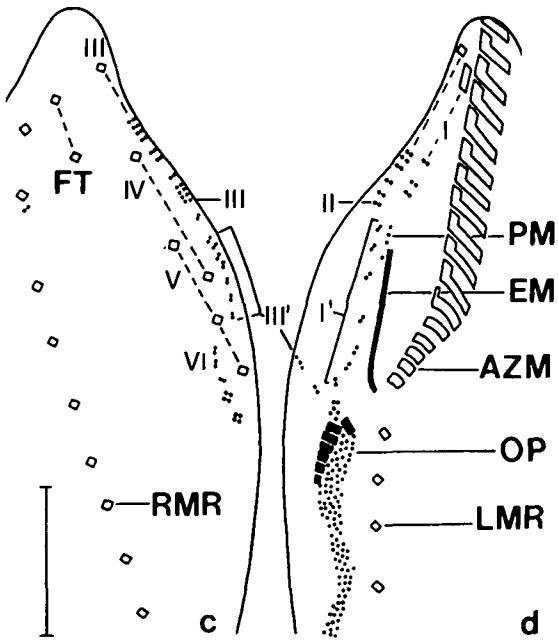


Fig. 175a–f. *Gonostomum algicola*, infraciliature of early dividers after protargol impregnation. **a–d:** Origin of cirral anlagen and adoral membranelles, which commence to differentiate at the anterior end of the oral primordium. Basal bodies from the anterior end of the oral primordium migrate anteriad and organize to two streaks (arrowheads). The left streak becomes opisthe's anlage I, the right (III') touches anlage III. In the specimen shown in Fig. 175a, we cannot exclude that the right anlage (left arrowhead) did not originate by migration of basal bodies from the oral primordium, but from a cirrus because about 15% of the specimens have a cirrus at this site. Note that anlage VI, which originates de novo, is distinctly separate from the oral primordium and the frontoterminal cirri. **e:** Anlagen IV and V are generated by the posteriormost cirrus of rows 2 and 3 (arrowheads). The paroral and endoral anlage separate at the right margin of the oral primordium. **f:** Maturation of the adoral zone of membranelles and growth of anlagen IV and V, which probably incorporate the remaining frontoventral cirri, except for the frontal and frontoterminal cirri. AZM – adoral zone of membranelles, EM – endoral membrane, FT – frontoterminal cirri, LMR – left marginal row, OP – oral primordium, PM – paroral membrane, RMR – right marginal row, I-VI – cirral anlagen, I', III' – opisthe anlagen. Scale bars 20 μm (a, b, e, f) and 10 μm (c, d).

by the posteriormost cirrus of rows 2 and 3 (Fig. 174q, 175e; 399f), elongate anteriad, probably incorporating the remaining frontoventral cirri (Fig. 175f, g). Thus, two short (anlagen I and I', which later form the left frontal cirrus in each proter and opisthe) and five long streaks (anlagen II–VI) are now recognizable in the proter frontal area. The long streaks (the so-called primary primordia) then divide transversely to form a set of cirral anlagen (secondary primordia) each for the proter and opisthe (Fig. 175i). Cirri segregate from anterior to posterior and very likely originate in the following manner (Fig. 175k, o, q, s; 399g; Table 155): frontal cirrus I/1 from anlage I; buccal and frontal cirrus II/1 from anlage II; frontal cirrus III/1 and usually one frontoventral cirrus from anlage III; usually two frontoventral cirri from anlage IV; one transverse cirrus and usually two frontoventral cirri from anlage V; two or three frontoterminal cirri from anlage VI. We must emphasize that this

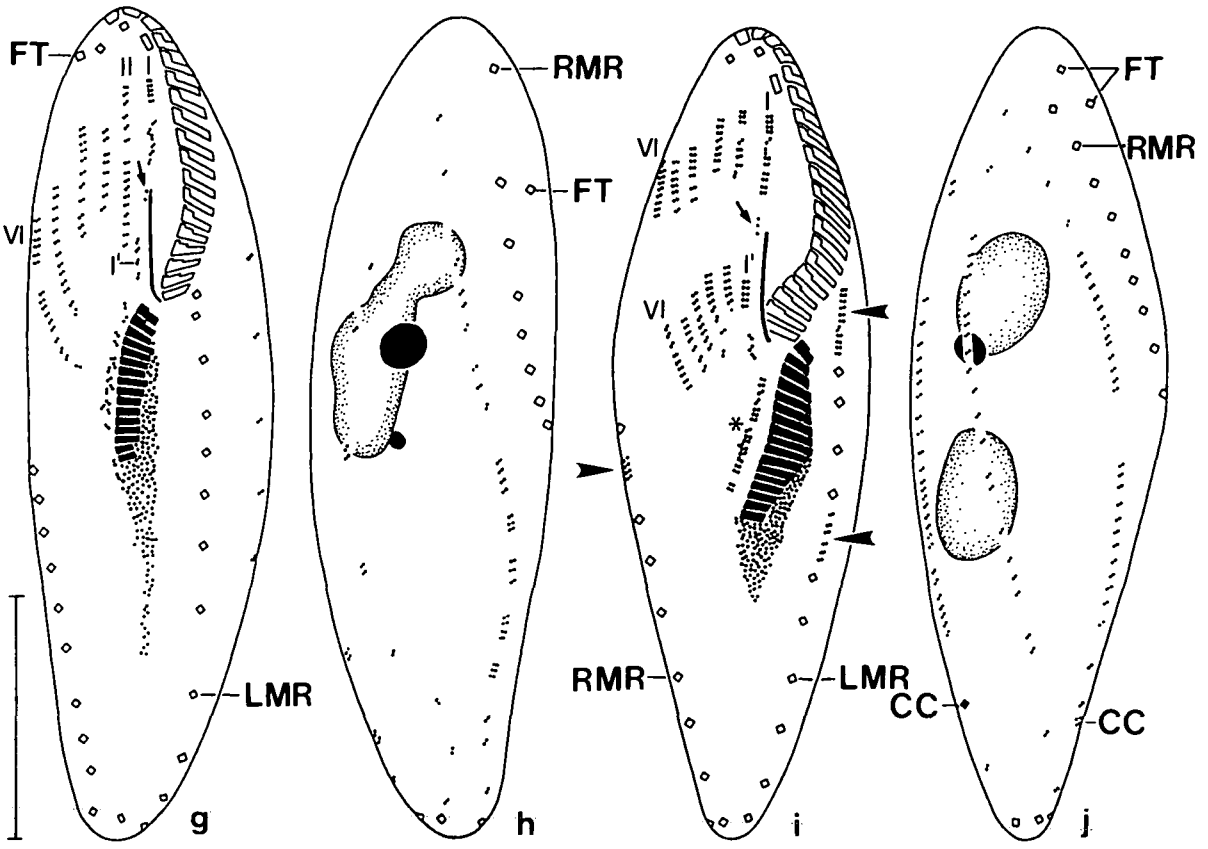


Fig. 175g–j. *Gonostomum algicola*, infraciliature of middle dividers after protargol impregnation. **g, h:** Ventral and dorsal view of same specimen showing five primary primordia (anlagen II–VI) in the frontal area and intrakinetal proliferation of basal bodies in the dorsal kineties. Proter's anlage I originates from the parental paroral (arrow), while the opisthe's anlage I is generated by the oral primordium. The new frontal cirrus I/1, which is generated by the anlagen I and I', assembles in the proter, while it still consists of widely spaced dikinetids in the opisthe. Note that the parental paroral (arrow), which is *left* of the endoral in morphostatic cells, moved to the *right*, very likely due to the flattening of the buccal cavity during the reorganization of the parental oral apparatus (see also Fig. 175i). **i, j:** Ventral and dorsal view of same specimen. The five primary primordia (Fig. 175g) split transversely to form five secondary primordia each in proter and opisthe. Arrow marks rest of parental paroral. The opisthe anlage I generates frontal cirrus I', and the basal bodies for the paroral and endoral anlage align (asterisk). Short streaks develop from dedifferentiated cirri at two sites in each marginal row (arrowheads). The dorsal kineties commence to split at mid-body and caudal cirri (CC) originate at their posterior ends. CC – newly formed caudal cirri, FT – frontoterminal cirri, LMR – left marginal row, RMR – right marginal row, I-VI – cirral anlagen, I' – opisthe anlage. Scale bar 20 μm.

pattern was deduced from stages like those shown in figures 175m, o and 399g. Accordingly, we cannot exclude that some cirral migration has already occurred and the pattern is thus different.

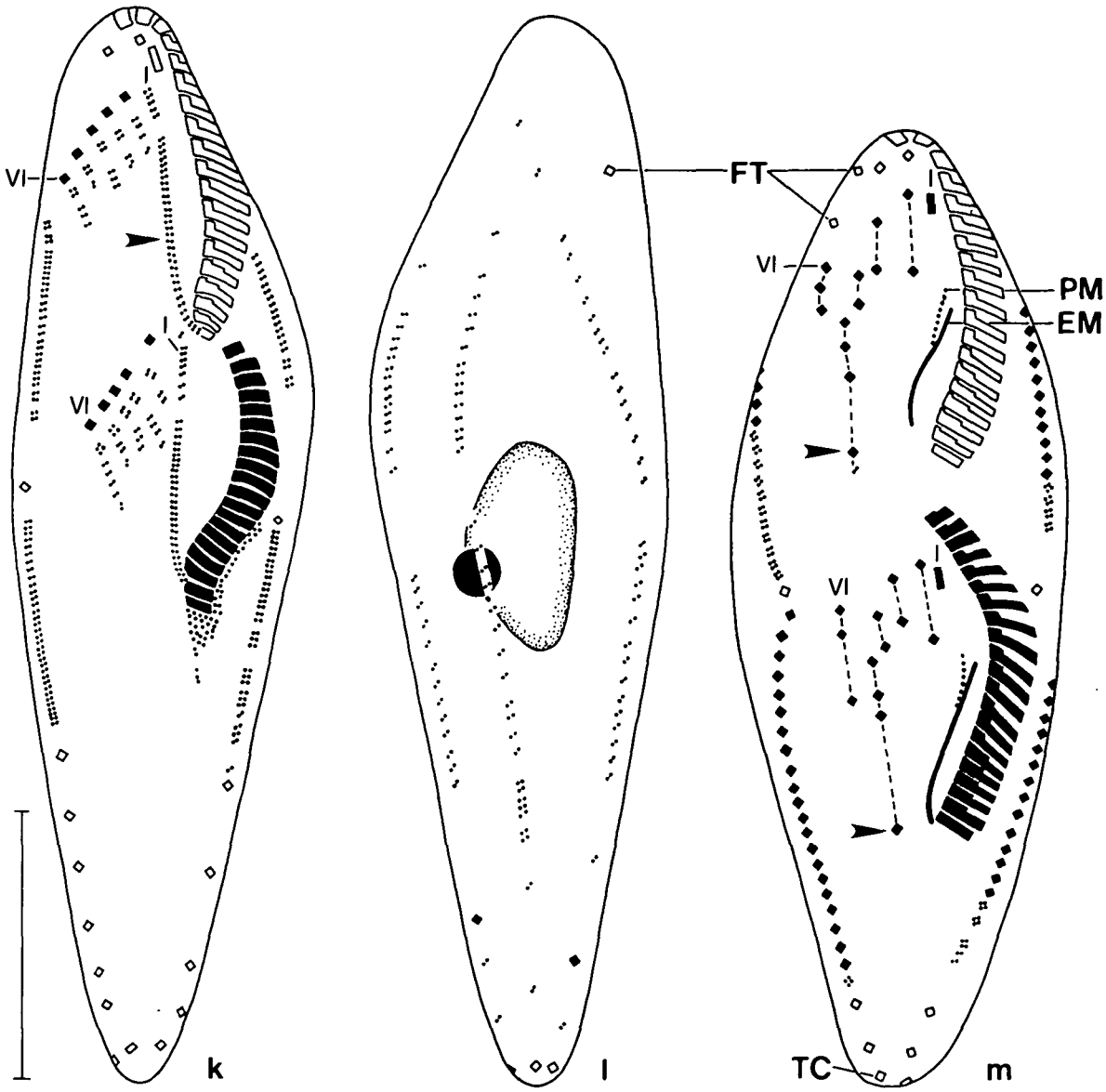


Fig. 175k–m. *Gonostomum algicola*, infraciliature of a middle and a late divider after protargol impregnation. Parental structures shown by contour, newly formed shaded black. **k, l:** Ventral and dorsal view of same specimen. Cirri segregate posteriad from the six fronto-ventral-transverse cirral anlagen in the proter and opisthe. The proter's paroral and endoral are reorganizing (arrowhead). The parental paroral has been either resorbed or incorporated into the anlage, which consists of distinct dikinetids. The macronuclear nodules fused to a globular mass. Note that caudal cirri formed only in rows 1 and 3 of the opisthe. The other caudal cirri are generated later (Fig. 175n, p). **m:** The formation of membranelles in the opisthe's adoral zone is complete. The new cirri arrange to the mature pattern, that is, the proter frontal cirrus I/1 replaces the old one and the posteriormost cirrus of anlage V migrates posteriad to become the transverse cirrus (arrowheads). However, we cannot exclude that some cirral migration has already occurred and the pattern is thus different. The anterior third of the proter's and opisthe's paroral and endoral anlage splits longitudinally: the left fork becomes the long endoral, while the right becomes the minute paroral. EM – endoral membrane, FT – frontoterminal cirri, PM – paroral membrane, TC – transverse cirrus, I-VI – cirral anlagen. Scale bar 20 µm.

Finally, the new cirri arrange to the mature pattern and replace the parental frontal and frontoterminal cirri in the proter and the transverse cirrus in the opisthe (Fig. 175m, o, q; 399g); the distinct migration of the latter, from the frontal field to the posterior body end, is highly remarkable (Fig. 175m, o, q, s; 399g). Proter's anlage VI never contacts the last frontoterminal cirrus (VI/2 or VI/3), only the newly formed frontoterminal cirri come rather close to the old ones when they migrate anteriad (Fig. 175m, o, q, r).

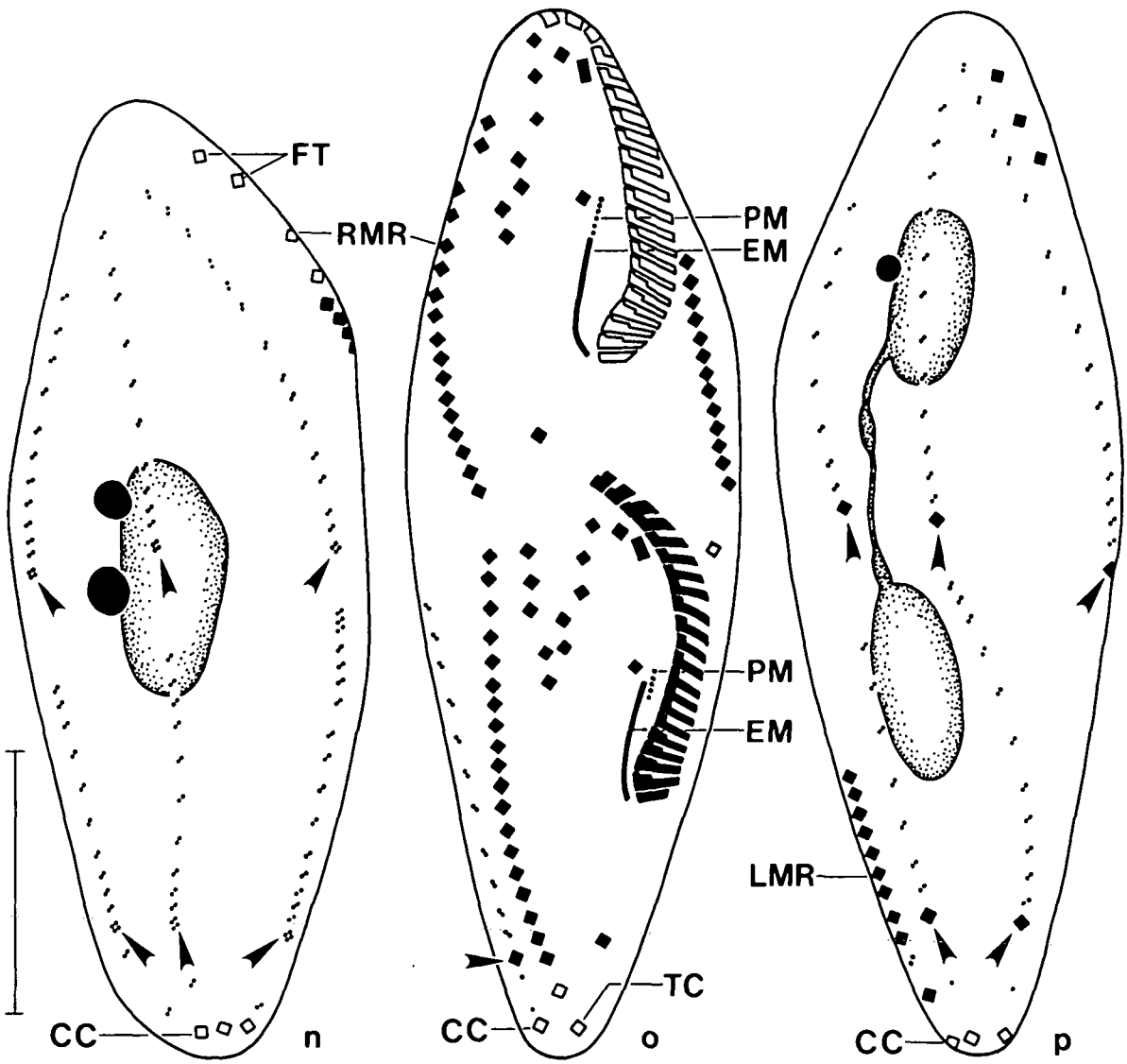


Fig. 175n–p. *Gonostomum algicola*, infraciliature of late dividers after protargol impregnation. Parental structures shown by contour, newly formed shaded black. **n:** The formation of caudal cirri commences at the posterior end of the dorsal ciliary rows (arrowheads), which split in mid-body. The newly formed marginal cirri are replacing the old ones. **o, p:** Ventral and dorsal view of same specimen. The paroral membrane of the opisthe is now left of the endoral (cp. figure 175m), possibly due to the shaping of the opisthe's buccal cavity and lip, while that of the proter is still moving to the left (cp. figure 175m with figure 175q). Caudal cirri were generated at the end of all dorsal ciliary rows (arrowheads). CC – parental caudal cirri, EM – endoral membrane, FT – parental frontoterminal cirri, LMR – left marginal row, PM – paroral membrane, RMR – right marginal row, TC – parental transverse cirrus. Scale bar 20 μm.

The marginal rows, the dorsal kineties and the nuclear apparatus divide as in congeners (Fig. 175h–t; BERGER & FOISSNER 1997, HEMBERGER 1982, OLMO & TÉLLEZ 1997, SONG 1990a). The three dorsal kineties form an anlage each in the proter and opisthe by intrakinetal proliferation of basal bodies and usually generate caudal cirri in a very specific time sequence: middle dividers produce a caudal cirrus each in rows 1 and 3 of the opisthe (Fig. 175j, l), late dividers generate a caudal cirrus in the middle row of the opisthe and in each row of the proter (Fig. 175n, p). This pattern is not entirely constant, that is, occasionally very late dividers produce caudal cirri only in rows 1 and 3 of the proter and in the middle row of the opisthe, while the caudal cirrus of the proter's middle row only assembles in early post-dividers (Fig. 175r, t).

Other temporal relationships are also somewhat variable. For instance, the macronuclear nodules may fuse before or after the primary primordia have split (Fig. 175g–j) and anlage I of the opisthe may develop at the beginning or after streak formation (Fig. 175a–f).

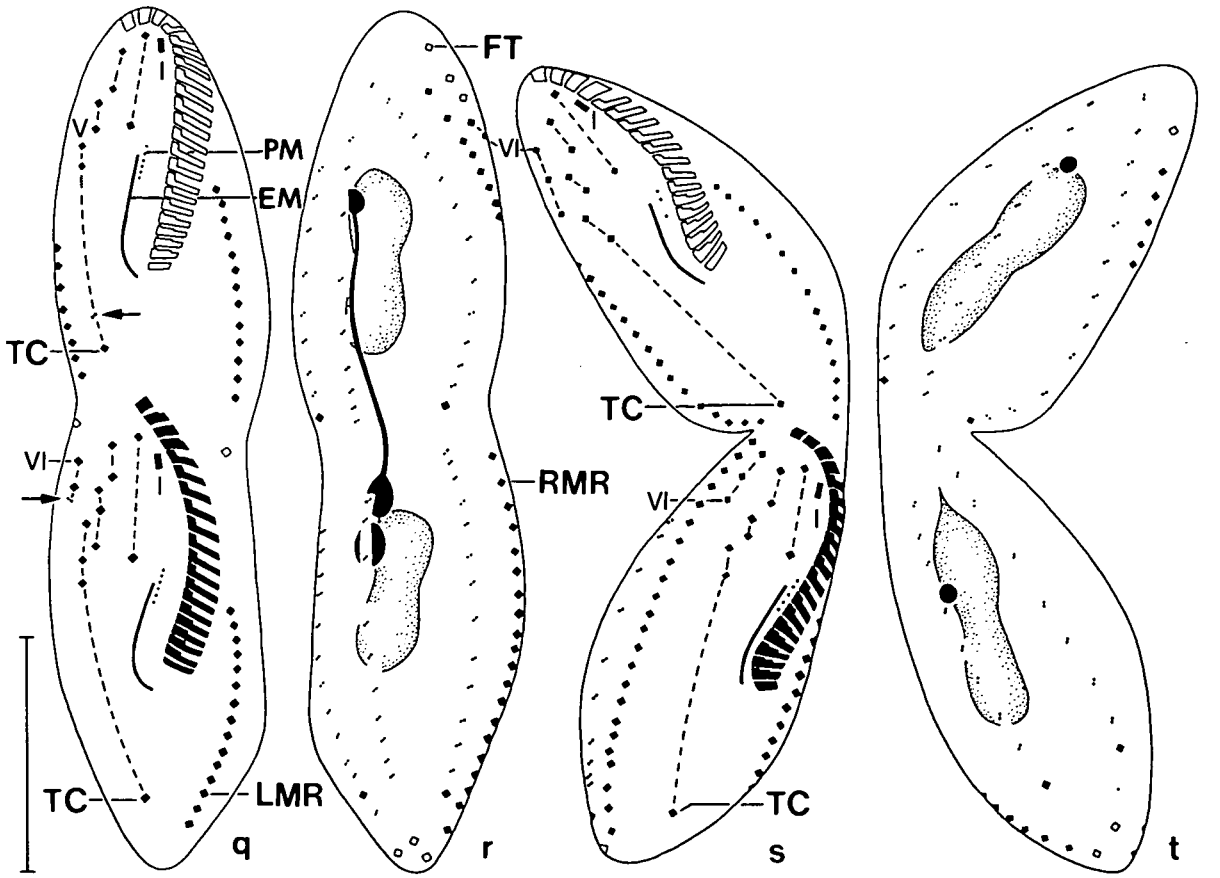


Fig. 175q–t. *Gonostomum algicola*, infraciliature of ventral and dorsal side of a late and a very late divider after protargol impregnation. Cirri possibly developing from the same anlage are connected by hatched lines (for details, see text). Parental structures shown by contour, newly formed shaded black. **q, r:** The parental transverse cirrus and the frontal cirri have been replaced. The paroral membrane is now left of the endoral in the proter and opisthe. Arrows mark kinetids which will be resorbed. **s, t:** The parental frontoterminal cirri were replaced by new ones, which derived from anlage VI. The old caudal cirri are replaced just before cell fission. The caudal cirrus of the proter's middle row occasionally only develops in post-dividers. EM – endoral membrane, FT – frontoterminal cirri, LMR – left marginal row, PM – paroral membrane, RMR – right marginal row, TC – transverse cirrus, I-VI – cirral anlagen. Scale bar 20 µm.

Table 155. Number of cirri formed in the fronto-ventral-transverse anlagen (FVT-anlagen) of *Gonostomum algicola*.

FVT-anlage	I	II	III	IV	V	VI
Number of cirri	1	2	2–3	2–3	3–4	2–3

Ontogenetic comparison: Our study focused on the formation of the six fronto-ventral-transverse cirral anlagen, especially anlage VI, because previous investigations differ in this respect. It is important to note that an Australian population of *G. strenuum*, which we investigated for comparison (data not shown), has virtually the same pattern as *G. algicola*.

Gonostomum affine, as described by HEMBERGER (1982): Anlage II is formed by the buccal cirrus *and* the oral primordium; the anterior portion of anlage VI is formed de novo, while the posterior half is generated by the oral primordium. In *G. algicola* and the Australian population of *G. strenuum*, the whole anlage II is formed by the buccal cirrus and anlage VI originates entirely de novo (Fig. 174w, 175a, b).

Gonostomum strenuum from China, as described by SONG (1990a): The anlagen streaks are formed mainly by the oral primordium (Fig. 9 in SONG's paper; showing a reorganizer in our opinion!). In *G. algicola* and the Australian population of *G. strenuum*, the anlagen streaks are formed by the frontoventral cirri (except for opisthe's streaks I and VI and possibly the posterior portion of anlage III; Fig. 174w, 175a, e, f, g, i). *Gonostomum strenuum* from Europe, as described by OLMO & TÉLLEZ (1997): anlage VI originates from the last fronto-terminal cirrus. In *G. algicola* and the Australian population of *G. strenuum*, anlage VI originates de novo (Fig. 174w, 175a, c).

Very recently, after the present text was written, EIGNER (1999) studied the ontogenesis of *G. kuehnelti* and *G. affine*. Unfortunately, the text is rather confusing and difficult to read. Furthermore, EIGNER (1999) hardly discussed previous results. Thus, a proper comparison is difficult. However, it seems that his data match ours: anlage VI originates de novo, without any participation of the parental frontoterminal cirri; proter's and opisthe's anlage I are not connected in *G. affine*; and the primary primordia develop mainly from the frontoventral cirri, not from the oral primordium, as stated by SONG (1990a). On the other hand, EIGNER (1999) denies any reorganization of the parental undulating membranes in *G. affine* and possibly also in *G. kuehnelti*. This is an incorrect statement because his figures 18 and 25 show the reorganization in *G. affine* very clearly and are virtually identical to our figure 175m. Thus, we also doubt that proter's and opisthe's anlage I are connected in *G. kuehnelti*.

Although some of the differences detailed in the previous paragraphs might be species-specific, we suggest that all populations have the same pattern as *G. algicola*, that is, we interpret most differences as observation errors.

Occurrence and ecology: *Gonostomum algicola* was discovered by GELLÉRT (1942) in Hungary in the algal layer covering tree bark. Our record is the first from mineral soil and the second world-wide; both habitats agree in being ephemeral. Also found at Namibian site (50) with the same features.

Comparison with original description and related species: Our specimens agree with *Gonostomum algicola* GELLÉRT, 1942 in several specific features (cp.

figures 174b, c with figures 174h, i): size (prepared specimens 52–95 µm respectively 60–100 µm), short adoral zone of membranelles (about 40% of body length; about 50% in congeners), and pattern and number of frontoventral and frontoterminal cirri. There are, however, some differences, namely, the number of transverse (1 vs. 4) and caudal cirri (3 vs. 2). Both are difficult to ascertain without ontogenetic data, even in protargol-impregnated specimens, because all cirri have a very similar size and are close together due to the narrowed body end. Thus, it is reasonable to assume that GELLÉRT, who studied only opal blue-treated, air-dried, morphostatic specimens, misidentified the posteriormost marginal cirri and the right caudal cirrus, which is often laterally inserted, as transverse cirri (cp. figures 174h, i with figures 174q, r); accordingly, he counted four ventral transverse and two dorsal caudal cirri. Some other small differences, for instance, in the arrangement of the dorsal kineties and the length of the right marginal row, are very likely also caused by GELLÉRT's insufficient preparation method.

Gonostomum algicola differs from the congeners so far investigated in detail (BERGER 1999, BUITKAMP 1977b, BUITKAMP & WILBERT 1974, EIGNER 1999, FOISSNER 1982, 1987b, HEMBERGER 1982, OLMO & TÉLLEZ 1997, SONG 1990a) by the short adoral zone of membranelles (37% vs. about 50% of body length), the slender body (4:1 vs. 2.6–3.4:1), the fine cirri (4 vs. ≥ 8 cilia), the low number of transverse cirri (1 vs. usually ≥ 3), and the minute paroral membrane (4 vs. ≥ 10 cilia). The single transverse cirrus is probably the most useful feature because it was found also in the population from site (50). The other differences occur also in → *G. namibiense*, which is probably the most closely related species, but has a distinct tail and thus cannot be mixed with *G. algicola*.

Gonostomum namibiense nov. spec. (Fig. 176a–j; Table 156)

Diagnosis: Size about 90 × 20 µm in vivo. Elongate lanceolate with tail-like posterior portion occupying about 15% of body length. 2 macronuclear nodules. Cortical granules about 1 × 0.3 µm, colourless, scattered. On average 26 right marginal, 17 left marginal, 2 frontoterminal, 6 frontoventral, 2 pretransverse, and 5 transverse cirri; 1 buccal cirrus in front of anterior end of paroral. Adoral zone of membranelles about 37% of body length, composed of 27 membranelles on average. 5–10, usually 6 paroral kinetids.

Type location: Highly saline soil from margin of Etosha Pan, Namibia, 19°10'S 15°55'E (site 61 in figures 2, 3 and chapter 2.1.2).

Etymology: Named after the country discovered.

Description: Size 80–110 × 15–25 µm in vivo, usually near 90 × 20 µm. Body elongate ellipsoidal or lanceolate, with short but distinct tail occupying about 15% of body length in vivo (Fig. 176a, c, d; Table 156). Cells acontractile but flexible and very fragile, prepared specimens thus considerably stouter (2.8–3.5:1, on average 3.1:1) and with broadened tail. Trunk flattened up to 2:1 and asymmetrical, left margin straight to slightly sigmoidal, right convex and narrowed in posterior quarter producing tail-like process. Anterior macronuclear nodule about in, posterior slightly left of midline, ellipsoidal (2:1) to elongate ellipsoidal (3:1), contain numerous globular nucleoli. Micronuclei near or attached to macronuclear

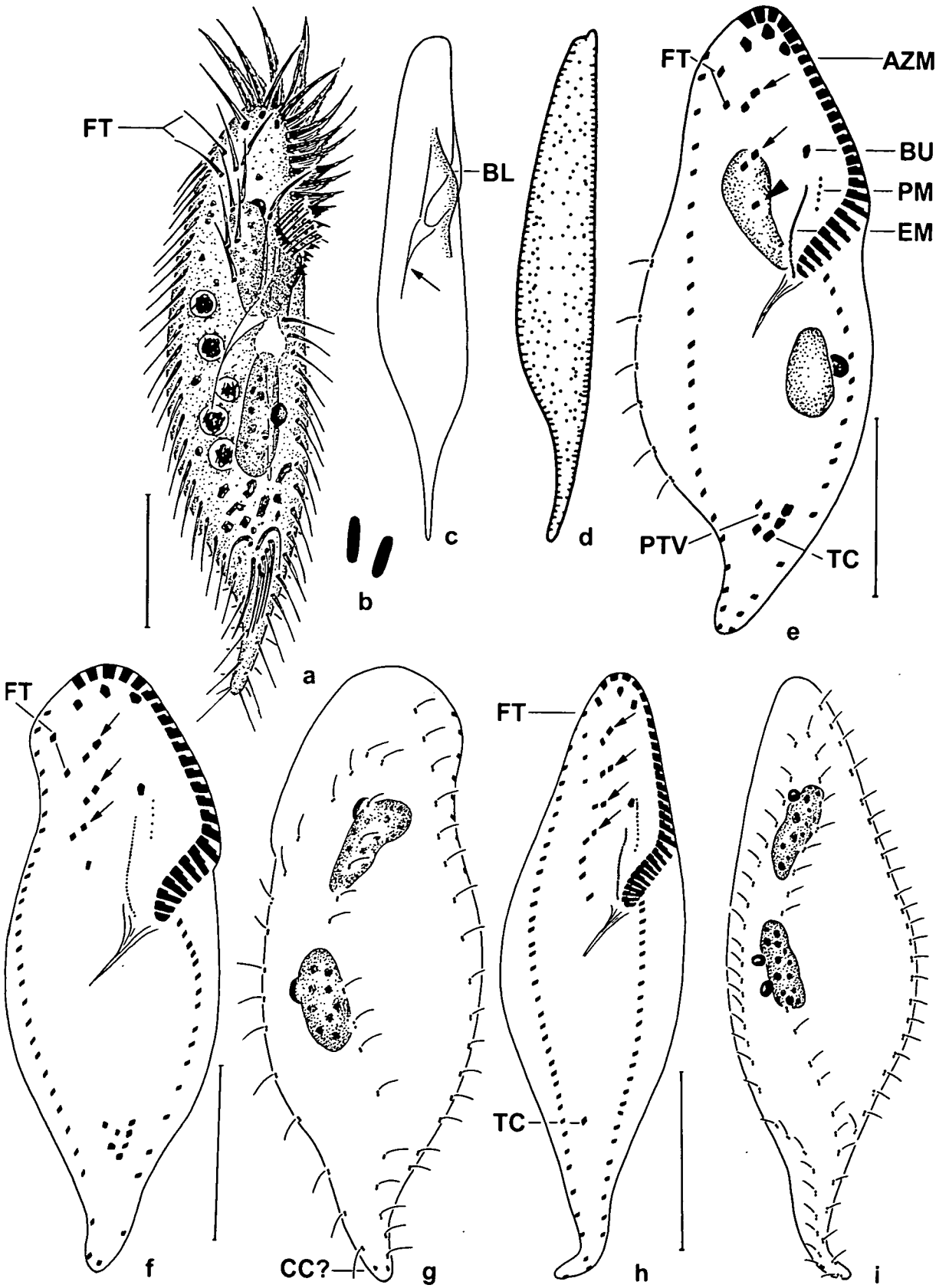
nodules, about 3 µm across in vivo. Contractile vacuole with two collecting canals near mid-body underneath buccal vertex. Cortical granules closely spaced, scattered, difficult to recognize because minute (1 × 0.3 µm) and colourless, stain red with methyl green-pyronin and increase to 2 × 1 µm (Fig. 176b, d); impregnate more or less intensely with protargol. Cytoplasm colourless but opaque, with 1–3 µm-sized crystals mainly in posterior body portion, and food vacuoles 4–5 µm across containing bacterial residues. Glides slowly to rather rapidly on microscope slide.

Cirral pattern rather constant and conspicuous because of midventral-like frontoventral cirral pairs; number of cirri of usual variability (Fig. 176e, f; Table 156). Most cirri about 10 µm long. Marginal cirri in two rows, both extend onto tail and posterior end, where they become cilia-like and are thus easily mistaken for dorsal bristles. Twelve frontoventral cirri on average. Frontal cirri moderately enlarged. Buccal cirrus slightly right and in front of paroral membrane. Frontoventral row usually distinctly shorter than adoral zone of membranelles, slightly right of midline, composed of two to four, usually three cirral pairs and a single cirrus at posterior end of row. Frontoterminal cirri near dorsolateral surface, form short, often slightly oblique row. Transverse cirri subterminally in midline, form hook-like pattern, slightly enlarged and about 15 µm long in vivo; pretransverse cirri very close to transverse cirri.

Dorsal bristles 3–4 µm long in vivo, arranged in three rows (Fig. 176g, i). Row 1 extends, except anteriorly, along left cell margin, commences, like row 2, subapically; row 3 commences apically and extends along right cell margin. Possibly two fine caudal cirri at top of tail; however, the arrangement and composition of the tail ciliature are difficult to analyze because both (marginal? caudal?) cirri and dorsal bristles are composed of basal body pairs; in vivo, the bristles (cirri) on the top of the tail are inconspicuous. Consequently, caudal cirri were not included in the diagnosis.

Oral apparatus in *Gonostomum* pattern (Fig. 176a, e, f). Adoral zone occupies only about 37% of body length (50% in most congeners), composed of an average of 26 membranelles, commences near midline of anterior body end and extends straight along left body margin, performing abrupt right bend and slight clockwise rotation to plunge into buccal cavity near left body margin. Largest membranelle bases about 5 µm wide. Proximal portion of adoral zone and buccal cavity almost entirely covered by a curved, rather prominent cortical process (buccal lip) bearing the paroral membrane, which consists of five to ten widely spaced, 10 µm long cilia. Buccal cavity flat and narrow, at right bordered by slightly curved endoral membrane composed of tightly spaced basal bodies. Pharyngeal fibres clearly recognizable in vivo, extend obliquely backwards.

Fig. 176a–i. *Gonostomum namibiense* from life (a–d) and after protargol impregnation (e–i). **a:** Ventral view of a representative specimen. **b:** The cortical granules are colourless and about 1 × 0.3 µm in size. **c:** Lanceolate shape variant showing large buccal lip. Arrow marks pharyngeal fibres. **d:** Right lateral view showing dorsoventral flattening and arrangement of cortical granules. **e:** Ventral infraciliature and nuclear apparatus of paratype. Arrows mark frontoventral cirral pairs, arrowhead denotes single cirrus at end of frontoventral row. **f, g:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrows mark three cirral pairs of frontoventral row. **h, i:** Infraciliature of ventral and dorsal side and nuclear apparatus of a specimen from site (30). Arrows mark four cirral pairs in the frontoventral row, which has a distinct tail. This population very likely lacks caudal cirri; however, this must be verified by ontogenetic data. AZM – adoral zone of membranelles, BU – buccal cirrus, BL – buccal lip, CC? – caudal (?) cirri, EM – endoral membrane, FT – frontoterminal cirri, PM – paroral membrane, PTV – pretransverse ventral cirri, TC – transverse cirri. Scale bars 20 µm (a, e, f, g) and 30 µm (h, i).


FT
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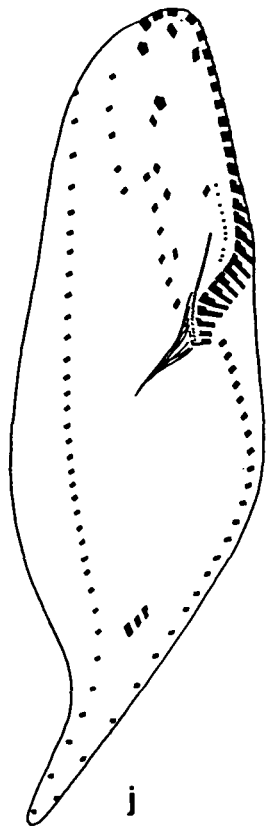


Fig. 176j. *Gonostomum namibiense* from site (49), length 100 µm. Infraciliature of ventral side after protargol impregnation. Specimens from this population usually have three transverse/pretransverse cirri, and are in this respect thus in between those from site 30 (Fig. 176h) and 61 (Fig. 176f). For labelling, see previous figures.

Occurrence and ecology: To date found only in Namibia, where it occurs in non-saline to highly saline habitats. However, the populations from sites (30) and (49) might be distinct subspecies because of considerable differences in quite a number of morphometrics (Table 156). On the other hand, body shape, cortical granules, and cirral pattern are rather similar in all populations. Comparable differences have been reported among *Gonostomum affine* populations (BERGER 1999, FOISSNER et al. 2001). Very recently, we found *G. namibiense* in a slightly saline soil sample from Saudi Arabia. This indicates that it has a wide geographical distribution and prefers saline habitats.

Comparison with related species: *Gonostomum namibiense* differs from all congeners by the tail-like elongation of the rear end, a very distinct feature facilitating in vivo identification. However, we have three further tailed species with similar extrusomes in our unpublished notes. Thus, identification must be checked by protargol impregnation. The tail is very likely produced by body elongation because the usual 50% *Gonostomum* ratio of body length: length of adoral zone of membranelles is obtained only when the tail is omitted.

In vivo *Gonostomum namibiense* is easily confused with → *Paragonostomum* spp. These species lack transverse cirri and cortical granules, and → *P. multinucleatum* has a row of 4–9 (7 on average) macronuclear nodules, while → *P. caudatum* lacks the frontoventral cirral pairs so distinct in *Gonostomum namibiense*. Inexperienced workers may confuse *Gonostomum namibiense* also with certain *Urosoma* species which, however, have only five frontoventral cirri.

Table 156. Morphometric data on *Gonostomum namibiense* from Namibian sites 61 (upper line; type population) and 30 (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	72.9	73.0	6.8	1.6	9.4	60.0	85.0	18
	100.2	102.0	9.2	2.0	9.2	84.0	115.0	21
Body, width	23.4	23.5	2.0	0.5	8.7	20.0	28.0	18
	27.0	27.0	4.8	1.1	17.6	19.0	36.0	18
Body length:width, ratio	3.1	3.0	0.4	0.1	12.5	2.7	4.3	16
	3.8	3.6	0.6	0.1	14.9	2.9	5.0	18
Anterior body end to proximal end of adoral	28.7	28.5	2.3	0.5	8.0	24.0	32.0	18
zone of membranelles, distance	40.8	4.0	4.9	1.1	12.1	29.0	52.0	21

(continued)

Characteristics [a]	$\bar{X}$	M	SD	SE	CV	Min	Max	n
Body length:length of adoral zone of membranelles, ratio	2.5	2.6	0.2	0.1	9.0	2.1	2.9	18
	2.5	2.5	0.3	0.1	12.3	1.7	3.2	21
Anterior body end to last frontoventral cirrus, distance	22.6	22.0	2.0	0.5	8.9	20.0	26.0	18
	38.3	37.0	5.1	1.1	13.3	32.0	57.0	21
Anterior body end to buccal cirrus, distance	15.1	15.0	2.3	0.5	15.0	11.0	21.0	18
	21.8	22.0	2.5	0.6	11.2	15.0	26.0	18
Anterior body end to anteriormost transverse cirrus, distance	54.2	55.0	5.3	1.3	9.8	43.0	65.0	18
	72.7	73.0	8.0	1.8	11.0	60.0	90.0	19
Anterior body end to anterior end of right marginal row, distance	5.3	5.5	1.5	0.4	28.0	3.0	9.0	18
	9.1	9.0	1.9	0.4	20.7	6.0	13.0	19
Anterior macronuclear nodule, length	11.7	12.0	2.1	0.5	18.0	8.0	16.0	18
	16.0	16.0	2.1	0.4	12.9	12.0	20.0	21
Anterior macronuclear nodule, width	5.3	6.0	1.0	0.2	18.2	4.0	6.0	18
	5.4	6.0	0.7	0.1	12.5	4.0	6.0	21
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	18
	2.0	2.0	–	–	–	2.0	3.0	21
Anterior micronucleus, length	2.2	2.2	–	–	–	1.6	3.2	18
	1.8	1.6	–	–	–	1.5	2.4	20
Anterior micronucleus, width	2.0	2.0	–	–	–	1.6	2.4	18
	1.7	1.6	–	–	–	1.6	2.5	20
Micronuclei, number	2.1	2.0	0.6	0.1	27.6	1.0	4.0	18
	2.8	2.5	1.3	0.3	45.8	1.0	7.0	20
Adoral membranelles, number	25.7	26.0	2.0	0.5	7.8	21.0	30.0	18
	29.4	29.5	3.4	0.8	11.6	19.0	33.0	18
Frontal cirri, number	2.9	3.0	–	–	–	2.0	3.0	18
	3.0	3.0	–	–	–	2.0	3.0	21
Frontoterminal cirri, number	2.2	2.0	–	–	–	2.0	3.0	17
	4.6	4.0	1.0	0.2	22.9	3.0	8.0	18
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	18
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	18
Remaining frontoventral cirri, number	6.4	7.0	1.1	0.3	17.0	5.0	9.0	18
	11.5	11.0	2.0	0.5	17.4	8.0	16.0	17
Frontoventral cirri, number of pairs	2.7	3.0	0.6	0.1	22.3	2.0	4.0	18
	4.1	4.0	0.9	0.2	22.2	2.0	6.0	17
Transverse cirri, number	4.7	5.0	–	–	–	4.0	5.0	17
	2.6	3.0	1.0	0.2	38.3	0.0	4.0	20
Pretransverse ventral cirri, number	1.9	2.0	–	–	–	1.0	2.0	17
	– [b]	–	–	–	–	–	–	–
Right marginal cirri, number	27.1	27.0	2.9	0.7	10.6	22.0	33.0	17
	32.6	32.0	5.2	1.2	15.9	26.0	44.0	19
Left marginal cirri, number	17.5	17.0	2.0	0.5	11.3	13.0	21.0	17
	21.6	21.0	3.1	0.7	14.3	17.0	29.0	19
Dorsal kineties, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	14
Kinetids in middle dorsal ciliary row, number	15.6	16.0	0.9	0.3	5.9	14.0	17.0	8
	24.6	25.0	1.5	0.5	6.1	23.0	27.0	10
Paroral kinetids, number	7.1	7.0	1.4	0.4	19.7	5.0	10.0	14
	12.9	13.0	2.3	0.5	17.9	8.0	18.0	18

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Paroral membrane, length	5.6	6.0	1.0	0.3	18.2	4.0	7.0	14
	9.4	9.0	1.3	0.3	14.2	6.0	12.0	18
Endoral membrane, length	10.8	11.0	1.3	0.3	12.2	8.0	12.0	15
	12.6	13.0	2.0	0.5	16.1	7.0	14.0	18

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Included in transverse cirri number.

Gonostomum strenuum (ENGELMANN, 1862) STERKI, 1878 (Fig. 177a–d; Table 157)

Neotype material: Neotypified from Namibian site (49) population, according to reasons 1, 4, 6 given in chapter 2.4.2.

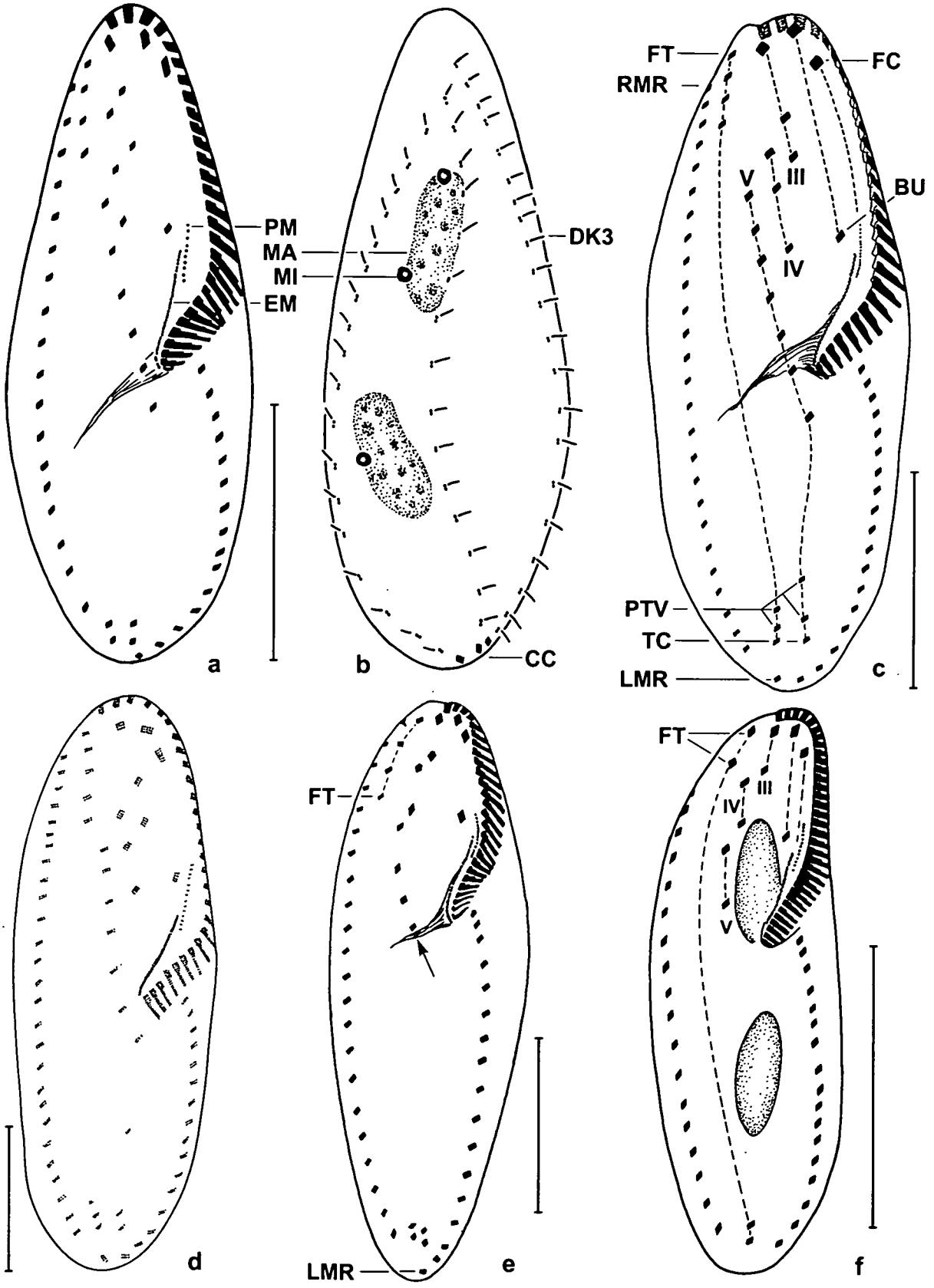
Improved diagnosis: Size 80–130 × 25–55 µm in vivo; ellipsoidal. 2 macronuclear nodules. Cortical granules colourless or yellowish, 1.0–1.5 × 0.6 µm in size, form indistinct fringe. On average 20–27 right marginal, 15–17 left marginal, 4–5 frontoterminal, 10–12 frontoventral, and 4–5 pretransverse and transverse cirri; 1 buccal cirrus right of anterior half of paroral; frontoventral cirral row V composed of 5–9 cirri, that is, long and surpassing buccal vertex. Adoral zone about 50% of body length, composed of 28–29 membranelles on average. Usually 10–13 paroral cilia.

Remarks: The Namibian specimens (Fig. 177a, b; Table 157) are highly similar to the populations described by SONG (1990a) from China (Fig. 157c), by OLMO & TÉLLEZ (1997) from Spain (Fig. 177d), and by FOISSNER et al. (2001) from Australia. Thus, data from all populations were used for the improved diagnosis, and only some supplementary observations are provided from the neotype population.

Fig. 177a–d. *Gonostomum strenuum* after protargol impregnation. **a, b:** Infraciliature of ventral and dorsal side and nuclear apparatus of Namibian neotype specimen. **c:** Chinese specimen, infraciliature of ventral side (from SONG 1990a). Cirri originating from same anlage connected by broken line. **d:** Spanish specimen, infraciliature of ventral side (from OLMO & TÉLLEZ 1997). Scale bars 30 µm.

Fig. 177e, f: *Gonostomum affine* after protargol impregnation (e, from FOISSNER 2000b; f, from BERGER & FOISSNER 1988b). **e:** A Venezuelan specimen with 15 frontal and ventral cirri; a value between *G. affine* (usually 11 cirri) and *G. strenuum* (usually 20–25 cirri). However, the four frontoterminal cirri indicate that it is nearer to *G. strenuum* than to *G. affine*. **f:** Typical *G. affine* with 11 frontoventral cirri. Likely, the number of frontoterminal cirri (2 vs. 4–6) is the most important character to distinguish *G. affine* from *G. strenuum*.

BU – buccal cirrus, CC – caudal cirri, DK3 – dorsal kinety 3, EM – endoral membrane, FC – left frontal cirrus, FT – frontoterminal cirri, LMR – left marginal row, MA – anterior macronuclear nodule, MI – micronucleus, PM – paroral membrane, PTV – pretransverse ventral cirri, RMR – right marginal row, TC – transverse cirri, III-V – frontoventral rows as revealed by ontogenesis.


PM
MA
MI
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a
DK3
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CC
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FC
RMR
V
III
BU
IV
PTV
TC
LMR
c
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FT
e
LMR
FT
III
IV
V
f

The four populations mentioned above can be clearly distinguished from a "typical" *Gonostomum affine* (STEIN, 1859) STERKI, 1878 (Fig. 157f) by the following features: 3–6, usually 4 frontoterminal cirri vs. usually 2; frontoventral row V long and composed of 5–9 cirri and thus usually surpassing buccal vertex vs. short usually composed of two cirri only and thus terminating ahead of buccal vertex. In total, *Gonostomum strenuum* has distinctly more frontoventral cirri (20–25) than *G. affine* (6–15, on average 11; data from 18 soil populations summarized by FOISSNER 2000b). Furthermore, *Gonostomum strenuum* has conspicuous cortical granules usually lacking or indistinct in *G. affine*. BERGER (1999, p. 369) also used the end of the left marginal row as a key feature: it is behind the transverse cirri in *G. strenuum* (Fig. 177c, d), while more or less left of the transverse cirri in *G. affine* (Fig. 177f). However, this feature is obviously not met by the Namibian specimens (Fig. 177a).

FOISSNER (2000b) described a *Gonostomum* population from Venezuela (Fig. 177e), which is difficult to assign because the total number of frontoventral cirri (14–18, on average 16) and the length of frontoventral row V are between the values mentioned above. The three to four frontoterminal cirri indicate that it is more closely related to *G. strenuum* than to the *G. affine* group (FOISSNER et al. 2001).

Additional observations from Namibian site (49) specimens (see table 157 for detailed morphometrics): Size about 80–110 × 25–35 µm in vivo. Flattened about 2:1 dorsoventrally. Contractile vacuole with longitudinal collecting canals. Cortical granules in loose rows, form distinct fringe; individual granules ellipsoidal, about 1.0–1.2 × 0.6 µm, yellowish, compact and thus bright, stain red with methyl green-pyronin but are not ejected, do not impregnate with the protargol method used. Cytoplasm colourless, posterior cell portion usually with many bright lipid droplets 2–3 µm across. Feeds on bacteria digested in vacuoles 6–10 µm across. Glides rather rapidly on microscope slide. Frontoventral, marginal and caudal cirri about 15 µm, transverse cirri about 20 µm, and dorsal bristles about 3 µm long in vivo. Adoral zone extends over 51% of body length on average, bases of largest membranelles about 5 µm wide in vivo. Paroral cilia about 6 µm long in vivo.

Occurrence and ecology: ENGELMANN (1862) discovered *Gonostomum strenuum* in a *Lemna* pond near Leipzig, Germany. Later, SONG (1990a) isolated it from a Chinese soil, while OLMO & TÉLLEZ (1997) found it in moss from emergent river stones in Spain, and FOISSNER et al. (2001) observed it in a soil sample from the Murray River floodplain in Australia. In Namibia, *G. strenuum* occurred in mud and soil from road puddles at the Bambatsi Guest Farm (site 49 in figure 2 and chapter 2.1.2), which is not a strictly edaphic site. These data show that *G. strenuum* is a cosmopolitan occurring in both freshwater and soil. See BERGER (1999) for a detailed review on distribution and ecology of *G. strenuum*. Generally, the species is much rarer than the common *G. affine*.

Table 157. Morphometric data on *Gonostomum strenuum*.

Characteristics[a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	81.5	80.0	7.8	2.2	9.6	72.0	98.0	13
Body, width	30.0	30.0	2.9	0.8	9.6	26.0	36.0	13
Body length:width, ratio	2.7	2.8	0.3	0.1	10.3	2.3	3.5	13
Anterior body end to end of adoral zone, distance	42.3	43.0	4.9	1.4	11.6	32.0	49.0	13
Body length:length of adoral zone, ratio	1.9	1.9	0.2	0.1	9.5	1.7	2.3	13
Anterior body end to buccal cirrus, distance	23.7	25.0	3.2	0.9	13.5	17.0	26.0	13
Anterior body end to left frontal cirrus, distance	5.2	5.0	0.7	0.2	13.9	4.0	6.0	13
Anterior body end to frontoventral (FV) row III, distance	7.3	7.0	1.1	0.3	15.2	6.0	9.0	13
Anterior body end to end of FV row III, distance	15.8	16.0	2.2	0.6	14.2	11.0	19.0	13
Anterior body end to FV row IV, distance	10.1	10.0	1.3	0.3	12.5	7.0	12.0	13
Anterior body end to end of FV row IV, distance	24.5	25.0	4.1	1.1	16.8	15.0	29.0	13
Anterior body end to FV row V, distance	19.2	19.0	2.0	0.6	10.4	16.0	22.0	13
Anterior body end to end of FV row V, distance	50.2	50.0	5.6	1.5	11.1	41.0	62.0	13
Anterior body end to end of frontoterminal cirri, distance	18.2	18.0	3.4	0.9	18.5	12.0	24.0	13
Anterior body end to right marginal row, distance	7.2	6.0	3.0	0.8	41.9	4.0	16.0	13
Anterior body end to paroral membrane, distance	23.8	25.0	3.1	0.9	13.0	17.0	27.0	13
Paroral membrane, length	8.1	8.0	1.4	0.4	17.8	6.0	10.0	13
Anterior body end to endoral membrane, distance	27.3	28.0	3.7	1.0	13.7	20.0	32.0	13
Endoral membrane, length	14.8	15.0	1.1	0.3	7.4	12.0	16.0	13
Anterior body end to dorsal kinety 1, distance	13.4	14.0	2.3	0.6	16.9	10.0	16.0	13
Anterior body end to dorsal kinety 2, distance	8.8	10.0	1.7	0.5	19.8	6.0	11.0	13
Anterior body end to dorsal kinety 3, distance	5.3	6.0	0.9	0.3	17.8	3.0	6.0	13
Posterior body end to transverse cirri, distance	3.4	3.0	0.9	0.3	26.6	2.0	5.0	13
Posterior body end to right marginal row, distance	4.0	4.0	1.4	0.4	35.1	2.0	6.0	13
Posterior body end to left marginal row, distance	1.1	1.5	–	–	–	0.0	2.0	13
Anterior body end to first macronuclear nodule, distance	18.9	19.0	2.8	0.8	14.9	15.0	26.0	13
Nuclear figure, length	43.0	42.0	4.2	1.2	9.8	37.0	51.0	13
Macronuclear nodules, distance in between	11.2	10.0	3.2	0.9	28.7	7.0	18.0	13
Anterior macronuclear nodule, length	16.7	17.0	1.8	0.5	10.5	14.0	20.0	13
Anterior macronuclear nodule, width	7.1	7.0	1.0	0.3	13.5	6.0	8.0	13
Anterior micronucleus, length	1.9	2.0	–	–	–	1.5	2.5	13
Anterior micronucleus, width	1.9	2.0	–	–	–	1.5	2.5	13
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	13
Micronuclei, number	4.6	5.0	1.5	0.4	32.5	3.0	8.0	13
Adoral membranelles, number	27.9	28.0	2.4	0.7	8.6	24.0	31.0	13
Paroral cilia, number	12.2	13.0	2.0	0.5	16.1	9.0	15.0	13
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13
Cirri in frontoventral row III, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	13
Cirri in frontoventral row IV, number	3.5	3.0	0.7	0.2	18.7	3.0	5.0	13
Cirri in frontoventral row V, number	6.9	7.0	1.3	0.4	19.1	5.0	9.0	13
Frontoterminal cirri, number	4.3	4.0	0.8	0.2	17.4	3.0	6.0	13
Frontoventral cirri, total number[b]	20.8	21.0	2.1	0.6	10.1	19.0	25.0	13
Pretransverse cirri ahead of left transverse cirrus, number	1.5	2.0	–	–	–	0.0	2.0	13
Pretransverse cirri ahead of right transverse cirrus, number	1.3	1.0	–	–	–	1.0	2.0	13
Transverse cirri, number	1.9	2.0	–	–	–	1.0	2.0	13

(continued)

Characteristics[a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Pretransverse plus transverse cirri, number	4.7	5.0	1.1	0.3	23.6	2.0	6.0	13
Right marginal cirri, number	20.5	19.0	3.5	1.0	17.2	16.0	27.0	13
Left marginal cirri, number	14.9	15.0	1.6	0.4	10.4	13.0	18.0	13
Caudal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13
Dorsal kineties, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13
Dorsal kinety 1, number of bristles	19.4	19.0	3.0	0.8	15.7	15.0	26.0	13
Dorsal kinety 2, number of bristles	17.2	17.0	2.7	0.8	15.7	12.0	22.0	12
Dorsal kinety 3, number of bristles	20.8	21.0	3.1	0.9	14.8	15.0	26.0	13

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in μm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Includes frontal cirri, buccal cirrus, cirri from frontoventral rows III-V, and frontoterminal cirri.

Paragonostomum nov. gen.

Diagnosis: Oxytrichinae without transverse cirri. Adoral zone of membranelles, undulating membranes, and ontogenesis in *Gonostomum* pattern. Posterior body portion more or less distinctly tail-like. Frontoventral cirri and frontoterminal cirri in Y-like pattern or single row. 1 right and left marginal row. 3 dorsal kineties.

Type species: *Paragonostomum caudatum* nov. spec.

Etymology: Composite of the Greek *para* (beside) and the generic name *Gonostomum*, meaning a ciliate related to *Gonostomum*. Neuter gender.

Comparison with related genera: *Paragonostomum* differs from → *Gonostomum* STERKI, 1878 by the lack of transverse cirri. Indeed, it is, beside → *Vermioxytricha*, the first oxytrichid without transverse cirri, although in some *Gonostomum affine* populations specimens without transverse cirri occur, but, on average, all possess at least two transverse cirri (BERGER 1999). All *Paragonostomum* species have a conspicuous tail, which is very fragile and thus difficult to preserve. Furthermore, the tail cirri are minute, sometimes consisting of two cilia only. Consequently, we could not ascertain unequivocally whether caudal cirri are present or not. Thus, the tail ciliature illustrated is possibly not entirely correct, and the feature, although important, not included in the species diagnoses. Detailed ontogenetic data are required to interpret the tail ciliature correctly.

Paragonostomum includes four species which differ in the nuclear apparatus, the arrangement of the frontoventral cirri, some morphometrics of the ciliature, and the structure of the paroral which is, uniquely within the hypotrichs, bipartite in most species (Fig. 179e, f, 180e, f, i, j, 181c). Usually, we assign such a peculiarity genus weight (see reviews by BERGER & FOISSNER 1997 and BERGER 1999). However, the feature is not entirely stable and thus perhaps better used as a species character.

Cladotricha GAIEVSKAÏA, 1925 also has a rather similar oral ciliature and lacks transverse cirri. However, the type species, *Cladotricha koltzowii* GAIEVSKAÏA, 1925, and some other species have one or more frontoventral cirral rows extending to near posterior body end (BLATTERER & FOISSNER 1988, BORROR & EVANS 1979, RUINEN 1938), whereas the frontoventral row of *Paragonostomum* hardly extends beyond the buccal vertex (Fig. 178h, i, l; 179e, f, 180c, e, 181c). Furthermore, there is an important ontogenetic difference: *Cladotricha koltzowii* and *C. variabilis* differentiate the frontoventral ciliature independently in the proter and opisthe (BORROR & EVANS 1979), while the *Gonostomum/Paragonostomum* group produces primary primordia (see BERGER 1999 and → *Gonostomum algicola* for details). Thus, synonymy of *Cladotricha* and *Paragonostomum* is unlikely.

***Paragonostomum caudatum* nov. spec.** (Fig. 178a–l; 381s, t; Table 158)

Diagnosis: Size about 85 × 20 µm in vivo. Lanceolate with conspicuous tail occupying about 25% of body length. 2 macronuclear nodules. On average 19 right marginal, 11 left marginal, and 4 frontoterminal cirri; frontoterminal and frontoventral cirral rows distinctly separate, the latter composed of an average of 6 cirri and ending at 30% of body length; 1 buccal cirrus at anterior end of paroral composed of 7–12, usually 9 kinetids. Adoral zone of membranelles about one third of body length, composed of 19 membranelles on average.

Type location: Soil from a meadow in the Botanical Garden of the town of Darwin, Australia, 12°26'S 130°50'E.

Etymology: The Latin *caudatum* (having a tail) refers to the tail, a main feature of this species.

Description: Size 70–110 × 15–25 µm in vivo, usually about 85 × 20 µm, length:width ratio of trunk 3.0–4.6:1, on average 3.6:1 in protargol preparations. Body clavate due to lanceolate to ellipsoidal trunk and cylindroidal tail occupying about 25% of body length in vivo and protargol preparations (Fig. 178a, c–l; 381s, t; Table 158); highly fragile, especially tail, and flexible, but acontractile. Trunk flattened up to 2:1 dorsoventrally and asymmetrical: left margin straight to slightly convex, right distinctly convex and narrowed in posterior quarter, producing conspicuous tail. Macronuclear nodules in middle third of trunk slightly left of midline, ellipsoidal (2:1) to elongate ellipsoidal (4:1), contain numerous globular nucleoli. Micronuclei near or attached to macronuclear nodules, about 3 × 2 µm in vivo. Contractile vacuole underneath buccal vertex. Cortical granules recognizable neither in vivo nor in protargol and methyl green-pyronin (Saudi Arabian population) preparations. Cytoplasm colourless, with few, about 3 µm-sized crystals and some lipid droplets 1–4 µm across. Feeds on bacteria digested in vacuoles 4–5 µm in diameter. Glides rather rapidly on microscope slide, often motionless for some time, tail occasionally adheres to soil particles with a slimy thread (Fig. 178g).

Cirral pattern very constant, number of cirri of usual variability (Fig. 178h, i, k, l; Table 158). Marginal cirri about 8 µm long in vivo, right row extends onto dorsal side anteriorly and usually terminates at base of tail; left row distinctly shortened posteriorly, that is, usually terminates above base of tail. Fourteen frontoventral cirri on average. Frontal cirri about 13 µm long in vivo, moderately enlarged. Buccal cirrus slightly right and ahead of paroral

membrane. Frontoventral row usually slightly shorter, occasionally as long as adoral zone of membranelles, right of midline, with anteriormost cirrus shifted slightly to left (arrow in Fig. 178h) and thus behind right frontal cirrus. Frontoterminal cirri near or on right dorsolateral surface, form short row. Transverse cirri absent.

Dorsal bristles about 3 µm long in vivo, arranged in three rows (Fig. 178j, k), of which two or all extend onto tail. Row 1 commences near level of buccal cirrus and extends along left cell margin; row 2 extends slightly left of midline from near anterior body end to posterior trunk end; row 3 commences subapically and extends along right cell margin. Two or three (caudal?) cirri at top of tail, conspicuous in vivo because about 20 µm long and usually widely spread (Fig. 178a). Arrangement and composition of tail ciliature difficult to analyze because the tail is only 1.0–2.5µm wide (see genus introduction).

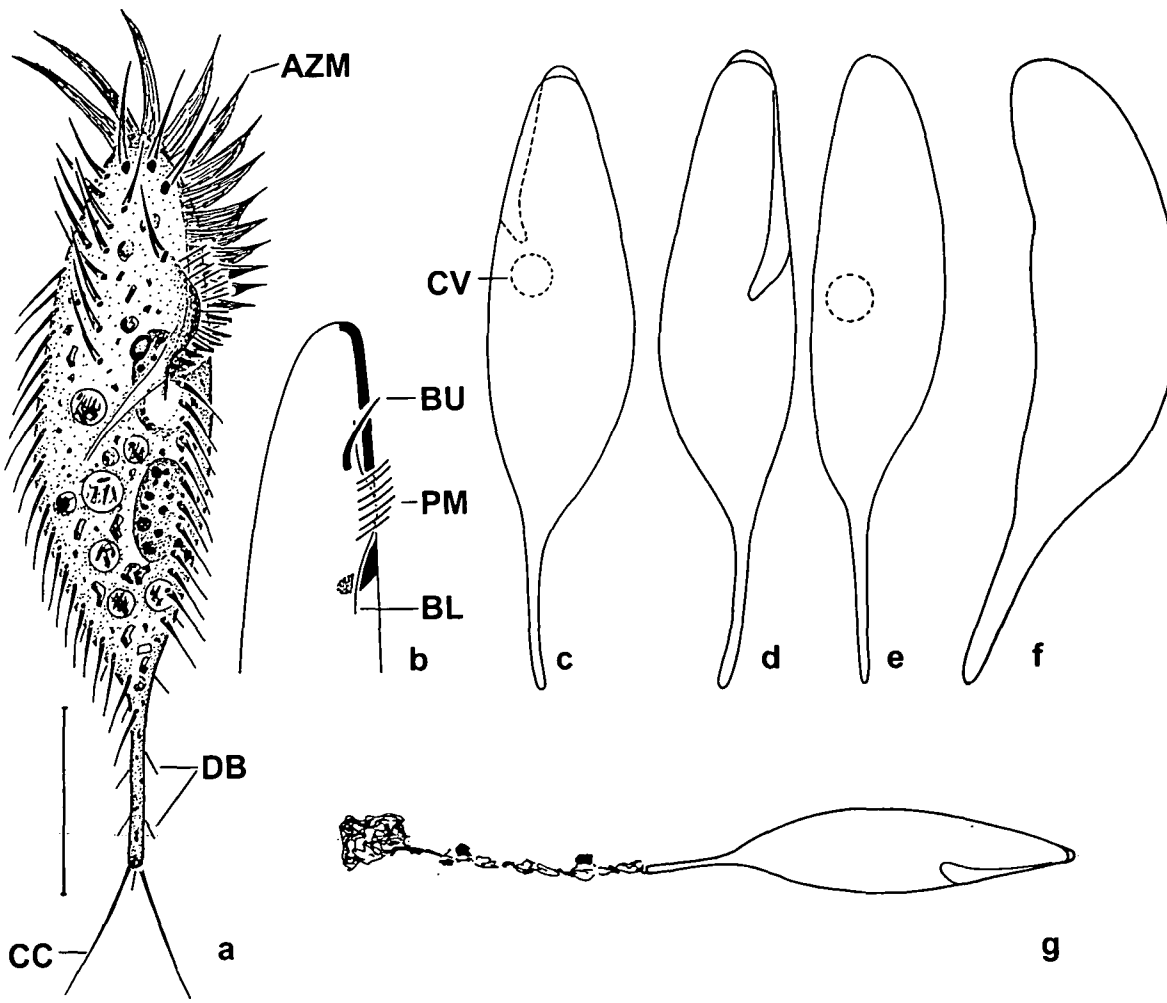

Fig. 178a–f. *Paragonostomum caudatum* from life (a, c, g, Australian type population; b, f, Saudi Arabian specimens; d, e, Corsican specimens). **a:** Ventral view of a representative specimen. **b:** Anterior body portion at higher magnification. Note the conspicuous buccal lip covering the buccal cavity and the posterior portion of the adoral zone of membranelles. Furthermore, the lip carries the paroral membrane. **c–f:** Ventral (d) and dorsal (c, e, f) views of shape variants. **g:** Specimen dragging a thread of mucous material recognizable by adhering debris. AZM – adoral zone of membranelles, BU – buccal cirrus, BL – buccal lip, that is, cortical process covering part of buccal cavity, CC – caudal (?) cirri, CV – contractile vacuole, DB – dorsal bristles on tail, PM – paroral membrane on buccal lip. Scale bar 20 µm.

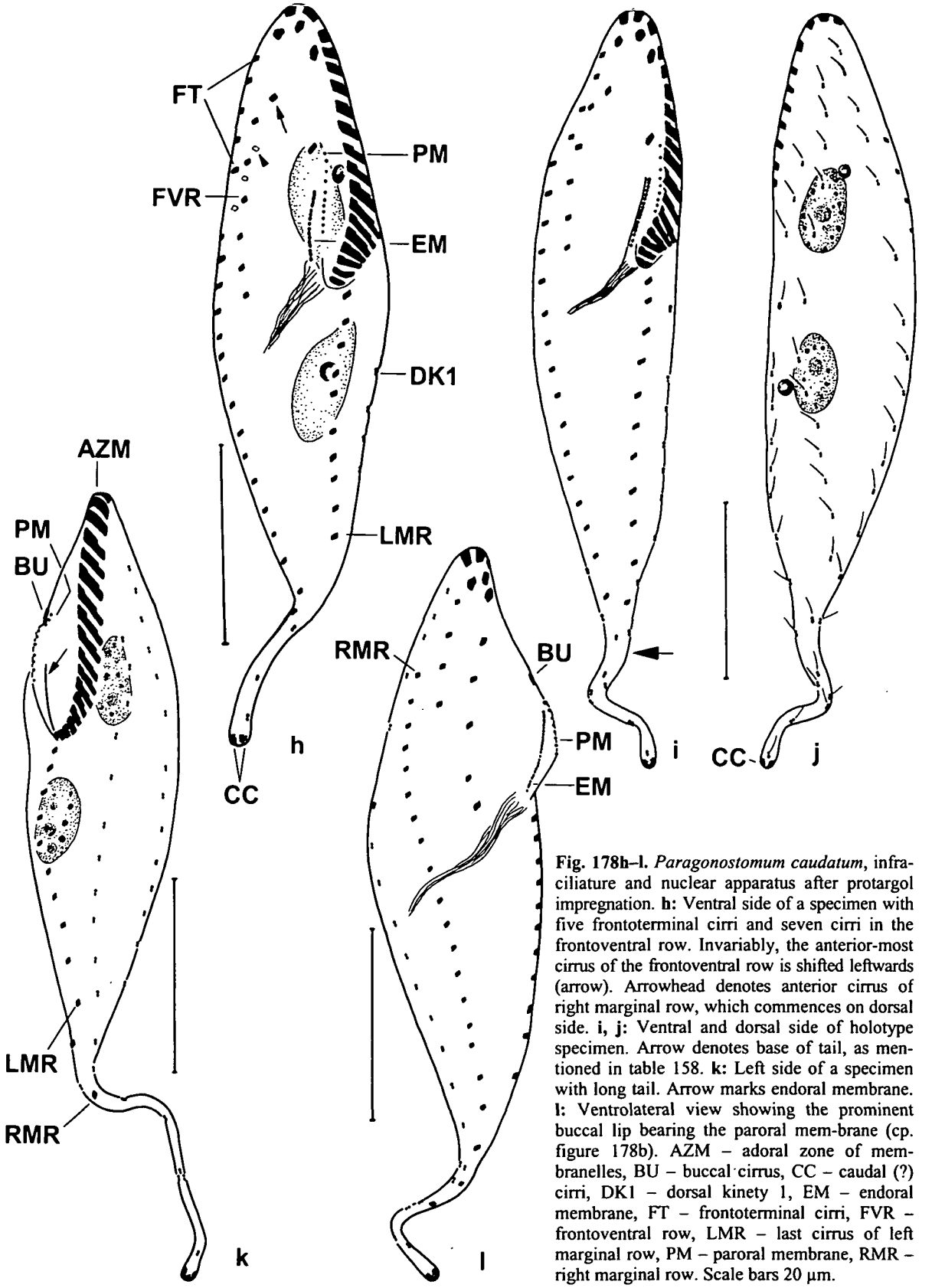

Fig. 178h–l. *Paragonostomum caudatum*, infraciliature and nuclear apparatus after protargol impregnation. **h:** Ventral side of a specimen with five frontoterminal cirri and seven cirri in the frontoventral row. Invariably, the anterior-most cirrus of the frontoventral row is shifted leftwards (arrow). Arrowhead denotes anterior cirrus of right marginal row, which commences on dorsal side. **i, j:** Ventral and dorsal side of holotype specimen. Arrow denotes base of tail, as mentioned in table 158. **k:** Left side of a specimen with long tail. Arrow marks endoral membrane. **l:** Ventrolateral view showing the prominent buccal lip bearing the paroral mem-brane (cp. figure 178b). AZM – adoral zone of membranelles, BU – buccal cirrus, CC – caudal (?) cirri, DK1 – dorsal kinety 1, EM – endoral membrane, FT – frontoterminal cirri, FVR – frontoventral row, LMR – last cirrus of left marginal row, PM – paroral membrane, RMR – right marginal row. Scale bars 20 µm.

Oral apparatus in *Gonostomum* pattern (Fig. 178a, b, h, i, k, l; BERGER 1999). Adoral zone occupies approximately 44% of trunk length, but only about one third of body length, commences near midline of anterior body end and extends straight along left body margin, performing abrupt right bend and slight clockwise rotation to plunge into buccal cavity near left body margin; composed of an average of 19 membranelles, bases of largest membranelles about 4 µm wide. Proximal portion of adoral zone and buccal cavity partially covered by a curved, rather prominent cortical process (buccal lip) bearing the paroral membrane, which consists of 7–12 widely spaced, at least 5 µm long cilia. Buccal cavity narrow and flat, at right bordered by slightly curved endoral membrane composed of tightly spaced basal bodies. Pharyngeal fibres clearly recognizable in vivo and after protargol impregnation, extend obliquely backwards.

Table 158. Morphometric data on *Paragonostomum caudatum* (PC), *P. binucleatum* (PB), and *P. multinucleatum* (PM [d]).

Characteristics [a]	Species	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Trunk or body, length [b]	PC	61.8	62.0	5.2	1.1	8.4	51.0	72.0	21
	PB	64.1	63.0	8.4	2.1	13.1	54.0	83.0	16
	PM1	59.6	61.0	7.1	1.6	11.9	48.0	72.0	19
	PM2	54.0	52.0	5.7	1.7	10.6	48.0	65.0	11
Trunk or body, width	PC	16.6	17.0	2.1	0.4	12.4	12.0	20.0	21
	PB	21.8	21.0	3.5	0.9	16.0	14.0	27.0	15
	PM1	15.8	16.0	1.3	0.3	8.4	13.0	18.0	20
	PM2	15.7	15.0	1.7	0.5	10.7	14.0	19.0	11
Trunk or body length:width, ratio [b]	PC	3.8	3.7	0.4	0.1	11.7	3.0	4.6	21
	PB	3.0	2.9	0.7	0.2	21.5	2.1	4.0	15
	PM1	3.8	3.8	0.4	0.1	9.8	3.0	4.5	18
	PM2	3.5	3.5	0.4	0.1	12.9	2.7	4.1	11
Tail, length [b]	PC	18.8	19.0	4.2	1.2	22.3	12.0	26.0	12
Tail, width in mid-region [b]	PC	1.5	1.6	0.4	0.1	23.4	1.0	2.5	19
Anterior body end to proximal end of adoral zone, distance	PC	27.4	27.0	1.7	0.4	6.1	25.0	30.0	21
	PB	24.2	24.0	1.7	0.4	7.0	21.0	27.0	16
	PM1	21.2	22.0	2.3	0.5	10.9	16.0	26.0	21
	PM2	18.8	19.0	1.7	0.5	9.1	16.0	21.0	11
Trunk or body length:length of adoral zone of membranelles, ratio [b]	PC	2.3	2.3	0.2	0.0	8.9	1.9	2.6	21
	PB	2.7	2.6	0.3	0.1	11.1	2.2	3.3	16
	PM1	2.8	2.9	0.4	0.1	12.5	2.2	3.6	19
	PM2	2.9	2.9	0.3	0.1	11.0	2.3	3.4	11
Anterior body end to last frontoventral cirrus, distance	PC	24.6	25.0	3.3	0.7	13.5	15.0	30.0	21
	PB	15.3	15.0	1.9	0.5	12.2	13.0	18.0	15
	PM1	12.2	12.0	1.6	0.4	13.5	9.0	15.0	20
Anterior body end to buccal cirrus, distance	PC	13.4	13.0	1.0	0.2	7.3	12.0	15.0	21
	PB	10.4	10.0	–	–	–	10.0	11.0	16
	PM1	9.4	9.0	1.7	0.4	17.9	6.0	14.0	18
Anterior body end to anterior end of right marginal row, distance	PC	12.0	12.0	1.9	0.4	15.6	9.0	15.0	21
	PB	4.9	4.0	1.4	0.4	28.1	3.0	8.0	15
	PM1	3.5	3.5	0.9	0.2	24.4	2.0	5.0	16

(continued)

Characteristics [a]	Species	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Anterior body end to posterior end of left marginal row, distance	PC	53.6	54.0	5.5	1.2	10.3	45.0	66.0	21
	PM1	56.0	57.0	6.4	1.8	11.4	45.0	64.0	13
Nuclear figure, length	PB	27.1	25.5	5.0	1.2	18.3	20.0	36.0	16
	PM1	28.9	29.0	3.0	0.6	10.3	22.0	35.0	21
Macronuclear nodules, distance in between	PB	10.8	11.0	3.1	0.8	29.1	6.0	18.0	16
Anterior macronuclear nodule, length	PC	10.7	11.0	1.5	0.3	14.2	8.0	13.0	21
	PB	9.3	9.0	1.9	0.5	20.3	6.0	12.0	16
	PM1	5.0	5.0	1.3	0.3	26.8	3.0	8.0	21
	PM2	4.6	4.0	1.2	0.3	25.2	3.0	7.0	11
Anterior macronuclear nodule, width	PC	4.6	5.0	0.7	0.2	16.3	3.0	6.0	21
	PB	5.7	6.0	0.6	0.2	10.6	4.0	6.0	16
	PM1	3.5	3.5	0.6	0.1	17.7	2.5	5.0	21
	PM2	3.2	3.0	–	–	–	3.0	4.0	11
Macronuclear nodules, number	PC	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	PB	2.0	2.0	0.0	0.0	0.0	2.0	2.0	16
	PM1	6.9	7.0	1.8	0.4	25.5	4.0	9.0	21
	PM2	7.5	7.0	2.3	0.7	30.2	4.0	13.0	11
Anterior micronucleus, length	PC	1.7	1.6	–	–	–	1.2	2.4	21
	PB	1.6	1.5	–	–	–	1.5	2.0	15
	PM1	1.3	1.2	–	–	–	1.0	2.0	17
	PM2	2.1	2.0	–	–	–	1.5	3.0	11
Anterior micronucleus, width	PC	1.5	1.6	–	–	–	1.0	1.6	21
	PB	1.5	1.5	–	–	–	1.5	2.0	15
	PM1	1.1	1.0	–	–	–	1.0	1.6	17
	PM2	1.6	1.5	–	–	–	1.3	2.0	11
Micronuclei, number	PC	1.9	2.0	–	–	–	1.0	2.0	21
	PB	1.8	2.0	–	–	–	1.0	2.0	15
	PM1 [c]	2.8	2.5	–	–	–	1.0	5.0	10
	PM2	1.4	1.0	–	–	–	1.0	2.0	11
Adoral membranelles, number	PC	18.7	19.0	1.2	0.3	6.6	17.0	21.0	21
	PB	20.5	21.0	2.3	0.6	11.4	16.0	23.0	16
	PM1	19.2	19.0	1.3	0.3	7.0	16.0	22.0	17
	PM2	14.5	14.0	1.1	0.3	7.8	13.0	17.0	11
Frontal cirri, number	PC	3.0	3.0	–	–	–	3.0	3.0	21
	PB	3.0	3.0	–	–	–	3.0	3.0	14
	PM1	3.0	3.0	–	–	–	3.0	3.0	17
	PM2	3.0	3.0	–	–	–	3.0	3.0	11
Frontoterminal cirri, number	PC	4.4	4.0	–	–	–	4.0	5.0	21
	PB	2.1	2.0	–	–	–	2.0	3.0	14
	PM1	2.1	2.0	–	–	–	1.0	3.0	16
Frontoventral cirri, number	PC	6.7	6.0	1.0	0.2	14.9	5.0	9.0	22
	PB	3.2	3.0	0.7	0.2	21.1	2.0	5.0	15
	PM1	3.1	3.0	–	–	–	3.0	4.0	19
	PM2 [c]	5.4	5.0	–	–	–	5.0	7.0	11
Buccal cirri, number	PC	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	PB	1.0	1.0	0.0	0.0	0.0	1.0	1.0	16
	PM1	1.0	1.0	0.0	0.0	0.0	1.0	1.0	18
	PM2	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11

(continued)

Characteristics [a]	Species	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Right marginal cirri, number	PC	19.5	20.0	2.9	0.6	14.9	12.0	25.0	21
	PB	20.6	20.5	2.6	0.6	12.4	16.0	27.0	16
	PM1	21.6	22.0	3.6	1.0	16.5	17.0	29.0	14
	PM2	22.1	22.0	2.6	0.8	11.9	18.0	28.0	11
Left marginal cirri, number	PC	11.1	11.0	1.7	0.4	15.1	8.0	14.0	21
	PB	14.6	15.0	1.7	0.4	11.9	12.0	17.0	16
	PM1	16.8	16.0	3.1	0.8	18.7	12.0	22.0	15
	PM2	16.5	16.0	2.4	0.7	14.6	13.0	21.0	11
Dorsal kineties, number	PC	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	PB [f]	3.0	3.0	0.0	0.0	0.0	3.0	3.0	14
	PM1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	17
	PM2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
Kinetids in middle dorsal ciliary row, number	PC	14.5	14.0	1.9	0.5	13.1	12.0	18.0	16
	PB	10.0	9.5	1.2	0.4	12.0	9.0	12.0	8
	PM1	9.8	9.5	1.0	0.4	10.0	9.0	11.0	6
Paroral kinetids, number	PC	9.4	9.0	1.2	0.3	13.1	7.0	12.0	20
	PB	6.4	7.0	1.0	0.3	15.4	4.0	8.0	15
	PM1	5.4	6.0	1.0	0.3	18.4	4.0	7.0	12
	PM2	5.3	5.0	1.6	0.5	29.5	3.0	8.0	11
Paroral membrane, length	PC	8.2	8.0	1.1	0.2	13.1	7.0	11.0	19
	PB	6.1	6.0	0.7	0.2	11.6	5.0	8.0	15
	PM1	5.3	5.0	0.7	0.2	13.5	4.0	6.0	11
Endoral membrane, length	PC	7.9	8.0	1.2	0.3	14.8	6.0	10.0	17
	PB	9.6	10.0	0.7	0.2	7.0	8.0	10.0	11
	PM1	5.9	6.0	0.7	0.2	12.7	5.0	7.0	10

[a] Data based on mounted, protargol-impregnated (FOISSNER's protocol), and slightly selected specimens (most inflated and/or distorted cells were excluded) from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] In *Paragonostomum caudatum*, the distance from anterior body end to tail base was measured (arrow in Fig. 178i), while in *P. binucleatum* and *P. multinucleatum* total body length is given because the tail is too indistinctly set off from body proper.

[c] Uncertain because difficult to recognize.

[d] PM1 – type population, PM2 – USA population.

[e] Frontoterminal cirri included.

[f] Specimens with four dorsal kineties occur rarely.

Occurrence and ecology: The type population was discovered in loamy soil (pH 7.1) from a meadow with some shrubs and trees in the Botanical Garden of the town of Darwin, Australia. Furthermore, we found *Paragonostomum caudatum* in fine, blackish soil (pH 5.3) from the bank of the Rizzanes River near the town of Propriano, Corsica (collected by Dr. Bruno GANNER in September 1985); in a soil sample from the USA; in mouldy, about 10 cm thick, sandy *Casuarina* litter (pH 7.2) on a dam near the village of Safwa, Saudi Arabia; and at several sites in Namibia (Table 4). Thus, *P. caudatum* is a common and very likely cosmopolitan species preferring fine-grained mineral soils.

Comparison with related species: *Paragonostomum caudatum* is a conspicuous species due to the distinct tail, which is very likely produced by body elongation because the usual 50% *Gonostomum* ratio of body length:length of adoral zone of membranelles is obtained only when the tail is omitted. It differs from → *P. multinucleatum* by the number of macronuclear nodules (2 versus 4–9) and the shape of the paroral (continuous versus bipartite); and from → *G. namibiense*, inter alia, by the lack of transverse cirri. → *Paragonostomum rarisetum* has distinctly fewer frontoventral cirri, which uniquely form a single short row with the frontoterminal cirri. → *Paragonostomum binucleatum* has distinctly fewer frontoventral cirri (5 vs. 10), a much less distinct tail, and a conspicuous gap in the paroral.

***Paragonostomum binucleatum* nov. spec.** (Fig. 179a–g; 381u; Table 158)

Diagnosis: Size about 70 × 23 µm in vivo. Pisciform with tail-like posterior portion occupying about 10% of body length. 2 macronuclear nodules. On average 21 right marginal, 15 left marginal, 2 frontoterminal, and 3 frontoventral cirri; 1 buccal cirrus at anterior end of paroral composed of 4–8, usually 6 kinetids divided into an anterior and posterior segment by a small gap. Adoral zone of membranelles about 37% of body length, composed of 21 membranelles on average.

Type location: Artificial (?) soil from lawn of a hotel in the village of Sharm el Sheik, Sinai, Egypt, 27°N 34°E.

Etymology: The Latin adjective *binucleatum* (two nuclei) refers to the two macronuclear nodules, a main feature of this species.

Description and comparison with related species: This species is very similar to → *P. multinucleatum*, differing only by the number of macronuclear nodules, namely two vs. seven. Thus, the reader is referred to the description of *P. multinucleatum*, and the detailed figures and morphometrics of *P. binucleatum* (Fig. 179a–g; Table 158). The tail is usually slightly longer in *P. multinucleatum* than in *P. binucleatum* (Fig. 381u). However, it is rather variable and thus should not be used as a distinguishing feature. Like the other members of the genus, *Paragonostomum binucleatum* is very fragile and thus usually more or less inflated and distorted in ordinary protargol preparations (Fig. 179f, g).

→ *Paragonostomum rarisetum*, which has a similar size and the same nuclear pattern, has a more distinct tail (25% vs. 10% of body length), and slightly more frontoventral and frontoterminal cirri (7 vs. 5), but fewer adoral membranelles (15 on average vs. 21).

→ *Gonostomum namibiense*, which has also a similar size and shape and the same nuclear pattern, possesses transverse cirri and cortical granules, which are, however, difficult to recognize because they are minute (1 × 0.3 µm) and colourless. Likewise, → *Gonostomum algicola* is rather similar, but usually lacks any indication of a tail, has only four paroral kinetids in a short, uninterrupted row, and possesses one transverse cirrus, which is, however, difficult to recognize. Thus, reliable species identification requires protargol impregnation or very careful in vivo observation.

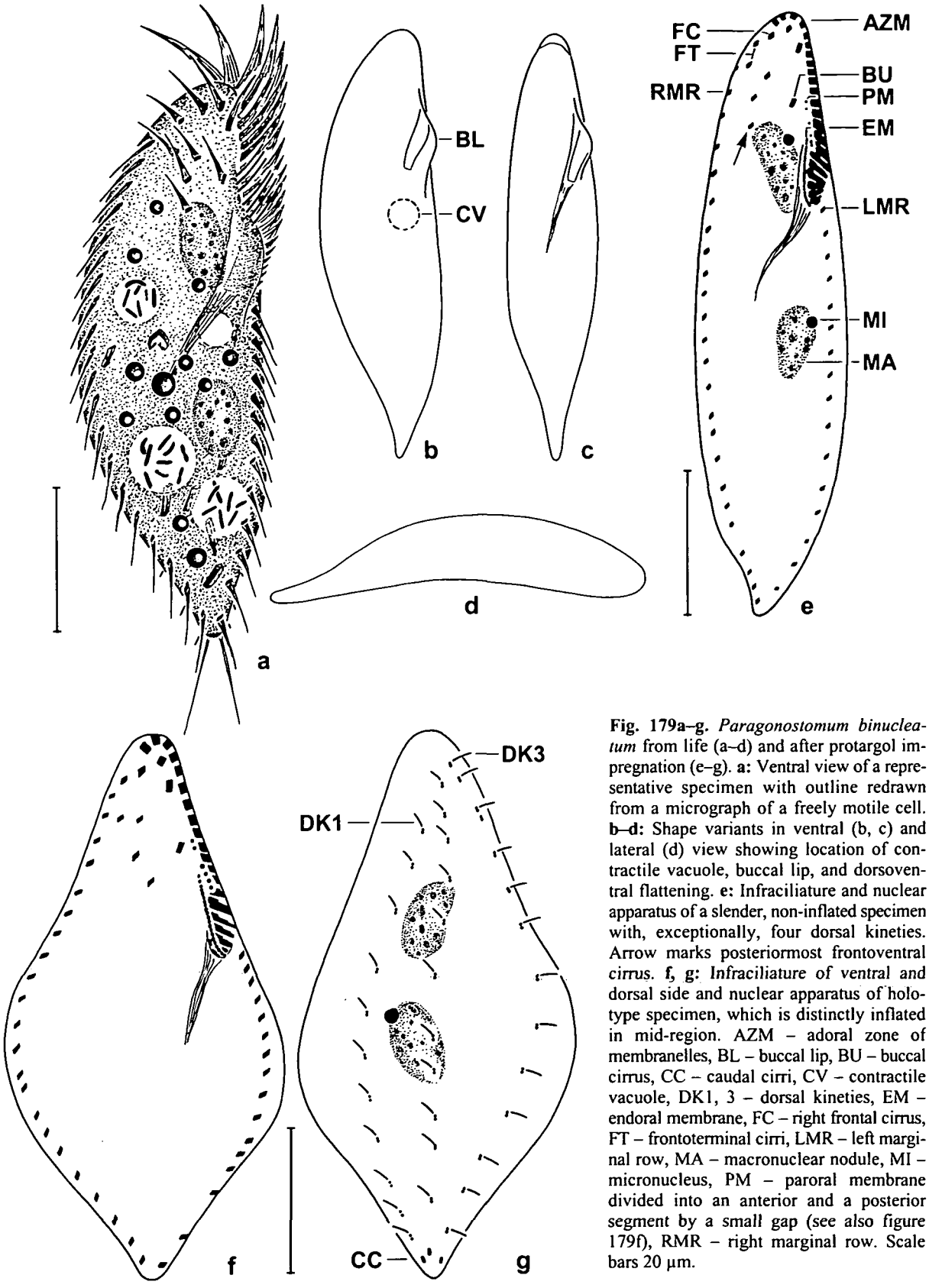

Fig. 179a–g. *Paragonostomum binucleatum* from life (a–d) and after protargol impregnation (e–g). **a:** Ventral view of a representative specimen with outline redrawn from a micrograph of a freely motile cell. **b–d:** Shape variants in ventral (b, c) and lateral (d) view showing location of contractile vacuole, buccal lip, and dorsoventral flattening. **e:** Infraciliature and nuclear apparatus of a slender, non-inflated specimen with, exceptionally, four dorsal kineties. Arrow marks posteriormost frontoventral cirrus. **f, g:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen, which is distinctly inflated in mid-region. AZM – adoral zone of membranelles, BL – buccal lip, BU – buccal cirrus, CC – caudal cirri, CV – contractile vacuole, DK1, 3 – dorsal kineties, EM – endoral membrane, FC – right frontal cirrus, FT – frontoterminal cirri, LMR – left marginal row, MA – macronuclear nodule, MI – micronucleus, PM – paroral membrane divided into an anterior and a posterior segment by a small gap (see also figure 179f), RMR – right marginal row. Scale bars 20 µm.

Occurrence and ecology: To date found at type location, where it was moderately abundant, and at Namibian sites (33, 49, 52, 56), where it was rare. The soil where *P. binucleatum* was discovered, is very likely artificial (compost or composted activated sludge) because it was only an about 5 cm thick layer above the sandy ground. It was black and "fat", hardly contained any litter, had a pH of 8.2, and was sown with lawn grasses a few days previously.

Paragonostomum multinucleatum **nov. spec.** (Fig. 180a–k; Table 158)

Diagnosis: Size about 75 × 15 µm in vivo. Pisciform with tail-like posterior portion occupying about 20% of body length. On average 7 macronuclear nodules forming distinct strand, 22 right marginal, 16 left marginal, 2 frontoterminal, and 3 frontoventral cirri; 1 buccal cirrus in front of paroral composed of 4–7, usually 6 kinetids divided into an anterior and posterior segment by a small gap. Adoral zone of membranelles about one third of body length, composed of 19 membranelles on average.

Type location: Highly saline crust soil from small quartz stones about 1 km inshore of the Great Bay of the town of Lüderitz, Namibia, 26°40'S 15°10'E (site 11 in figure 2 and chapter 2.1.2).

Etymology: The Latin adjective *multinucleatum* (many nuclei) refers to the numerous macronuclear nodules, a main feature of this species.

Description: Size 60–90 × 13–25 µm in vivo, usually about 75 × 15 µm, length:width ratio 3.0–4.5:1, on average 3.8:1 in protargol preparations, where specimens are more or less inflated since they are rather fragil (Table 158). Body elongate and tail-like posteriorly in vivo and protargol preparations; only slightly flattened and asymmetrical, left margin straight to slightly sigmoidal, right slightly to distinctly convex and narrowed in posterior quarter producing tail-like elongation; acontractile but very flexible (Fig. 180a–c). Macronuclear nodules mainly left of midline in series, sometimes in C-shaped pattern, some nodules occasionally separated by small gaps; individual nodules globular to ellipsoidal (2:1), rarely dumb-bell-shaped or elongate ellipsoidal indicating that two or three nodules have not separated, contain globular nucleoli. Micronuclei near or attached to macronuclear nodules, globular, inconspicuous because tiny and rather hyaline. Contractile vacuole with two collecting canals right of buccal vertex, that is, in or near body midline. Cortical granules recognizable neither in vivo nor in protargol preparations. Cytoplasm colourless, with few, about 2–3 µm-sized crystals and some lipid droplets 1–3 µm across in posterior body portion. Feeds on bacteria and coccal green algae digested in vacuoles 4–6 µm across. Glides rather rapidly on microscope slide.

Cirral pattern very constant, number of cirri of usual variability (Fig. 180c–f, i, j; Table 158). Marginal cirri about 7 µm long in vivo, arranged in two rows extending to or near to posterior body end, right row extends onto dorsal side anteriorly; posterior marginal cirri composed of two basal bodies only and thus very fine. Only nine frontoventral cirri on average. Frontal cirri about 10 µm long in vivo, moderately enlarged. Buccal cirrus slightly right and ahead of paroral membrane. Frontoventral row distinctly shorter than adoral zone of membranelles, in or right of midline, except for anteriormost cirrus, which is invariably shifted leftwards and

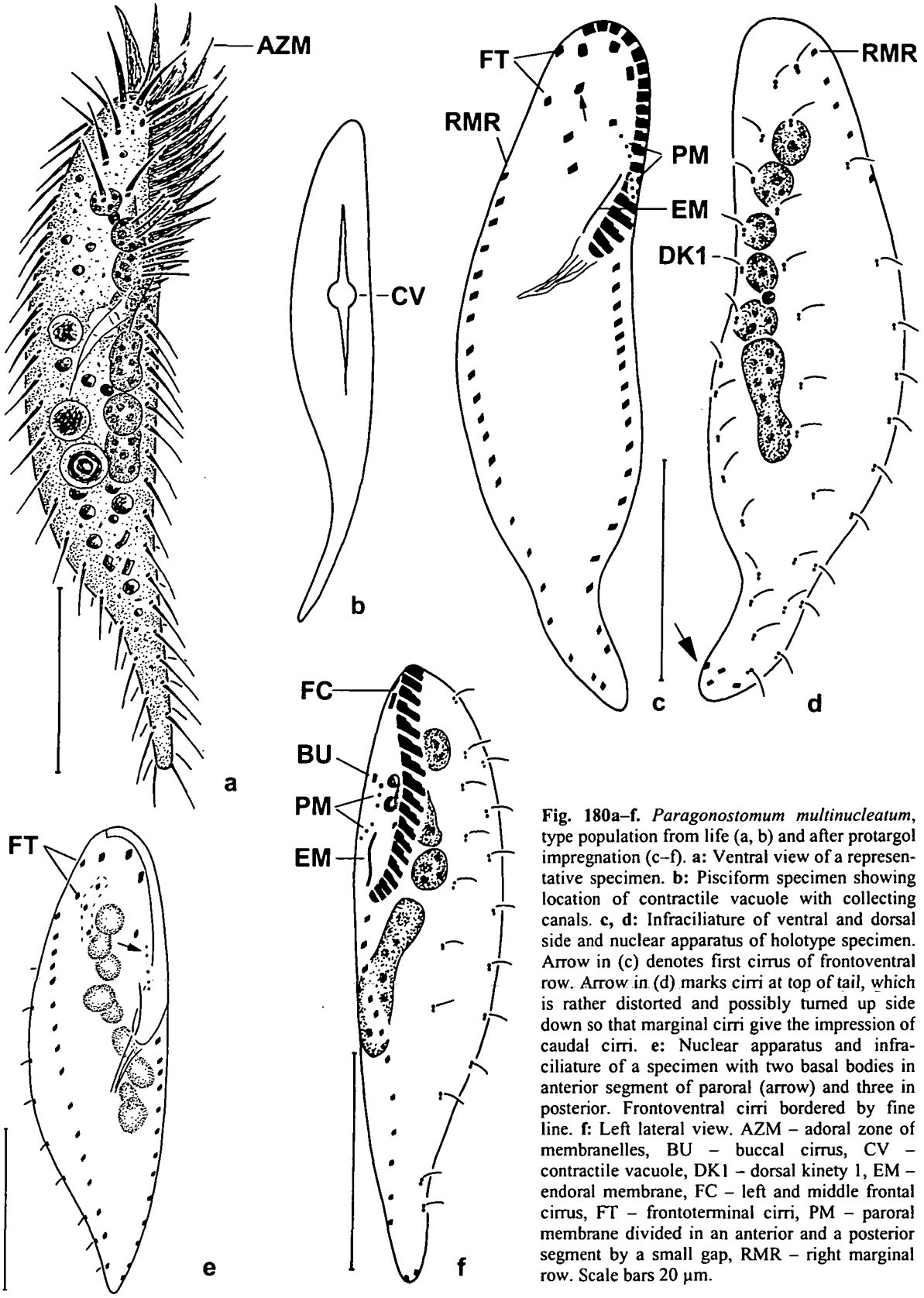

Fig. 180a–f. *Paragonostomum multinucleatum*, type population from life (a, b) and after protargol impregnation (c–f). **a:** Ventral view of a representative specimen. **b:** Pisciform specimen showing location of contractile vacuole with collecting canals. **c, d:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrow in (c) denotes first cirrus of frontoventral row. Arrow in (d) marks cirri at top of tail, which is rather distorted and possibly turned up side down so that marginal cirri give the impression of caudal cirri. **e:** Nuclear apparatus and infraciliature of a specimen with two basal bodies in anterior segment of paroral (arrow) and three in posterior. Frontoventral cirri bordered by fine line. **f:** Left lateral view. AZM – adoral zone of membranelles, BU – buccal cirrus, CV – contractile vacuole, DK1 – dorsal kinety 1, EM – endoral membrane, FC – left and middle frontal cirrus, FT – frontoterminal cirri, PM – paroral membrane divided in an anterior and a posterior segment by a small gap, RMR – right marginal row. Scale bars 20 μm.

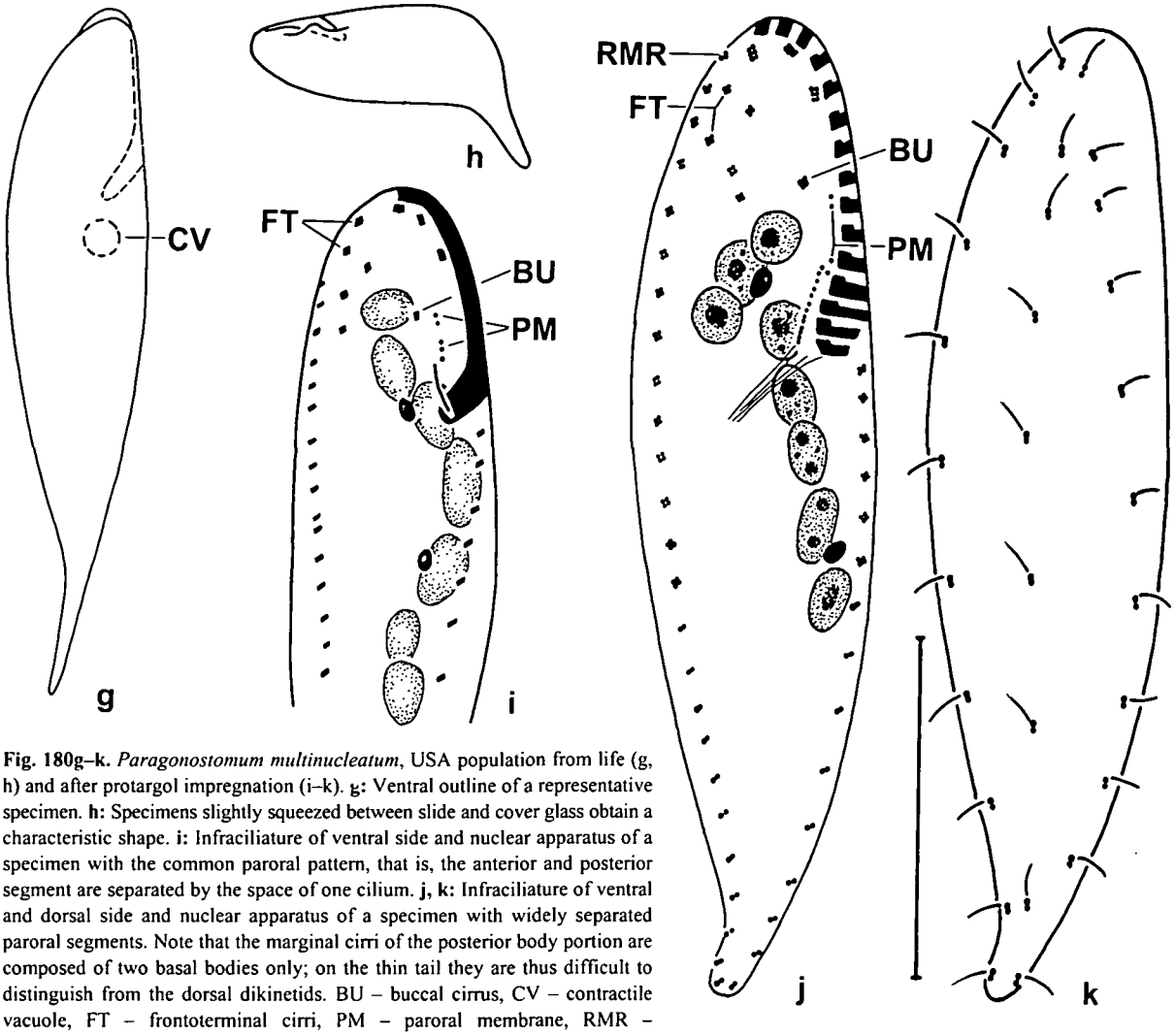

Fig. 180g–k. *Paragonostomum multinucleatum*, USA population from life (g, h) and after protargol impregnation (i–k). **g:** Ventral outline of a representative specimen. **h:** Specimens slightly squeezed between slide and cover glass obtain a characteristic shape. **i:** Infraciliature of ventral side and nuclear apparatus of a specimen with the common paroral pattern, that is, the anterior and posterior segment are separated by the space of one cilium. **j, k:** Infraciliature of ventral and dorsal side and nuclear apparatus of a specimen with widely separated paroral segments. Note that the marginal cirri of the posterior body portion are composed of two basal bodies only; on the thin tail they are thus difficult to distinguish from the dorsal dikinetids. BU – buccal cirrus, CV – contractile vacuole, FT – frontoterminal cirri, PM – paroral membrane, RMR – anteriormost cirrus of right marginal row. Scale bar 20 µm.

thus behind right frontal cirrus. Frontoterminal cirri near or on right dorsolateral surface, form short, slightly oblique row. Transverse cirri absent.

Dorsal bristles about 3 µm long in vivo, arranged in three rows; details of pattern and presence/absence of caudal cirri difficult to analyze for reasons mentioned in genus section, very likely as shown in figures 180d, f, k; in vivo, the cirri at the peak of the tail are inconspicuous.

Oral apparatus in → *Gonostomum* pattern (Fig. 180a, c, e, i, j). Adoral zone occupies only slightly more than one third of body length (50% in most *Gonostomum* species), commences near midline of anterior body end and extends straight along left body margin, performing abrupt right bend and slight clockwise rotation to plunge into buccal cavity near left body margin; composed of an average of 19 membranelles, bases of largest membranelles about 4 µm wide. Proximal portion of adoral zone and buccal cavity almost entirely covered by a curved, rather prominent cortical process (buccal lip) bearing the paroral membrane. Paroral as in → *P. binucleatum*, that is, divided into an anterior segment with 1–3 and a posterior

segment with 2–4 widely spaced, about 8 µm long cilia (Fig. 180a, c, e, f, i, j). Buccal cavity very narrow and flat, at right bordered by slightly curved endoral membrane composed of tightly spaced basal bodies. Pharyngeal fibres clearly recognizable in vivo and after protargol impregnation, extend obliquely backwards.

Occurrence and ecology: The type population was discovered at Namibian site (11), that is, in a highly saline crust soil. The second population is also from an extreme habitat, viz., the Warm Sonoran Desert of Arizona, USA, where *P. multinucleatum* occurred in the litter and upper soil layer under *Ephedra* sp. ("mormon tea", jointed firs), a gymnospermous belonging to the Ginetophyta (collected by Prof. Dr. Stuart BAMFORTH on 21. May 1988 at 11 h 30, when soil temperature was 40° C under *Ephedra*). The USA specimens match the type population very well, both in morphology and main morphometrics (Fig. 180g–k; Table 158). Likely, *Paragonostomum multinucleatum* is euryhaline and cosmopolitan.

Comparison with related species: *Paragonostomum multinucleatum* is, like → *P. rarisetum*, → *P. binucleatum*, → *P. caudatum* and → *Gonostomum namibiense*, a conspicuous species due to the distinct tail. It differs from the congeners and → *G. namibiense*, inter alia, by the number of macronuclear nodules (4–9 versus 2). As concerns the infraciliature, *P. multinucleatum* is indistinguishable from → *P. binucleatum*. In vivo, it is easily identified by the gonostomoid oral apparatus, the tailed body, the macronuclear strand, and the lack of transverse cirri.

Paragonostomum rarisetum **nov. spec.** (Fig. 181a–e; Table 159)

Diagnosis: Size about 85 × 20 µm in vivo. Lanceolate with conspicuous tail occupying about 25% of body length. 2 macronuclear nodules. On average 21 right marginal and 15 left marginal cirri; frontoventral and frontoterminal cirri form single row composed of 6 cirri on average and ending at 20% of body length; 1 buccal cirrus at anterior end of paroral composed of 6–9, usually 7 kinetids. Adoral zone of membranelles about 27% of body length, composed of 15 membranelles on average.

Type location: Soil from *Aloe dichotoma* forest near the Gariganus Guest Farm, Namibia, 26°30'S 18°25'E (site 5 in figure 2 and chapter 2.1.2).

Etymology: Composite of the Latin words *rarus* (few) and *saeta* (bristle ~ cirrus), referring to the reduced number of frontoventral cirri.

Description and comparison with related species: In vivo, *P. rarisetum* was identified as → *P. caudatum*, from which it is indistinguishable in size, shape and general appearance. However, protargol impregnation revealed several distinct features, suggesting species status.

(i) *Paragonostomum rarisetum* seemingly lacks frontoterminal cirri, that is, has only a single row of cirri extending slightly obliquely from the distal end of the adoral zone to the mid of the frontal field (Fig. 181a, e). The lack of frontoterminal cirri would be a highly deviating feature in an oxytrichid ciliate (BERGER 1999). Fortunately, we found a late divider, which shows

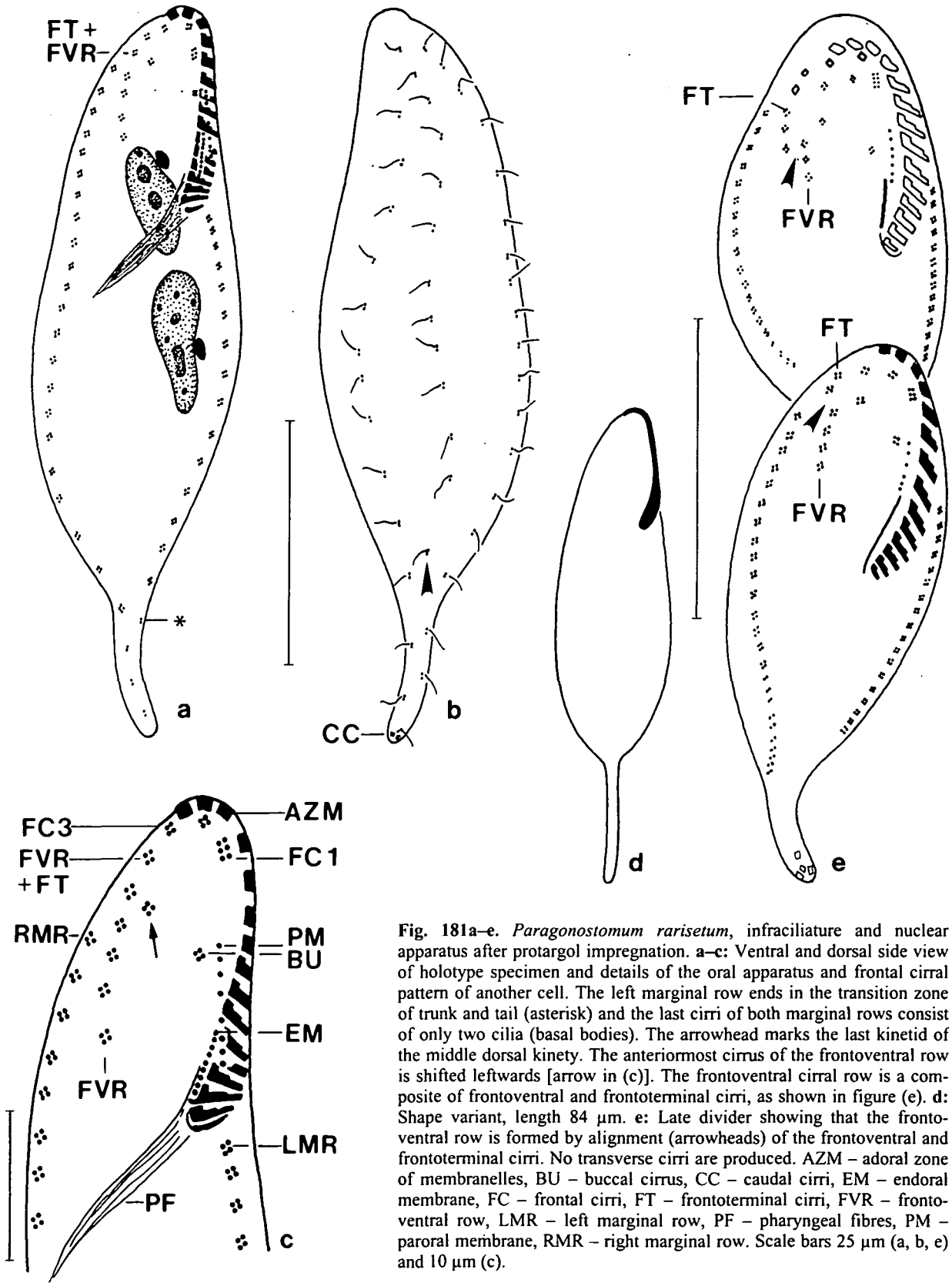

Fig. 181a–e. *Paragonostomum rarisetum*, infraciliature and nuclear apparatus after protargol impregnation. **a–c:** Ventral and dorsal side view of holotype specimen and details of the oral apparatus and frontal cirral pattern of another cell. The left marginal row ends in the transition zone of trunk and tail (asterisk) and the last cirri of both marginal rows consist of only two cilia (basal bodies). The arrowhead marks the last kinetid of the middle dorsal kinety. The anteriormost cirrus of the frontoventral row is shifted leftwards [arrow in (c)]. The frontoventral cirral row is a composite of frontoventral and frontoterminal cirri, as shown in figure (e). **d:** Shape variant, length 84 µm. **e:** Late divider showing that the frontoventral row is formed by alignment (arrowheads) of the frontoventral and frontoterminal cirri. No transverse cirri are produced. AZM – adoral zone of membranelles, BU – buccal cirrus, CC – caudal cirri, EM – endoral membrane, FC – frontal cirri, FT – frontoterminal cirri, FVR – frontoventral row, LMR – left marginal row, PF – pharyngeal fibres, PM – paroral membrane, RMR – right marginal row. Scale bars 25 µm (a, b, e) and 10 µm (c).

that two or three frontoterminal cirri are present but aligned to the anterior end of the frontoventral row (Fig. 181e). In the congeners, the frontoterminal and frontoventral cirri form separate rows.

(ii) The frontoventral cirral row of *P. rarisetum*, although containing the frontoterminal cirri, is distinctly shorter than that of → *P. caudatum* (extending 15 vs. 25 µm back from anterior body end; Tables 158, 159), although it consists of six cirri in both. Obviously, the cirri are more closely spaced and the row commences more anteriorly in *P. rarisetum*.

(iii) → *Paragonostomum caudatum* has a total of ten frontoventral and frontoterminal cirri, while *P. rarisetum* has only six on average, similar to → *P. multinucleatum*.

(iv) The adoral zone of *P. rarisetum* is composed of 15 membranelles, while that of → *P. caudatum* consists of 19. Accordingly, the membranellar zone is shorter in *P. rarisetum* than in → *P. caudatum*: 36% vs. 44% of trunk length; ratio total body length:length of adoral zone 3.6:1 vs. 2.9:1.

Further observations from protargol-impregnated specimens: (i) Macronuclear nodules obliquely arranged, as described in → *Gonostomum namibiense* and shown in figure 181a. (ii) Two to three cirri, each composed of two long cilia, at peak of tail. These cirri must be caudal cirri because no transverse cirri are recognizable in the late divider (Fig. 181e). (iii) Dorsal bristles 3–5 µm long. (iv) Cilia of paroral membrane about 10 µm long and loosely spaced, occasionally with a distinct gap, as in → *P. multinucleatum*.

Occurrence and ecology: To date found at four sites in Namibia (Table 4), all in the Namib Escarpment, indicating that it prefers hot and dry conditions. We cannot exclude having mixed *P. rarisetum* with *P. caudatum* when in vivo identifications were not checked in protargol slides.

Table 159. Morphometric data on *Paragonostomum rarisetum*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Trunk, length [b]	59.9	60.0	3.8	1.0	6.4	52.0	68.0	15
Trunk, width	16.7	16.0	2.0	0.5	12.1	13.0	22.0	15
Trunk, length:width ratio [b]	3.6	3.7	0.4	0.1	11.2	2.9	4.5	15
Tail, length	17.5	17.0	3.7	1.0	21.0	13.0	23.0	15
Tail, width	2.3	2.0	–	–	–	2.0	3.0	15
Anterior body end to proximal end of adoral zone, distance	21.3	21.0	0.8	0.2	3.8	20.0	23.0	15
Trunk length: length of adoral zone, ratio [b]	2.8	2.8	0.2	0.1	7.6	2.4	3.2	15
Anterior body end to last frontoventral cirrus, distance	15.2	15.0	1.8	0.5	12.0	13.0	20.0	15
Anterior body end to buccal cirrus, distance	9.4	10.0	1.9	0.5	20.0	7.0	14.0	15
Anterior body end to anterior end of right marginal row, distance	7.0	7.0	1.6	0.4	22.9	4.0	10.0	15
Anterior body end to posterior end of left marginal row, distance	59.9	60.0	3.8	1.0	6.4	52.0	68.0	15
Nuclear figure, length	26.5	27.0	2.9	0.8	11.0	22.0	31.0	15
Anterior macronuclear nodule, length	11.4	11.0	1.4	0.4	11.9	10.0	14.0	15
Anterior macronuclear nodule, width	4.9	5.0	0.7	0.2	14.3	4.0	6.0	15
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15

(continued)

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Macronuclear nodules, distance in between	2.2	2.0	1.1	0.3	49.2	1.0	5.0	15
Anterior micronucleus, length	2.5	3.0	0.5	0.1	20.4	2.0	4.0	15
Anterior micronucleus, width	1.8	2.0	–	–	–	1.5	2.0	15
Micronuclei, number	1.9	2.0	0.5	0.1	27.7	1.0	3.0	15
Adoral membranelles, number	15.0	15.0	0.9	0.2	6.2	14.0	17.0	15
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
Frontoterminal cirri, number				see text				
Frontoventral cirri, number (see also text!)	6.5	6.0	0.8	0.2	12.8	5.0	8.0	15
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Right marginal cirri, number	21.1	21.0	3.3	0.9	15.8	13.0	25.0	15
Left marginal cirri, number	15.4	15.0	2.5	0.7	16.4	13.0	23.0	15
Dorsal kineties, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
Kinetids in middle dorsal ciliary row, number	10.9	11.0	1.2	0.3	11.2	9.0	13.0	15
Paroral kinetids, number	7.1	7.0	0.9	0.2	12.9	6.0	9.0	15
Paroral membrane, length	7.3	8.0	0.9	0.2	12.1	6.0	8.0	15
Endoral kinetids, number	7.9	8.0	1.0	0.3	12.6	6.0	9.0	10
Endoral membrane, length	4.7	4.5	0.9	0.3	18.9	4.0	7.0	12

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Measured as in → *P. caudatum*.

Hemiurosoma nov. gen.

Diagnosis: Oxytrichidae with oral apparatus in *Gonostomum* pattern and frontoventral cirri in *Urosoma* pattern. 2 or less postoral cirri. 5 or less pretransverse and transverse cirri. 1 right and 1 left row of marginal cirri. 4 dorsal kineties. Caudal cirri present. Fronto-ventral-transverse cirri originate from 5 anlagen, four of which are primary primordia. Dorsal ontogenesis in *Urosomoida* pattern.

Type species: *Hemiurosoma terricola* nov. spec.

Etymology: Composite of the Greek word *hemi* (half) and the generic name *Urosoma* (tailed body), referring to the similarity with the genus *Urosoma* KOWALEWSKIEGO, 1882. Feminine gender.

Comparison with related genera: This genus is established to contain two species described by FOISSNER (1982, 1984) and two new species found in Namibia. FOISSNER (1982, 1984) assigned his species to *Hemisincirra* (*H. similis*, *H. polynucleata*), while BERGER (1999) combined them with *Urosoma*, emphasizing "that they very likely form a distinct clade within that genus". We could study the ontogenesis in one such form, viz., → *Hemiurosoma terricola*. It differs from most oxytrichids s. str. and especially from that of *Urosoma*

by generating not six but only five fronto-ventral-transverse cirral anlagen, possibly due to the reduced number of cirri. Furthermore, the reduction of the postoral cirri causes all or most (possibly in the two species still having one postoral cirrus) opisthe anlagen to originate de novo via the de novo developing oral primordium. This is unusual in *Oxytricha* but typical for *Hemisincirra* (HEMBERGER 1982, 1985) and possibly also some other oxytrichids with a reduced number of postoral cirri, e.g., → *Erimophrya arenicola* and → *Vermioxytricha arenicola*. The occurrence of only five fronto-ventral-transverse cirral anlagen in *Hemiurosoma* is more than a simple quantitative difference because most other oxytrichids with fewer (e.g. *Urosomoida*) or more (e.g. → *Gastrostyla*) than the usual 18 frontoventral cirri still have six anlagen (for a review, see BERGER 1999).

Long after having written this paragraph, we discovered two further groups of oxytrichids with only five fronto-ventral-transverse cirral anlagen, namely → *Erimophrya* and → *Vermioxytricha*. However, the anlagen reduction likely evolved convergently in these three groups because they have a different oral apparatus (see diagnoses and relevant figures).

Hemiurosoma differs from *Urosoma* by the reduced number of postoral (0–1 vs. 3) and transverse (2 vs. 5) cirri, and cirral anlagen during ontogenesis (5 vs. 6). The reduction of the transverse cirri is very likely not caused by simple spatial constraints, that is, the narrowed posterior body end, because tailed *Urosoma* species still have the usual five transverse cirri, but at the base of the tail, where sufficient space is available (for a review, see BERGER 1999).

Hemiurosoma differs from *Urosomoida* by the different arrangement of the frontoventral cirri and adoral zone (*Urosoma* vs. *Oxytricha* pattern), and the number of cirral anlagen during ontogenesis (5 vs. 6). *Hemiurosoma* differs from *Hemisincirra* by the arrangement of the frontoventral cirri (*Urosoma* vs. zigzag-like pattern; see *Hemisincirra* species described in this monograph) and oral apparatus (*Urosoma* vs. *Urosomoida* pattern), while ontogenesis is very similar (HEMBERGER 1982, 1985). However, *Hemisincirra* is still insufficiently defined and holds mostly small, slender species that do not fit any other genus well. Several species were transferred to new genera, such as → *Terricirra* BERGER & FOISSNER, 1989a and *Circinella* FOISSNER, 1994a.

As mentioned above, two species have to be transferred to the new genus: *Hemiurosoma similis* (FOISSNER, 1982) nov. comb. (basionym: *Perisincirra similis* FOISSNER, 1982) and *Hemiurosoma polynucleata* (FOISSNER, 1984) nov. comb. (basionym: *Hemisincirra polynucleata* FOISSNER, 1984).

***Hemiurosoma terricola* nov. spec.** (Fig. 182a–u; 381q, 400a–j; Table 160)

Diagnosis: Size about 150 × 20 µm in vivo; slenderly lanceolate. 4 macronuclear nodules and 21 adoral membranelles on average.

Type location: Soil from the ghost tree forest (*Moringa ovalifolia*) in the Etosha National Park, 19°S 15°40'E (site 56 in figures 2, 3 and chapter 2.1.2).

Etymology: The Latin *terricola* (living in soil) refers to the habitat the species was discovered.

Description: Size 120–180 × 15–25 µm in vivo, length:width ratio 5.3–8.7:1, on average 7.3:1 in vivo, scanning electron micrographs, and protargol preparations; slightly flattened dorsoventrally, very flexible but acontractile. Outline very elongate lanceolate with anterior end usually transversely truncate and posterior distinctly narrowed; specimens from Namibian site (29) almost parallel-sided and tail-like narrowed posteriorly, very much like *H. similis* (Fig. 182a–c, h, i; 381q, 400a, b, g; Table 160). Cells difficult to preserve, usually inflated and/or wrinkled in ordinary protargol preparations (FOISSNER's method), while well-preserved with DIECKMANN's technique (Fig. 182h, i). Macronuclear nodules left of midline in middle third of cell, ellipsoidal, contain many minute nucleoli; one or two nodules incompletely separated in about 25% of specimens, quadrinuclear pattern, however, always recognizable; nodules sometimes in two more or less distinct pairs, especially in Costa Rican and Namibian site (29) specimens; cells with five or six nodules more frequent in Costa Rican than Namibian population. Usually two ellipsoidal micronuclei, one each in anterior and posterior portion of nuclear figure, frequently not impregnated with protargol. Contractile vacuole with fine collecting canals near mid-body left of midline. Cortical granules lacking; subcortical mitochondria as conspicuous as in *Urosoma* spp., about 2–3 × 1–2 µm in size. Cytoplasm colourless, contains many sand-like crystals 1–3 µm across, mainly in rear body quarter, and innumerable, about 1 µm-sized fat droplets forming short rows and reticular structures (Fig. 182d). Usually packed with 4–6 µm-sized food vacuoles containing remnants of bacteria and, likely, heterotrophic flagellates. Glides slowly on microscope slide and soil particles. Resting cysts of a population from the Zambezi floodplain globular with smooth, colourless wall (Fig. 400j).

Cirral pattern constant, number of cirri of usual variability (Fig. 182a, h, i; 381q, 400a–i; Table 160). Marginal cirri about 10 µm long in vivo, likely composed of 3–4 × 2 basal bodies, except for posterior cirri comprising only four cilia. Frontal cirri slightly enlarged, right one behind distal end of adoral zone. Buccal cirrus right of anterior half of paroral membrane. Frontoventral cirri right of a minute crest, arranged in typical *Urosoma* pattern, that is, in a slightly oblique row with anterior cirrus (= cirrus III/2 in Fig. 182h; for details, see Fig. 381q, 400f, i and BERGER 1999) somewhat dislocated to left and indistinctly enlarged. No postoral cirri. Transverse cirri of about same size as marginal cirri, but 15–20 µm long, very near to body end and thus distinctly projecting, just as in *H. similis* and *H. polynucleata*, while distinctly subterminal in → *H. goertzi* (Fig. 183a, j, k). Caudal cirri also 15–20 µm long and near posterior body end and thus difficult to separate from transverse cirri. Dorsal bristles 3–4 µm long in vivo, much more closely spaced in anterior than posterior half of cell, arranged in four rows: row 1 slightly shortened anteriorly; rows 2 and 3 bipolar; row 4 consists of only three to four bristles in anterior body third.

Adoral zone short, occupies only 14–21%, on average 18% of body length, roughly in *Gonostomum* pattern, that is, extends straight along left body margin, performing right bend and slight clockwise rotation to plunge into buccal cavity; composed of an average of 21 membranelles, bases of largest membranelles 5–6 µm wide in vivo. Buccal cavity very flat and narrow, right margin forms hyaline lip bearing undulating membrane and covering buccal cavity and proximal third of adoral zone. Undulating membranes almost straight and in series or slightly overlapping, both minute and likely dikinetidal; paroral with a small fibre bundle anteriorly and cilia about 7 µm long in vivo. Pharyngeal fibres distinct in vivo and protargol preparations, of ordinary length and structure, extend obliquely backwards (Fig. 182a, f, h; 400a, c, f, h, i; Table 160).

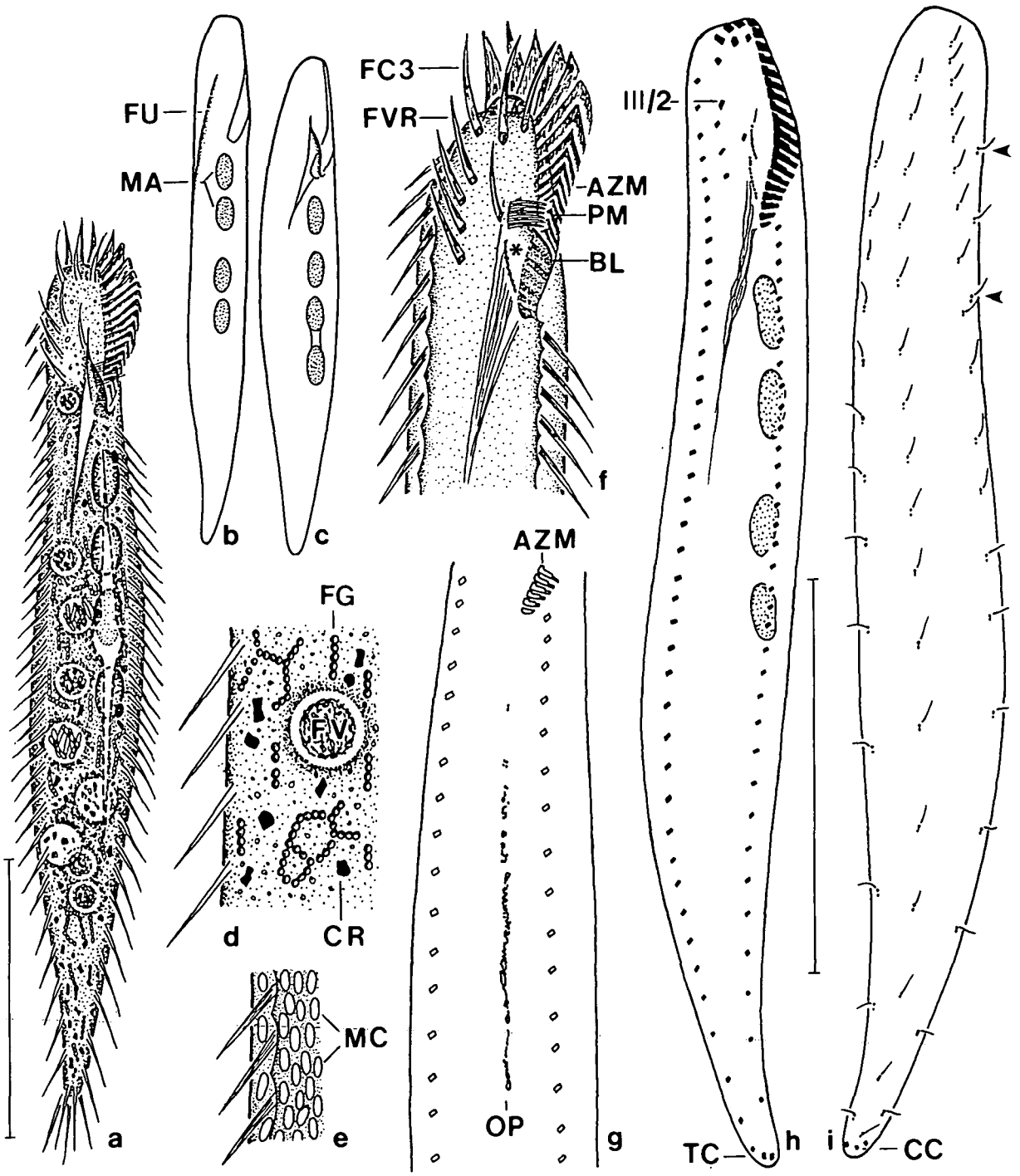

Fig. 182a–i. *Hemiurosoma terricola* from life (a–f) and after protargol impregnation (g–i). **a:** Ventral view of a representative specimen. **b, c:** Shape variants. **d:** Optical section showing aggregates of minute fat globules in the cytoplasm. **e:** Surface view showing subcortical mitochondria. **f:** Anterior ventral body portion. Note the broad buccal lip (BL) covering the minute buccal cavity (asterisk) and part of the adoral zone. **g:** Very early divider with oral primordium in anterior body half. **h, i:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrowheads mark short dorsal kinety 4. AZM – adoral zone of membranelles, CC – caudal cirri, BL – buccal lip, CR – crystal, FC3 – third frontal cirrus, FG – fat globules, FU – dorsal furrow, FV – food vacuole, FVR – frontoventral row, MA – macronuclear nodules, MC – mitochondria, OP – oral primordium, PM – paroral, TC – transverse cirri, III/2 – frontoventral cirrus. Scale bars 50 μm.

Table 160. Morphometric data on *Hemiurosoma terricola*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	138.5	138.0	10.5	2.4	7.6	117.0	161.0	19
Body, width	19.2	20.0	2.1	0.5	11.1	15.0	22.0	19
Body length:width, ratio	7.3	7.3	0.8	0.2	10.9	5.3	8.7	19
Anterior body end to end of adoral zone, distance	24.5	25.0	2.1	0.5	8.8	19.0	28.0	19
Body length:length of adoral zone, ratio	5.7	5.6	0.7	0.2	11.6	4.7	7.3	19
Anterior body end to paroral membrane, distance	11.8	12.0	1.5	0.4	13.0	9.0	15.0	19
Paroral membrane, length	3.6	4.0	0.6	0.1	17.0	3.0	5.0	19
Anterior body end to endoral membrane, distance	16.4	16.0	2.3	0.5	14.0	14.0	21.0	19
Endoral membrane, length	5.6	6.0	0.6	0.1	10.6	5.0	7.0	19
Anterior body end to first frontoventral cirrus, distance	9.0	9.0	0.8	0.2	9.1	7.0	10.0	19
Anterior body end to last frontoventral cirrus, distance	19.1	19.0	1.3	0.3	7.0	17.0	22.0	19
Anterior body end to buccal cirrus, distance	11.7	12.0	1.6	0.4	13.4	8.0	14.0	19
Anterior body end to right marginal row, distance	7.4	7.0	1.0	0.2	13.7	6.0	9.0	19
Anterior body end to first macronuclear nodule, distance	31.7	31.0	1.9	0.4	6.1	28.0	35.0	19
Nuclear figure, length	45.0	45.0	4.8	1.1	10.7	35.0	51.0	19
Anterior macronuclear nodule, length	8.5	9.0	1.8	0.4	21.2	6.0	13.0	19
Anterior macronuclear nodule, width	4.3	4.0	0.6	0.1	13.5	3.0	5.0	19
Macronuclear nodules, number	4.1	4.0	–	–	–	4.0	5.0	30
Anterior micronucleus, length	3.3	3.0	–	–	–	3.0	4.0	19
Anterior micronucleus, width	1.8	2.0	–	–	–	1.5	2.0	19
Micronuclei, number	2.1	2.0	–	–	–	2.0	3.0	19
Posterior body end to transverse cirri, distance	1.3	1.0	–	–	–	1.0	2.0	19
Adoral membranelles, number	21.1	21.0	0.9	0.2	4.4	19.0	23.0	19
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
Frontoventral cirri, number	4.1	4.0	–	–	–	4.0	5.0	19
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
Postoral cirri, number	0.0	0.0	0.0	0.0	0.0	0.0	0.0	30
Transverse cirri, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
Right marginal cirri, number	37.0	37.0	1.8	0.4	4.7	35.0	41.0	19
Left marginal cirri, number	31.8	31.0	2.9	0.7	9.2	28.0	40.0	19
Caudal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
Dorsal kineties, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	19

[a] Data based on mounted, protargol-impregnated (DIECKMANN 1995 method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max –maximum, Min – minimum, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Ontogenesis (Fig. 182g, j–u): Division was studied in specimens from type location and Costa Rica (Fig. 182n, u), which together provided a complete series of events. Ontogenesis of *H. terricola* is similar to that of oxytrichids in general and *Urosoma* in particular because the proter cirral anlagen are entirely or partially produced by the opisthe via long primary primordia, a highly characteristic apomorphy uniting the genera *Urosoma*, *Hemiurosoma*, and *Gonostomum* (BERGER 1999, FOISSNER & ADAM 1983a).

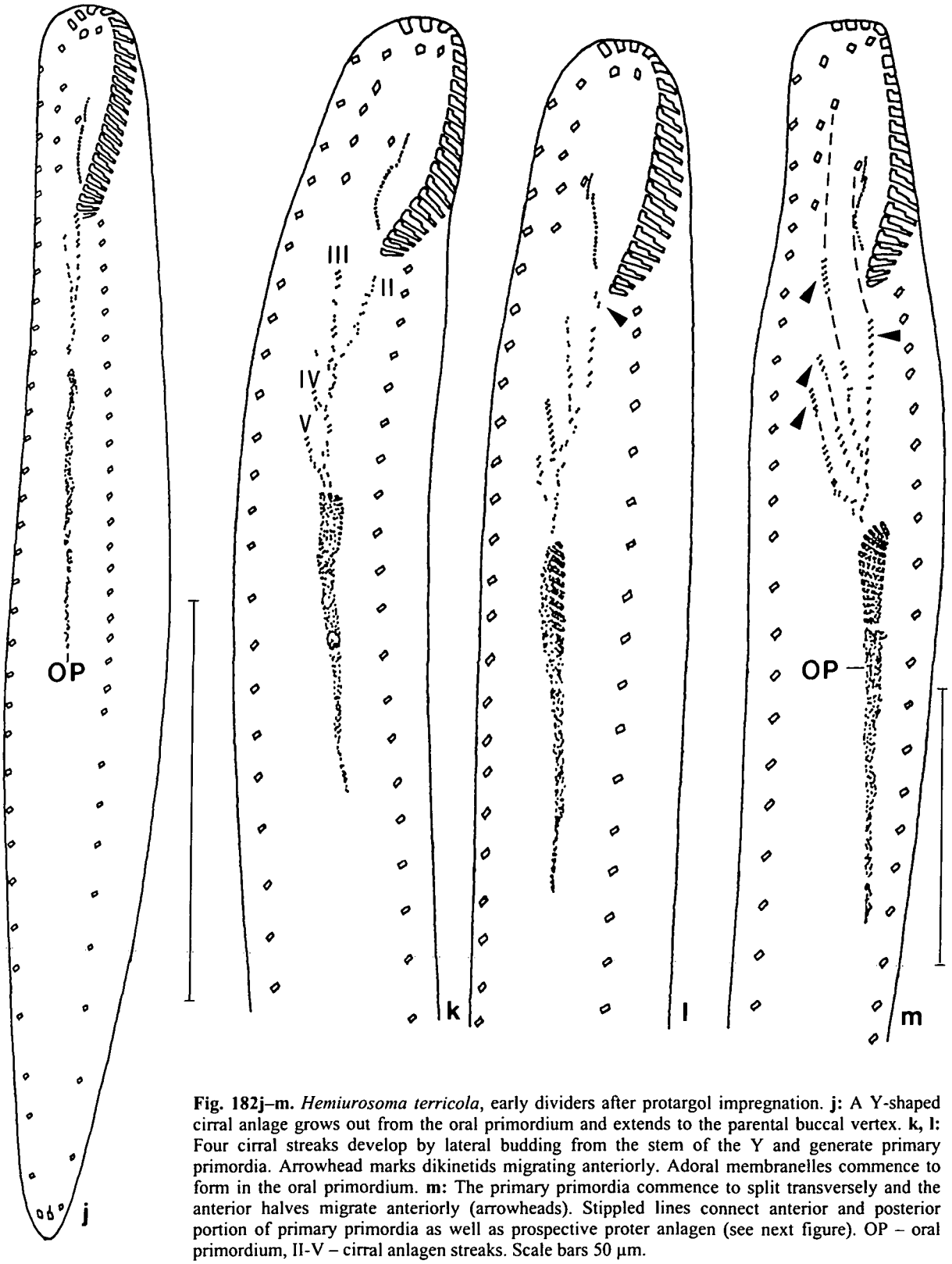

Fig. 182j–m. *Hemiurosoma terricola*, early dividers after protargol impregnation. **j:** A Y-shaped cirral anlage grows out from the oral primordium and extends to the parental buccal vertex. **k, l:** Four cirral streaks develop by lateral budding from the stem of the Y and generate primary primordia. Arrowhead marks dikinetids migrating anteriorly. Adoral membranelles commence to form in the oral primordium. **m:** The primary primordia commence to split transversely and the anterior halves migrate anteriorly (arrowheads). Stippled lines connect anterior and posterior portion of primary primordia as well as prospective proter anlagen (see next figure). OP – oral primordium, II-V – cirral anlagen streaks. Scale bars 50 µm.

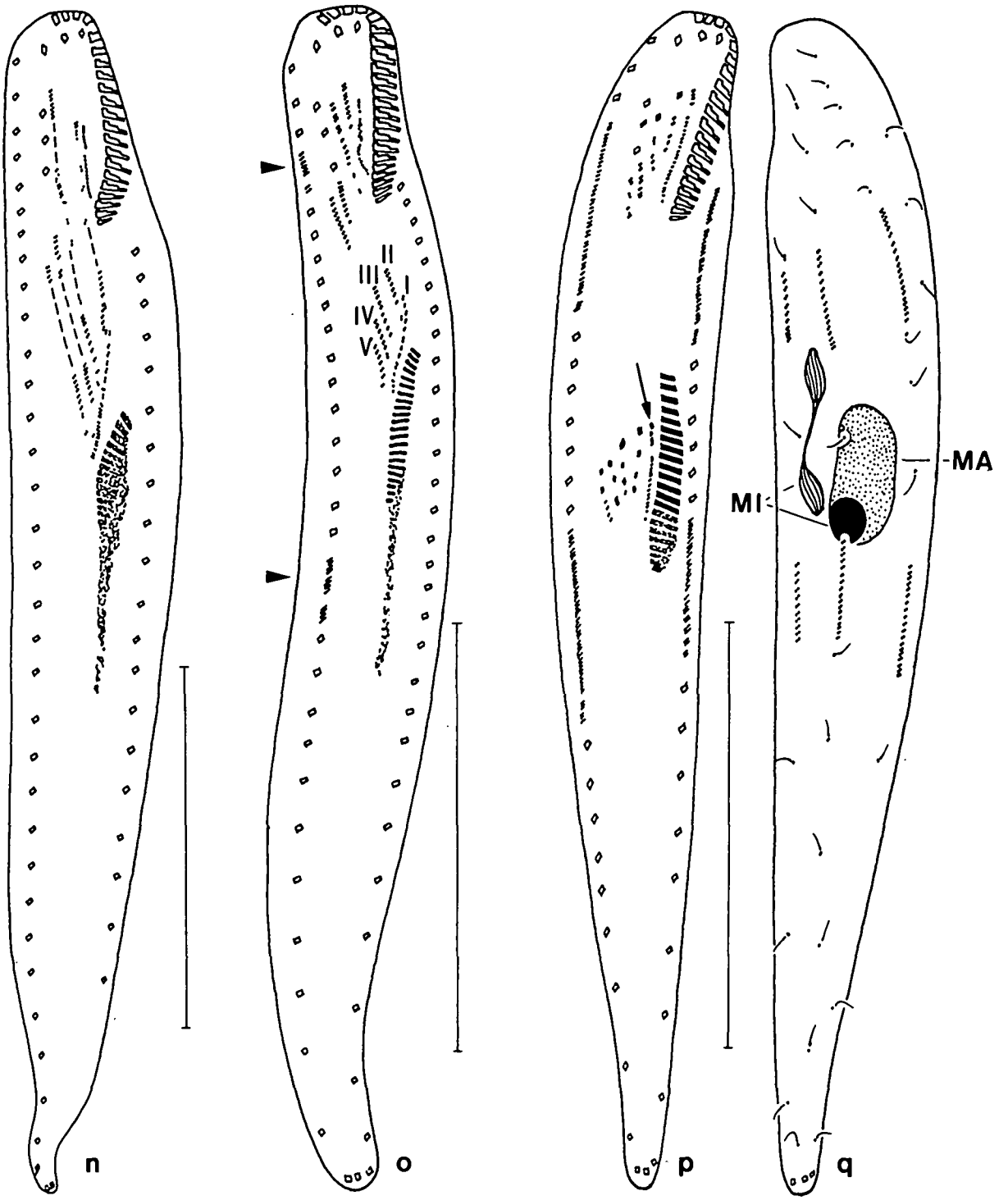

Fig. 182n–q. *Hemiurosoma terricola*, early (n, o) and middle (p, q) dividers after protargol impregnation. **n, o:** The anterior portion of the primary primordia migrates to the proter, where it unites with anlagen formed by the parental buccal cirrus and the anteriormost cirrus (III/2) of the frontoventral row (stippled lines). Thus, five anlagen streaks each are recognizable in proter and opisthe. Arrowheads mark anlagen within marginal cirral rows. **p, q:** Cirri form within the anlagen and three dorsal primordia develop. Arrow marks first frontal cirrus of opisthe generated by the newly formed undulating membranes. MA – condensed macronucleus, MI – micronuclei, I-V – cirral anlagen. Scale bars 50 μm.

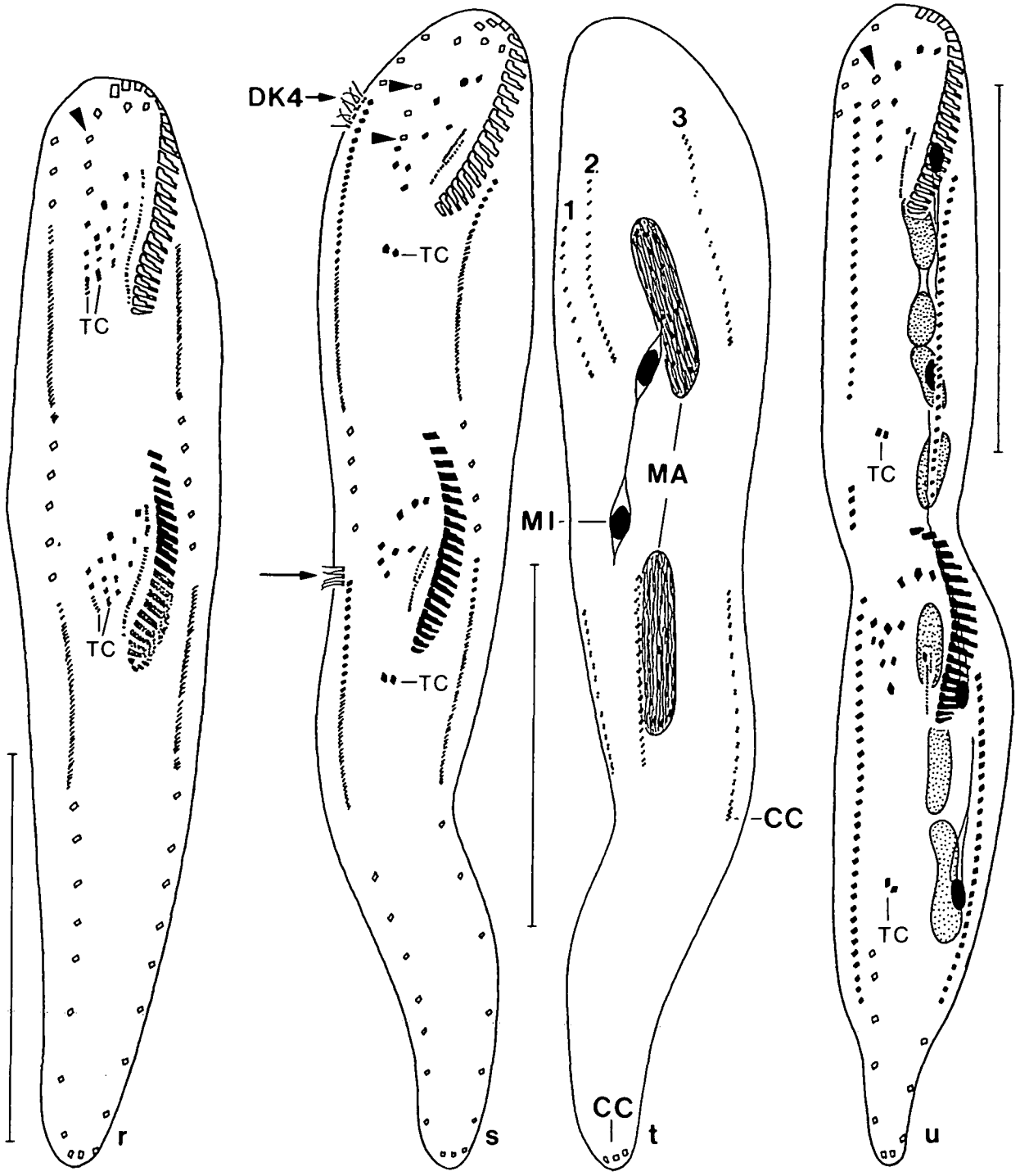

Fig. 182r–u. *Hemiurosoma terricola*, late dividers after protargol impregnation. Parental structures shown by contour, newly formed shaded black. Arrowheads mark not yet resorbed cirri of the frontoventral row, of which only the leftmost cirrus (III/2) transformed into a cirral anlage (III). The transverse cirri (TC) originate from the rightmost anlagen and perform a conspicuous migration to rear body end. Caudal cirri develop at posterior end of dorsal anlagen 1–3 (t), while dorsal kinety 4, which develops dorsomarginally (arrows), does not generate a caudal cirrus. Note that more cirri are produced than present in the interphase specimens. CC – caudal cirri, DK4 – dorsal kinety 4, MA – macronuclear nodules, MI – micronuclei, TC – transverse cirri, 1-3 – dorsal kineties. Scale bars 50 μm.

Ontogenesis commences with the formation of a long, narrow oral primordium extending anteriorly from mid-body (Fig. 182g). Then, two cirral anlagen streaks arise from the anterior end of the oral primordium and extend to the parental buccal vertex in characteristic Y-pattern (Fig. 182j). Next, two further anlagen develop from the stem of the Y. Thus, four long cirral anlagen streaks are recognizable at this stage (Fig. 182k, l). The long anlagen are primary primordia, which split transversely, producing a cirral anlagen set each in the proter and opisthe (Fig. 182m, n). In detail, the process runs as follows: the posterior half of the leftmost anlage becomes opisthe's undulating membranes and frontal cirrus 1, while the anterior portion unites with proter's anlage II produced by the parental buccal cirrus; proter anlage I originates, as is usual, from the reorganizing undulating membranes (Fig. 182o, p, r); the anterior portion of opisthe's anlage III unites with the proter anlage III produced by cirrus III/2, that is, the slightly left-shifted cirrus of the frontoventral row; proter's anlagen IV and V are entirely generated by the anterior half of opisthe's anlagen IV and V (Fig. 182n, o) because the other cirri of the frontoventral row are ontogenetically inactive and will be resorbed in very late dividers (Fig. 182r, s, u).

When the macronuclear nodules have fused to a globular mass and micronuclear division commences, five widely separated cirral anlagen streaks and three dorsal primordia are recognizable in both the proter and the opisthe. Furthermore, the new adoral zone of membranelles is almost complete (Fig. 182p, r). Next, cirri begin to segregate in the anlagen and the last cirrus of anlagen IV and V separates from its streak to migrate posteriorly; the migration of these cirri, which will become the transverse cirri, is very conspicuous in both filial products because of the short anlagen fields and long body (Fig. 182r, s, u). In late dividers, the undulating membranes are completed, the cirri migrate to their specific sites, supernumerary and parental cirri are resorbed, caudal cirri develop at end of dorsal primordia 1–3, and the globular macronuclear mass divides twice to produce the species-specific four nodules (Fig. 182s–u). Furthermore, a very short dorsomarginal row, which will become dorsal kinety 4, develops at the right anterior end of the marginal anlage in each filial product (Fig. 182s).

Occurrence and ecology: *Hemiurosoma terricola* occurred at several sites in Namibia (Table 4), in a desert soil from Arizona, USA (sample kindly provided by Prof. Klaus HAUSMANN, Berlin), and in a soil sample from Costa Rica (horse pasture near peak of Monte Verde, pH 5.5; originally a fog rain forest), indicating a broad ecological (mud of ephemeral pools to "true" soil) and geographical range. Abundances were considerable in the non-flooded Petri dish cultures with many active specimens when the cultures were discarded four weeks after re-wetting. The occurrence at site (56) indicates some salt tolerance. Recently, a population from the Zambezi floodplain in Botswana could be cultivated in Eau de Volvic enriched with some wheat grains. The scanning electron micrographs match the description based on in vivo observations and protargol slides (Fig. 400a–j). *Hemiurosoma terricola* is well adapted to the habitat by its long and slender body.

Comparison with related species: *Hemiurosoma terricola* has four macronuclear nodules and is thus easily distinguished from *H. similis* (FOISSNER, 1982), which has only two. However, all other features are highly similar and would not justify separation at species level. Generally, *H. terricola* is easily confused with the congeners and several → *Urosomoida* species. Thus, the following combination of features is important for in vivo identification: body long and slender (about 150 × 20 µm), four macronuclear nodules, frontoventral cirri in *Urosoma* pattern, no postoral cirri, transverse cirri very near to posterior body end, buccal field very flat and narrow.

Hemiurosoma goertzi nov. spec. (Fig. 183a–i; 381a–d; Table 161)

Diagnosis: Size about 150 × 20 µm in vivo, under certain circumstances about 250 × 40 µm. Slenderly lanceolate with short tail. 2 macronuclear nodules, a single postoral cirrus, and 27 adoral membranelles on average.

Type location: Highly saline soil from the *Sporobolus* zone around the Etosha Pan, Namibia, 19°10'S 15°55'E (site 60 in figures 2, 3 and chapter 2.1.2).

Dedication: We dedicate this new species to Prof. Dr. Hans-Dieter GÖRTZ, Stuttgart University, for his scientific excellence and editorial activities.

Description: This species showed an extraordinary size variability. When it was studied and prepared from an about ten days old, ordinary non-flooded Petri dish culture, it measured about 150 × 20 µm. After three weeks, the Petri dish was flooded, which caused strong reproduction and size increase to about 250 × 40 µm within two weeks! Interestingly, all other main diagnostics, such as the number of adoral membranelles and marginal cirri as well as the size of the macronuclear nodules, remained stable (Fig. 183i; Table 161). A similar size variability has been reported for *Urosoma cienkowskii*, which was considerably smaller in protargol slides from terrestrial (FOISSNER 1982) than limnetic material (FOISSNER 1984). Thus, the following description is based on material as first obtained from the ordinary non-flooded Petri dish culture.

Size 115–180 × 15–30 µm in vivo, length:width ratio about 7:1 (range 6–8:1) in vivo, on average 6:1 in protargol preparations (Table 161); flattened about 2:1 dorsoventrally, very flexible but acontractile. Outline elongate lanceolate with anterior end usually transversely truncate and posterior tail-like and curved to right. Cells very fragile and thus difficult to preserve, tail often inflated in silver preparations (Fig. 183a, b, e, i; 381a, b). Macronuclear nodules slightly left of midline, about 17 × 8 µm in vivo, ellipsoidal, with many medium-sized nucleoli. Micronuclei about 6 × 3 µm in vivo, ellipsoidal, one usually attached to front of anterior macronuclear nodule, the other to rear of posterior nodule. Contractile vacuole with distinct collecting canals above mid-body at left cell margin. Cortical granules lacking; subcortical mitochondria, however, as conspicuous as in most *Urosoma*-like oxytrichids. Cytoplasm colourless, contains some ordinary crystals mainly in posterior third and food vacuoles 4–11 µm across with sporulating bacteria, golden-coloured fungal conidia (11 × 6 µm), and, rarely, small ciliates. Glides rather rapidly on microscope slide and soil particles.

Cirral pattern and number of cirri of usual variability (Fig. 183a, e, g–i; 381a–d; Table 161). Marginal cirri about 12 µm long in vivo, composed of 4 × 2 basal bodies, except for posterior cirri comprising only four cilia. Right marginal row usually ends slightly more subterminally than left. Frontal cirri frequently slightly enlarged, right one behind distal end of adoral zone. Buccal cirrus right of anterior end of paroral membrane, of variable size, that is, composed of 4 × 3, 4 × 2, or fewer basal bodies. Frontoventral cirri in typical *Urosoma* pattern, that is, longitudinally arranged with anterior cirrus (= cirrus III/2, arrowhead in figures 183h; 381c, d; for details, see BERGER 1999) somewhat shifted leftwards and slightly enlarged. Postoral cirrus at about 24% of body length and slightly left of midline, composed of 3 × 2, 4 × 2, or 3 × 3 basal bodies. Transverse cirri about 20 µm long in vivo and frequently slightly larger than marginal cirri, subterminal and thus not projecting posteriorly, usually in triangular pattern.

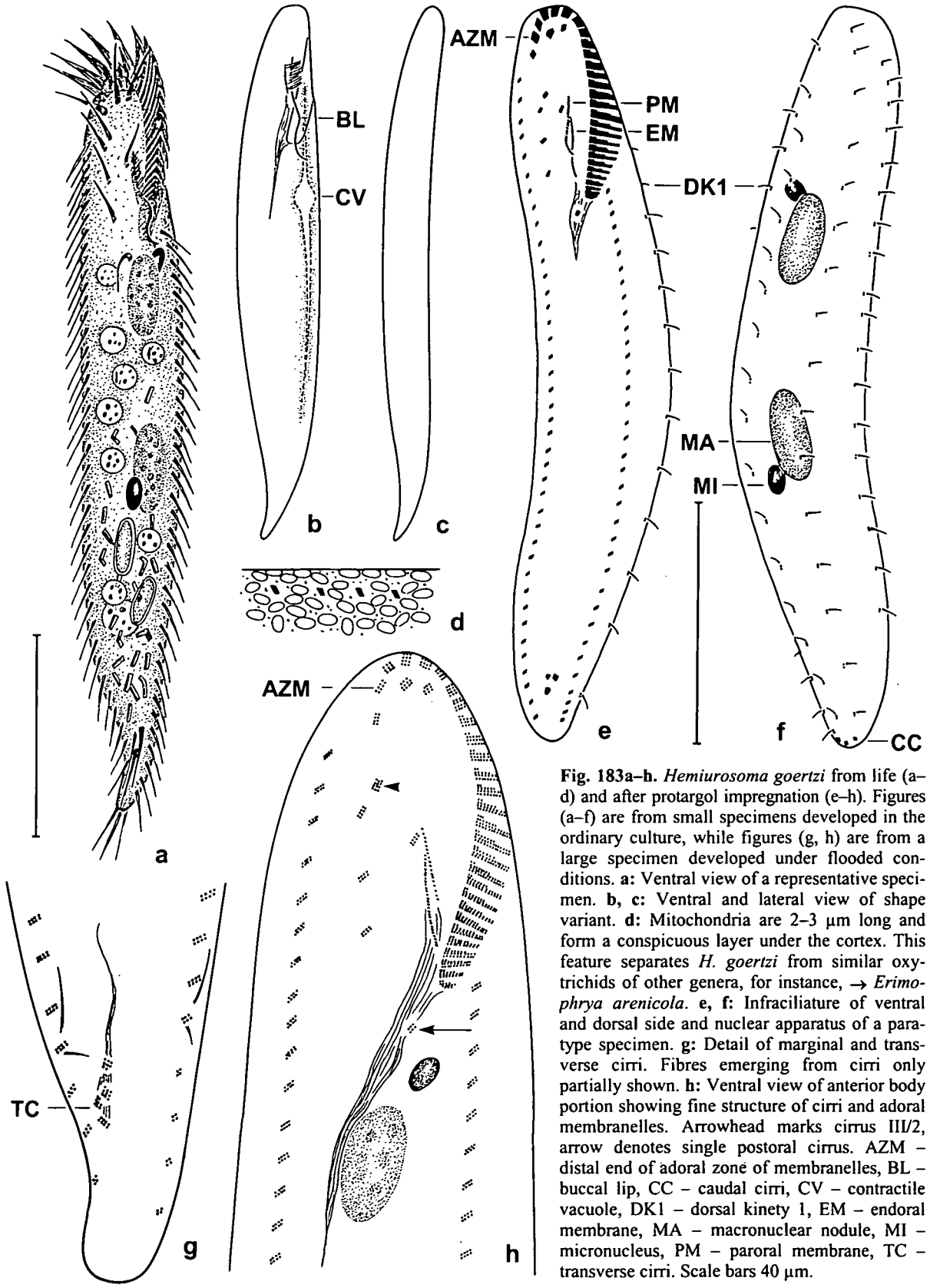

Fig. 183a–h. *Hemiurosoma goertzi* from life (a–d) and after protargol impregnation (e–h). Figures (a–f) are from small specimens developed in the ordinary culture, while figures (g, h) are from a large specimen developed under flooded conditions. **a:** Ventral view of a representative specimen. **b, c:** Ventral and lateral view of shape variant. **d:** Mitochondria are 2–3 µm long and form a conspicuous layer under the cortex. This feature separates *H. goertzi* from similar oxytrichids of other genera, for instance, → *Erimophrya arenicola*. **e, f:** Infraciliature of ventral and dorsal side and nuclear apparatus of a paratype specimen. **g:** Detail of marginal and transverse cirri. Fibres emerging from cirri only partially shown. **h:** Ventral view of anterior body portion showing fine structure of cirri and adoral membranelles. Arrowhead marks cirrus III/2, arrow denotes single postoral cirrus. AZM – distal end of adoral zone of membranelles, BL – buccal lip, CC – caudal cirri, CV – contractile vacuole, DK1 – dorsal kinety 1, EM – endoral membrane, MA – macronuclear nodule, MI – micronucleus, PM – paroral membrane, TC – transverse cirri. Scale bars 40 µm.

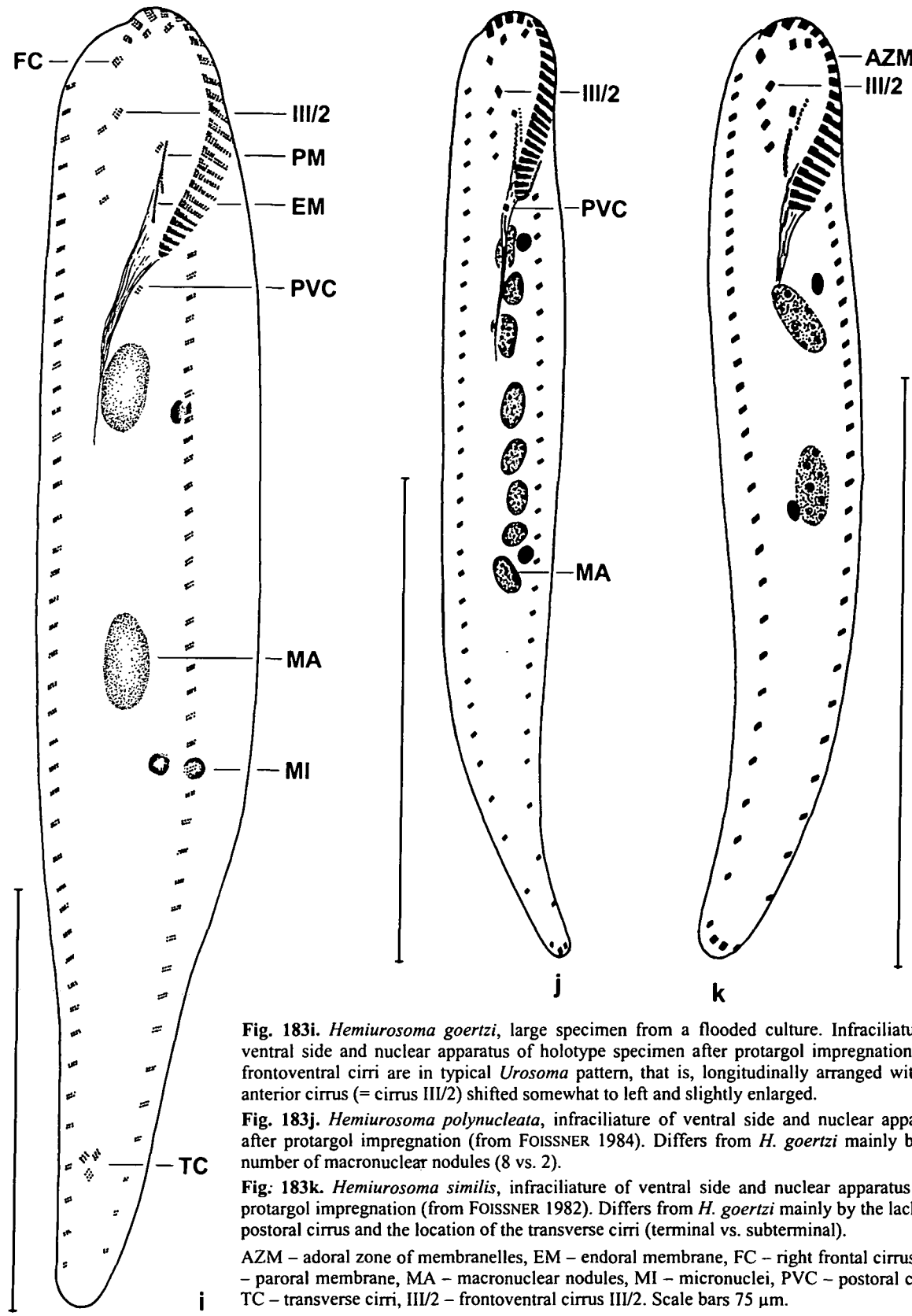

Fig. 183i. *Hemiurosoma goertzi*, large specimen from a flooded culture. Infraciliature of ventral side and nuclear apparatus of holotype specimen after protargol impregnation. The frontoventral cirri are in typical *Urosoma* pattern, that is, longitudinally arranged with the anterior cirrus (= cirrus III/2) shifted somewhat to left and slightly enlarged.

Fig. 183j. *Hemiurosoma polynucleata*, infraciliature of ventral side and nuclear apparatus after protargol impregnation (from FOISSNER 1984). Differs from *H. goertzi* mainly by the number of macronuclear nodules (8 vs. 2).

Fig. 183k. *Hemiurosoma similis*, infraciliature of ventral side and nuclear apparatus after protargol impregnation (from FOISSNER 1982). Differs from *H. goertzi* mainly by the lack of a postoral cirrus and the location of the transverse cirri (terminal vs. subterminal).

AZM – adoral zone of membranelles, EM – endoral membrane, FC – right frontal cirrus, PM – paroral membrane, MA – macronuclear nodules, MI – micronuclei, PVC – postoral cirrus, TC – transverse cirri, III/2 – frontoventral cirrus III/2. Scale bars 75 µm.

Dorsal bristles about 3 μm long in vivo, arranged in four rows: rows 1–3 about of body length, each with a single caudal cirrus; row 4 slightly shortened anteriorly and distinctly so posteriorly (Fig. 183f).

Adoral zone occupies 17–26%, on average 22% of body length, roughly in *Gonostomum* pattern, that is, extends straight along left body margin, performing right bend and slight clockwise rotation to plunge into buccal cavity; composed of an average of 27 membranelles, bases of largest membranelles about 4 μm wide in vivo. Buccal cavity very flat and narrow, right margin forms hyaline lip bearing undulating membrane and covering buccal cavity and proximal adoral membranelles. Undulating membranes almost straight and side by side, endoral on average 10 μm long, paroral 8 μm long and commencing about 3 μm ahead of endoral at level of buccal cirrus; both membranes likely composed of dikinetids. Pharyngeal fibres distinct in vivo and protargol preparations, of ordinary length and structure, extend obliquely backwards (Fig. 183a, b, e, h; 381c; Table 161).

Occurrence and ecology: To date found only at four sites in Namibia (Table 4), ranging from non-saline mud and soil from rock-pools on an Inselberg to a highly saline soil from the *Sporobolus* zone around the Etosha Pan.

Comparison with related species: *Hemiurosoma goertzi* differs from *H. polynucleata* (Fig. 183j), the sole congener with a single postoral cirrus, mainly by the macronuclear pattern (2 vs. 8 nodules in line), an excellent feature because of its high stability. Minor differences are found in the number (3 vs. 2) and location (subterminal vs. terminal) of the transverse cirri and the number of adoral membranelles (25–30 vs. 19–24). In vivo, *Hemiurosoma goertzi* is characterized by the following combination of features: slender, slightly tailed body with anterior end transversely truncate; two macronuclear nodules; single postoral cirrus; distinct mitochondria.

Table 161. Morphometric data on *Hemiurosoma goertzi*. Where two lines appear, the lower one is from the large specimens developed under flooded conditions (see introduction to description).

Characteristics[a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	132.3	130.0	16.4	4.2	12.4	95.0	157.0	15
	235.5	238.0	30.7	7.9	13.0	184.0	284.0	15
Body, width	22.3	22.0	3.2	0.8	14.5	16.0	27.0	15
	41.5	43.0	5.6	1.4	13.5	30.0	48.0	15
Body length:width, ratio	6.0	5.9	0.5	0.1	8.5	5.0	6.8	15
	5.8	5.4	1.0	0.3	18.0	4.6	8.8	15
Anterior body end to end of adoral zone, distance	28.9	29.0	3.0	0.8	10.4	23.0	33.0	15
	41.0	41.0	2.5	0.6	6.0	36.0	45.0	15
Body length:length of adoral zone, ratio	4.6	4.5	0.6	0.17	13.9	3.8	5.8	15
	5.8	5.9	0.8	0.2	14.2	4.1	7.1	15
Anterior body end to paroral membrane, distance	14.1	14.0	1.7	0.4	12.2	10.0	16.0	15
Paroral membrane, length	8.1	8.0	1.1	0.3	13.3	6.0	10.0	14
Anterior body end to endoral membrane, distance	16.7	17.0	1.7	0.4	10.1	13.0	18.0	15
Endoral membrane, length	9.8	10.0	1.1	0.3	11.2	8.0	12.0	13

(continued)

Characteristics[a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Anterior body end to first frontoventral cirrus, distance	10.5	10.0	0.8	0.2	8.0	9.0	12.0	15
Anterior body end to last frontoventral cirrus, distance	24.0	24.0	2.6	0.7	10.8	18.0	28.0	14
Anterior body end to buccal cirrus, distance	14.9	15.0	1.7	0.4	11.3	11.0	17.0	15
Anterior body end to right marginal row, distance	9.1	9.0	2.0	0.5	22.2	6.0	13.0	15
Anterior body end to postoral cirrus, distance	32.0	32.0	3.3	0.9	10.4	26.0	36.0	15
Anterior body end to first macronuclear nodule, distance	31.7	32.0	3.4	0.9	10.7	25.0	36.0	15
Macronuclear nodules, distance in between	14.5	16.0	5.2	1.3	35.7	7.0	24.0	15
Anterior macronuclear nodule, length	15.3	16.0	2.3	0.6	15.4	10.0	18.0	15
	16.6	17.0	1.5	0.4	9.1	14.0	20.0	15
Anterior macronuclear nodule, width	5.9	6.0	0.5	0.1	8.8	5.0	7.0	15
	6.7	6.0	1.0	0.3	14.6	5.0	8.0	15
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15
Anterior micronucleus, length	4.2	4.0	1.1	0.3	27.1	2.5	6.0	15
Anterior micronucleus, width	2.8	3.0	0.6	0.1	20.3	1.5	4.0	15
Micronuclei, number	1.7	2.0	–	–	–	1.0	2.0	15
	1.7	2.0	–	–	–	0.0	3.0	15
Nuclear figure, length	45.7	45.0	6.2	1.6	13.7	37.0	58.0	15
Posterior body end to rear transverse cirrus, distance	11.1	10.5	2.6	0.7	23.9	8.0	16.0	14
	22.0	22.0	4.9	1.3	22.1	10.0	30.0	15
Posterior body end to anterior transverse cirrus, distance	15.6	14.0	3.8	1.0	24.5	10.0	22.0	14
Adoral membranelles, number	27.3	27.0	2.1	0.6	7.9	25.0	30.0	11
	25.3	26.0	1.8	0.5	6.9	22.0	28.0	15
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
Frontoventral cirri, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	14
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Postoral cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Transverse cirri, number	3.1	3.0	–	–	–	3.0	4.0	14
Right marginal cirri, number	38.6	39.0	2.4	0.6	6.3	34.0	43.0	15
	39.1	39.0	3.1	0.8	8.0	34.0	46.0	15
Left marginal cirri, number	34.5	35.0	2.7	0.7	7.8	28.0	39.0	15
Caudal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	7
Dorsal kineties, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	8

[a] Data based on mounted, protargol-impregnated (FOISSNER's method, fixed in STIEVE's solution amended with some drops of osmium tetroxide for better preservation), and randomly selected specimens from a Petri dish culture. See table head and description for further details. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Sterkiella cavicola (KAHL, 1935) FOISSNER, BLATTERER, BERGER & KOHMANN, 1991 (Fig. 184a–z)

Material: Soil from Austria as described in BERGER & FOISSNER (1987), who investigated specimens from a non-flooded Petri dish culture. Specimens from this source were used to establish pure cultures in Eau de Volvic enriched with some crashed wheat grains and a species of the *Tetrahymena pyriformis* complex as main food source. The protargol slides containing the dividers shown in the following figures have been deposited at the same locality as the Namibian slides. Interestingly, this species occurs in Namibia only at site 55 (Table 4), while it is frequent in Germany and Austria (FOISSNER 2000a).

Morphostatic specimens: The interphase morphology of *S. cavicola* has been thoroughly described by BERGER & FOISSNER (1987) from an Austrian and a Japanese population. A critical review of this species has been published by BERGER (1999). Thus, there is no need to describe it again. The cultivated specimens show a higher variability in the number of fronto-ventral-transverse cirri than those from the non-flooded Petri dish culture studied by BERGER & FOISSNER (1987), namely, 17–24 ($\bar{x}$ = 19.0, M = 19, SD = 1.6, SE = 0.3, CV = 8.4%, n = 21). The increased number of cirri is recognizable also in the streaks of middle to very late dividers, both in the proter ($\bar{x}$ = 19.9, M = 19, SD = 3.3, Min = 17, Max = 24, n = 13) and opisthe ($\bar{x}$ = 20.2, M = 20, SD = 3.3, Min = 18, Max = 23, n = 13). Usually, the number of postoral ventral and/or transverse cirri is increased, while mostly eight (rarely 9, Fig. 184h) cirri are on the frontal field, as is common. Furthermore, giants with a disproportionally large oral apparatus occur in cultures (Fig. 184n). Such macrostomes often retain many parental dorsal bristles making the infraciliature rather confusing (Fig. 184q, r). Interestingly, there is no clear-cut relationship between macrostomy and number of fronto-ventral-transverse cirri.

Ontogenesis: Divisional morphogenesis of *S. cavicola* is highly similar to that of *S. nova*, as described by FOISSNER & BERGER (1999). Thus, it is not detailed here, but the reader is referred to the figures and figure explanations. Basically, the cirral primordia originate as in *S. histriomuscorum* (PETZ & FOISSNER 1997) and *S. nova* (FOISSNER & BERGER 1999): UM → Ip, II/2 → IIp, III/2 → IIIp, IV/3 → IVp, IV/3 → Vp, IV/3 → VIp; OP → Io, OP → IIo, OP → IIIo, IV/2 → IVo, V/4 → Vo, V/4 → VIo (nomenclature according to BERGER & FOISSNER 1997). Accordingly, FOISSNER's earlier claim (in BERGER & FOISSNER 1997) that the opisthe primordia V and VI of *S. cavicola* originate de novo is an unfortunate mistake caused by a too superficial investigation of the slides. The origin of proter primordium IV is as difficult to assess in *S. cavicola* as in *S. histriomuscorum* and *S. nova* because it is close to primordium V. Very likely, it is generated by cirrus IV/3; however, a contribution of cirrus III/2 cannot be entirely excluded (Fig. 184h–n). Furthermore, we cannot exclude that postoral cirrus IV/2 contributes to the oral primordium because a patch of basal bodies develops early and close to it (Fig. 184d–f); the cirrus, however, remains unchanged (Fig. 184g).

The ontogenetic data show that *Sterkiella cavicola*, type of the genus, *S. histriomuscorum* and *S. nova* form a distinct group of oxytrichid hypotrichs. See BERGER (1999) for further species possibly belonging to this genus.

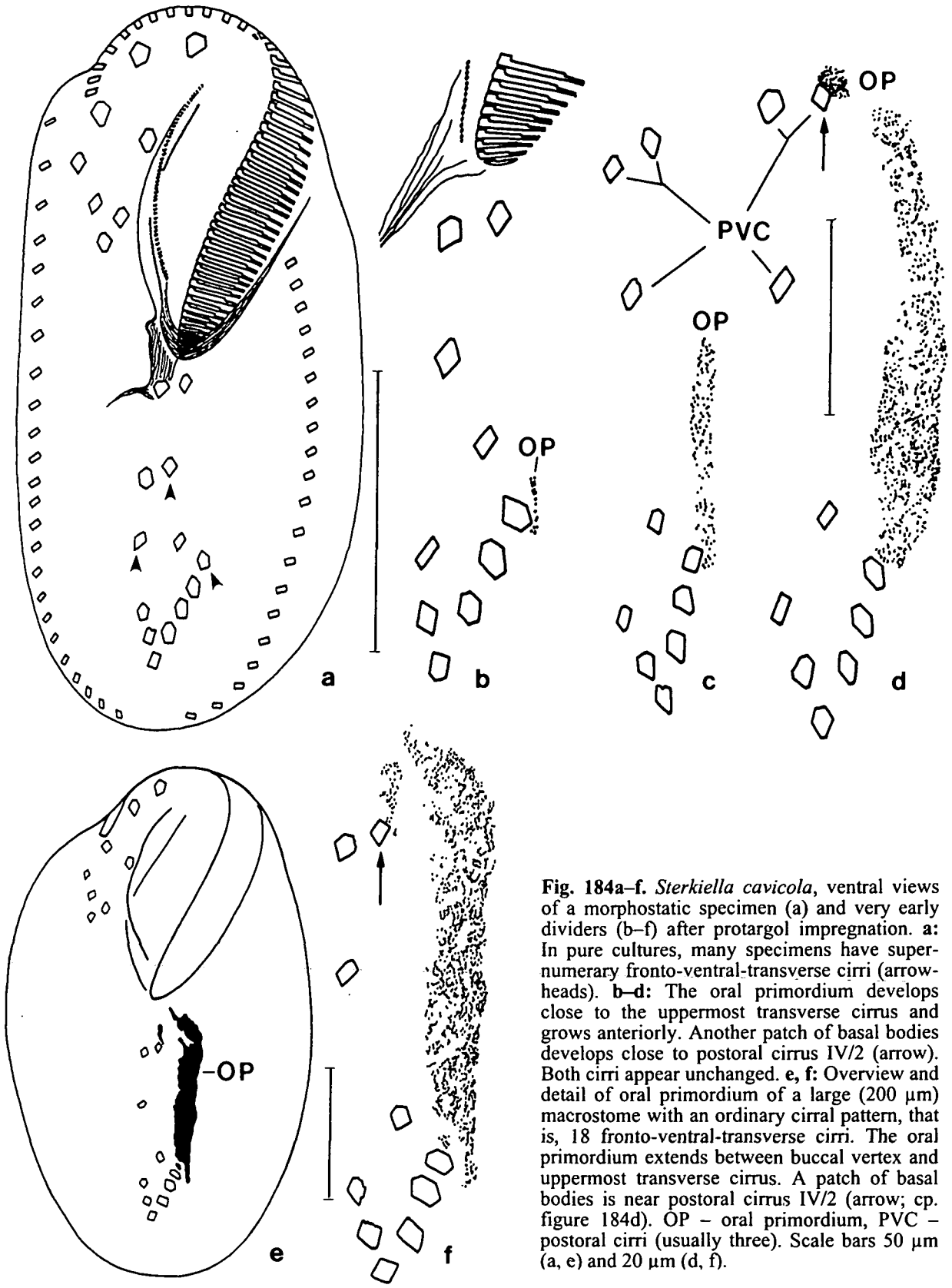

Fig. 184a–f. *Sterkiella cavicola*, ventral views of a morphostatic specimen (a) and very early dividers (b–f) after protargol impregnation. **a:** In pure cultures, many specimens have supernumerary fronto-ventral-transverse cirri (arrowheads). **b–d:** The oral primordium develops close to the uppermost transverse cirrus and grows anteriorly. Another patch of basal bodies develops close to postoral cirrus IV/2 (arrow). Both cirri appear unchanged. **e, f:** Overview and detail of oral primordium of a large (200 µm) macrostome with an ordinary cirral pattern, that is, 18 fronto-ventral-transverse cirri. The oral primordium extends between buccal vertex and uppermost transverse cirrus. A patch of basal bodies is near postoral cirrus IV/2 (arrow; cp. figure 184d). OP – oral primordium, PVC – postoral cirri (usually three). Scale bars 50 µm (a, e) and 20 µm (d, f).

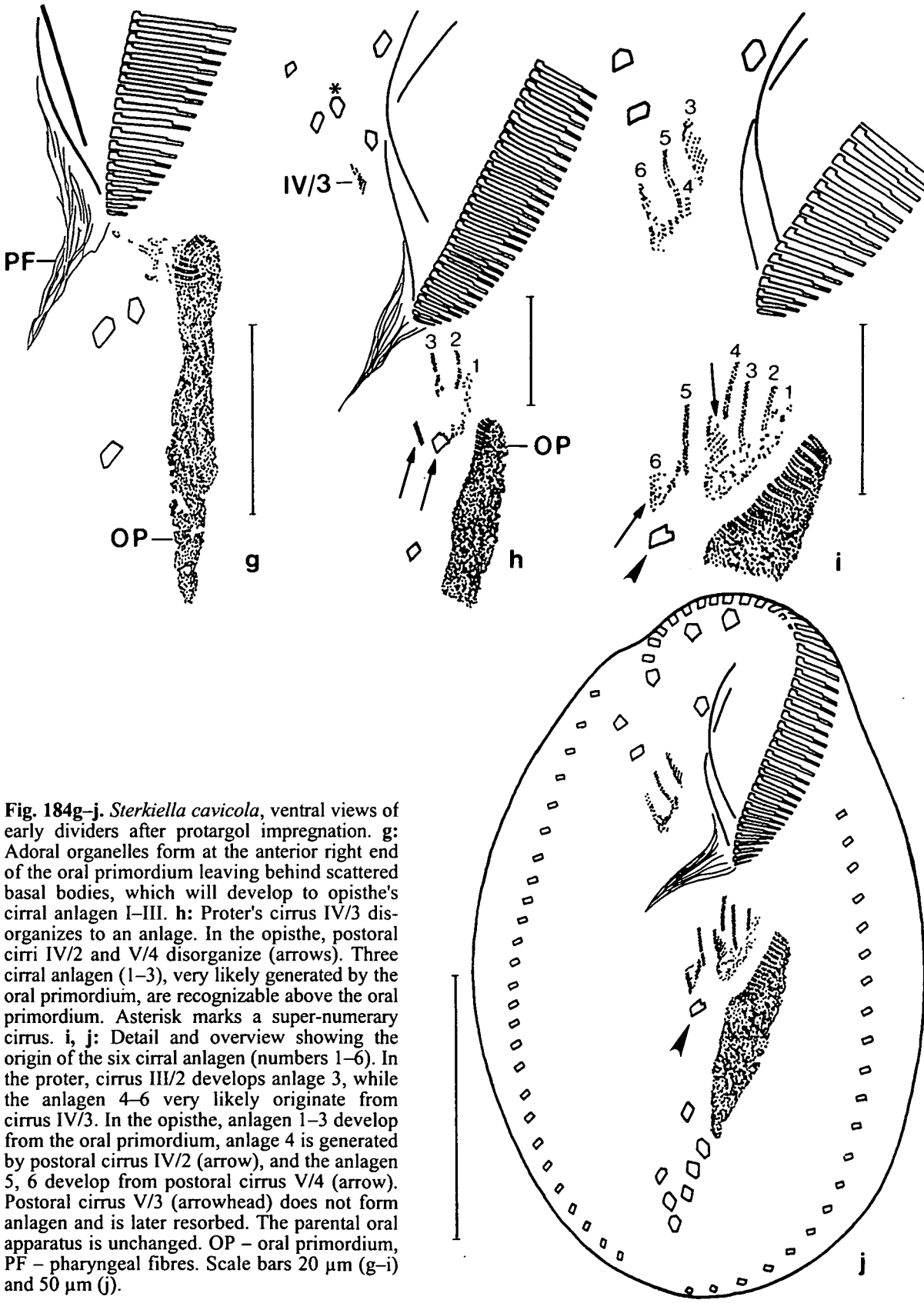

Fig. 184g–j. *Sterkiella cavicola*, ventral views of early dividers after protargol impregnation. **g:** Adoral organelles form at the anterior right end of the oral primordium leaving behind scattered basal bodies, which will develop to opisthe's cirral anlagen I–III. **h:** Proter's cirrus IV/3 disorganizes to an anlage. In the opisthe, postoral cirri IV/2 and V/4 disorganize (arrows). Three cirral anlagen (1–3), very likely generated by the oral primordium, are recognizable above the oral primordium. Asterisk marks a super-numerary cirrus. **i, j:** Detail and overview showing the origin of the six cirral anlagen (numbers 1–6). In the proter, cirrus III/2 develops anlage 3, while the anlagen 4–6 very likely originate from cirrus IV/3. In the opisthe, anlagen 1–3 develop from the oral primordium, anlage 4 is generated by postoral cirrus IV/2 (arrow), and the anlagen 5, 6 develop from postoral cirrus V/4 (arrow). Postoral cirrus V/3 (arrowhead) does not form anlagen and is later resorbed. The parental oral apparatus is unchanged. OP – oral primordium, PF – pharyngeal fibres. Scale bars 20 μm (g–i) and 50 μm (j).

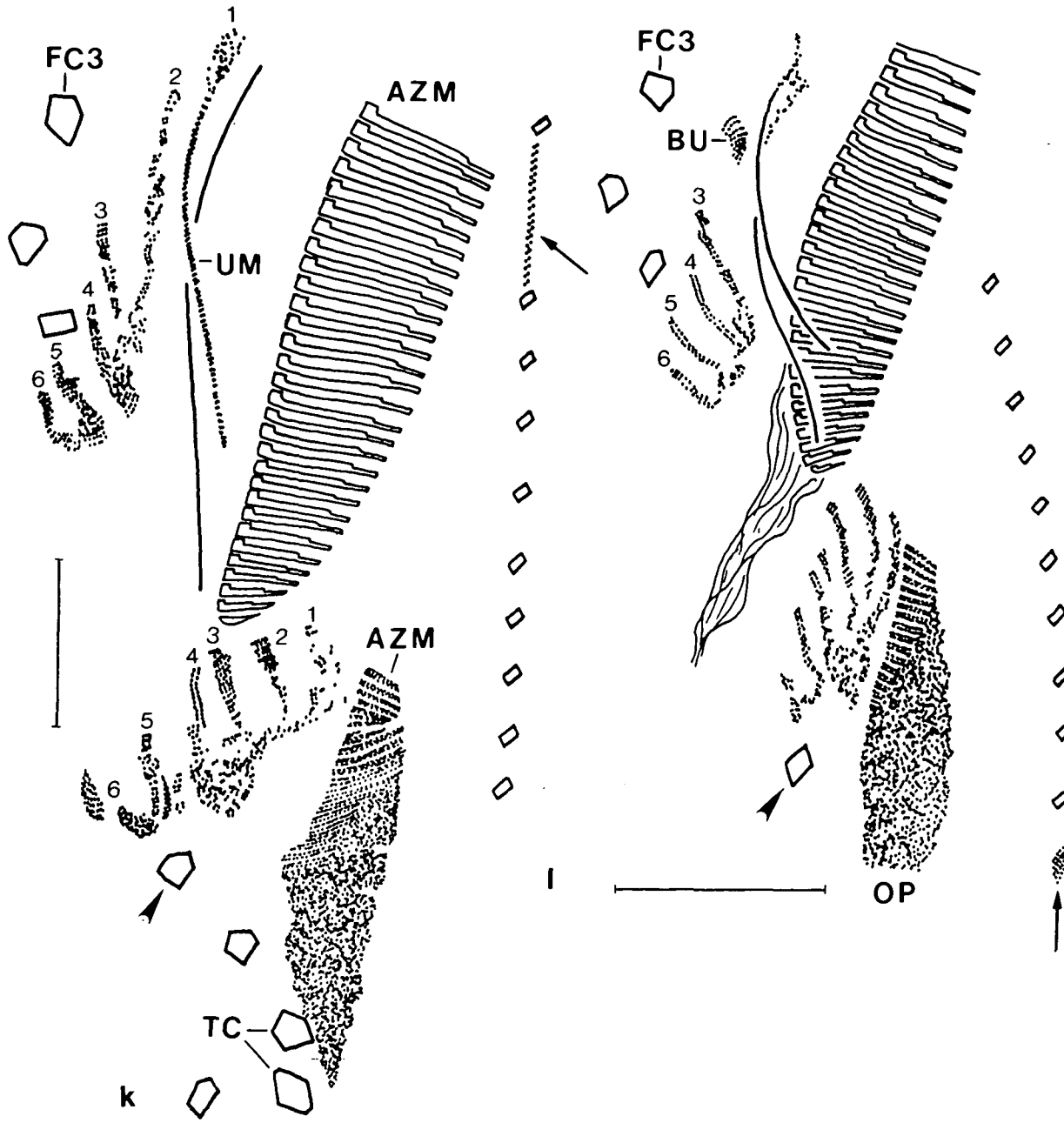

Fig. 184k, l. *Sterkiella cavicola*, ventral views of early dividers after protargol impregnation. These figures show a "critical" stage, namely, the formation of proter's cirral anlagen 4, 5 and 6 and of opisthe's cirral anlagen 5 and 6. Proter's anlagen 4–6 often form a W-shaped pattern (l) and very likely originate from cirrus IV/3, although we cannot entirely exclude that anlage 4 is generated, like anlage 3, by cirrus III/2 (k). This uncertainty is due to the spatial narrowness of the anlagen. The opisthe's anlagen 5 and 6 obviously originate from postoral cirrus V/4, that is, not de novo as previously stated (BERGER & FOISSNER 1997). Postoral cirrus V/3 (arrowheads) is, as in Stylonychinae, not involved in anlagen formation and later resorbed. Arrows mark anlagen in marginal rows. The anterior end of the undulating membranes disorganizes to anlage 1, which will generate frontal cirrus 1 and new undulating membranes. The anlagen of the proter and opisthe develop completely independently, but co-ordinated, that is, are always at a similar stage. New adoral membranelles are continuously formed in the opisthe's anarchic field from anterior to posterior. AZM – adoral zone of membranelles, BU – buccal cirrus, FC3 – frontal cirrus 3, OP – oral primordium, TC – transverse cirri, UM – paroral membrane. Scale bars 20 μm.

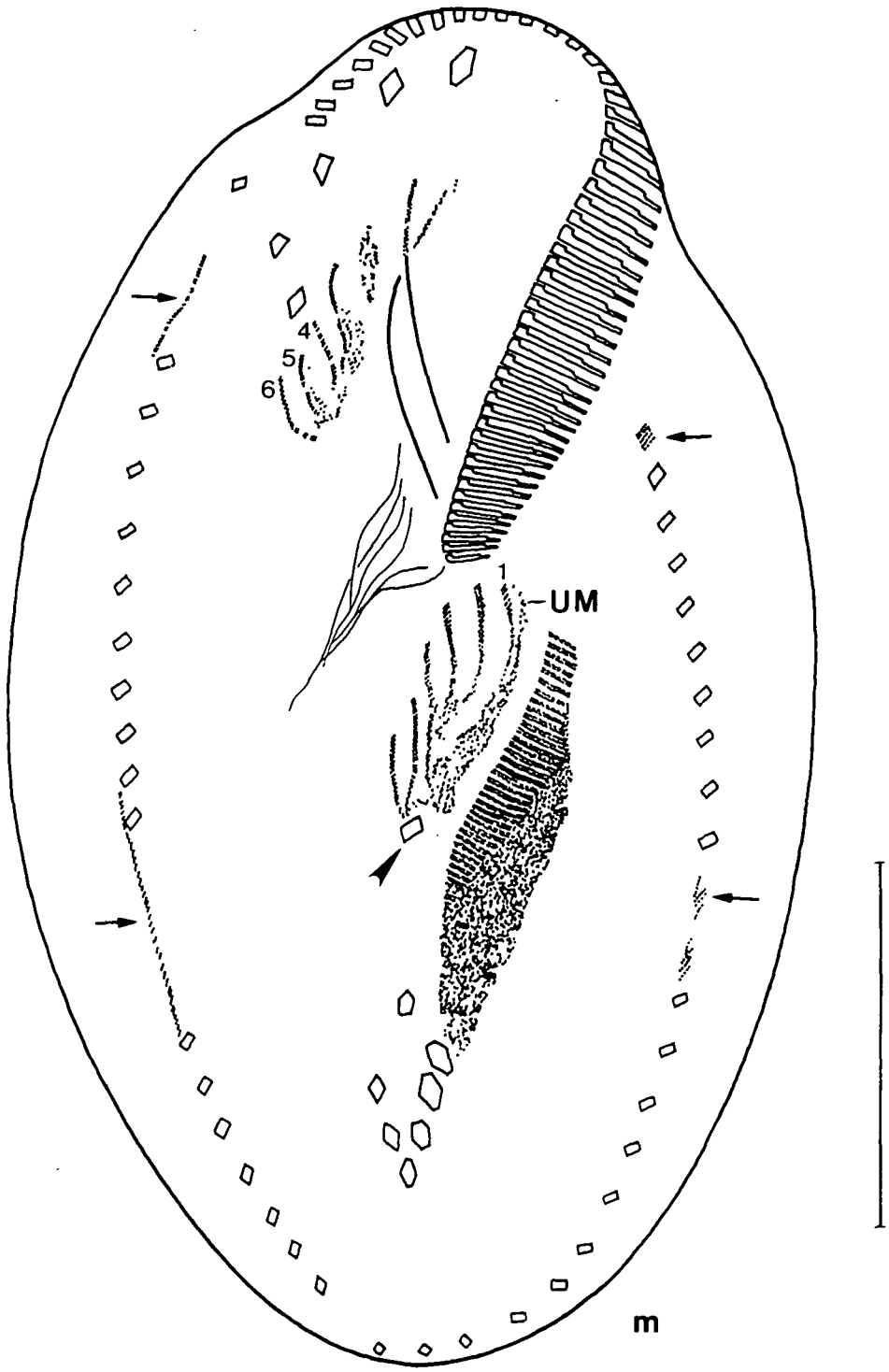

Fig. 184m. *Sterkiella cavicola*, ventral view of a middle divider after protargol impregnation. Six cirral anlagen each are recognizable in proter and opisthe. Proter's anlagen 4–6 form a W-shaped pattern, indicating that they evolved from a single cirrus (IV/3). In the opisthe, anlage 1 (frontal cirrus 1) separates from the primordium for the undulating membranes (UM). The parental undulating membranes disintegrate anteriorly. Arrowhead marks postoral cirrus V/3, which is not involved in anlagen formation. Arrows denote anlagen in marginal rows; those in the right row develop earlier than those in the left row. Adoral membranelles are formed in the oral primordium from anterior to posterior. Scale bar 50 μm.

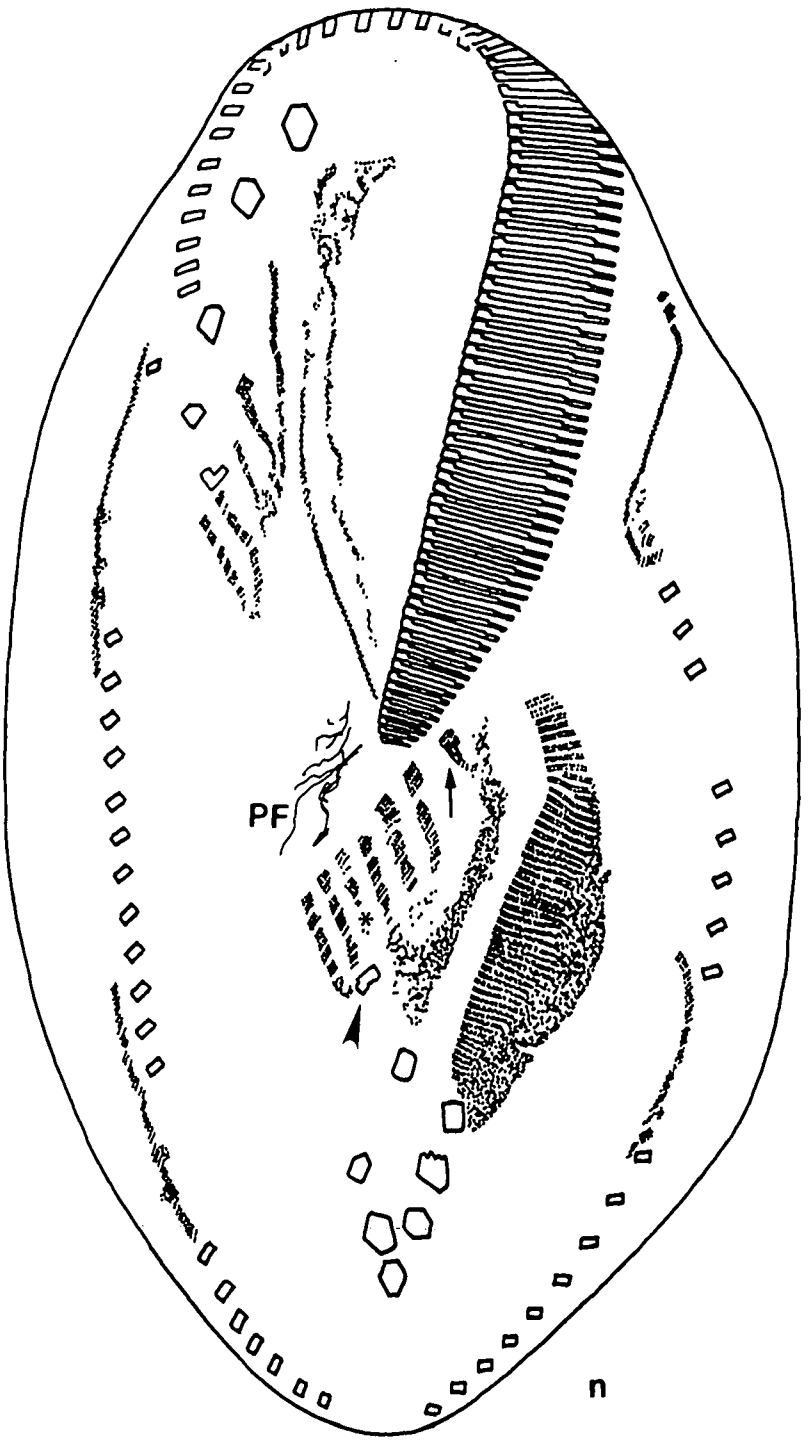

Fig. 184n. *Sterkiella cavicola*, ventral view of a middle divider after protargol impregnation. This is a large (length 182 μm), macrostome individual with 78 adoral membranelles and an ordinary set of 18 fronto-ventral-transverse cirri. Cirri are forming in the anlagen, and frontal cirrus 1 (arrow) has separated from the opisthe anlage for the undulating membranes. A small, supernumerary opisthe anlage is recognizable (asterisk). Arrowhead marks disintegrating postoral cirrus V/3, which is not involved in anlagen formation. The parental undulating membranes and pharyngeal fibres (PF) are reorganized. The marginal anlagen are distinct. Scale bar 50 μm.

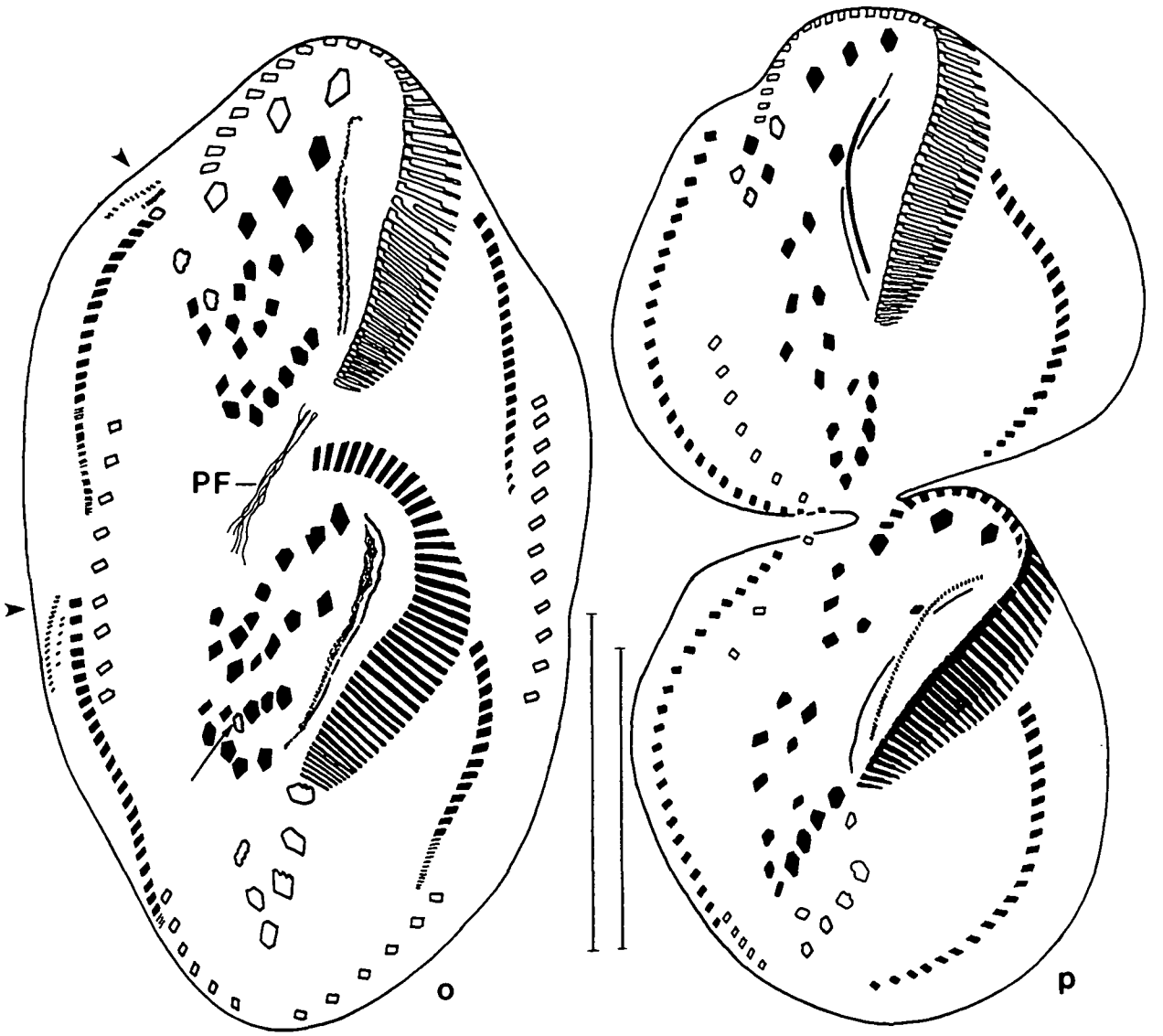

Fig. 184o, p. *Sterkiella cavicola*, ventral views of a late (o) and a very late (p) divider after protargol impregnation. Parental structures shown by contour, newly formed shaded black. Both specimens formed 7 anlagen in both the proter and the opisthe. **o:** The newly formed cirri are migrating to their final sites. The cirri not involved in anlagen formation are resorbed, for instance, cirrus V/3 (arrow), which is now smaller and has an irregular outline. The undulating membranes are forming in both daughters and still side by side. The new adoral zone of membranelles commences shaping, but the individual membranelles are not yet finished, that is, consist of three basal body rows of same length. The parental adoral membranelles do not reorganize. Arrowheads mark dorsomarginal bristle rows generated at the anterior end of the new marginal rows. **p:** In very late dividers, the final cirral pattern is recognizable and the new adoral membranelles obtain their final structure (two long ciliary rows, one slightly and one strongly shortened row). The new undulating membranes moved one over the other and thus intersect optically. Both daughters have 21 newly formed cirri, that is, three supernumerary cirri each. An increased number of cirri is often found in specimens from flourishing cultures. Most parental cirri that were not involved in anlagen formation are already resorbed. The dorsomarginal bristle rows (arrowheads in Fig. 184o) moved onto the dorsal side (Fig. 184v). Note that daughters separate at distal end of adoral zone and are smaller and rounder than morphostatic specimens. Thus, there is distinct post-divisional growth and elongation. PF – disorganizing pharyngeal fibres. Scale bars 50 μm.

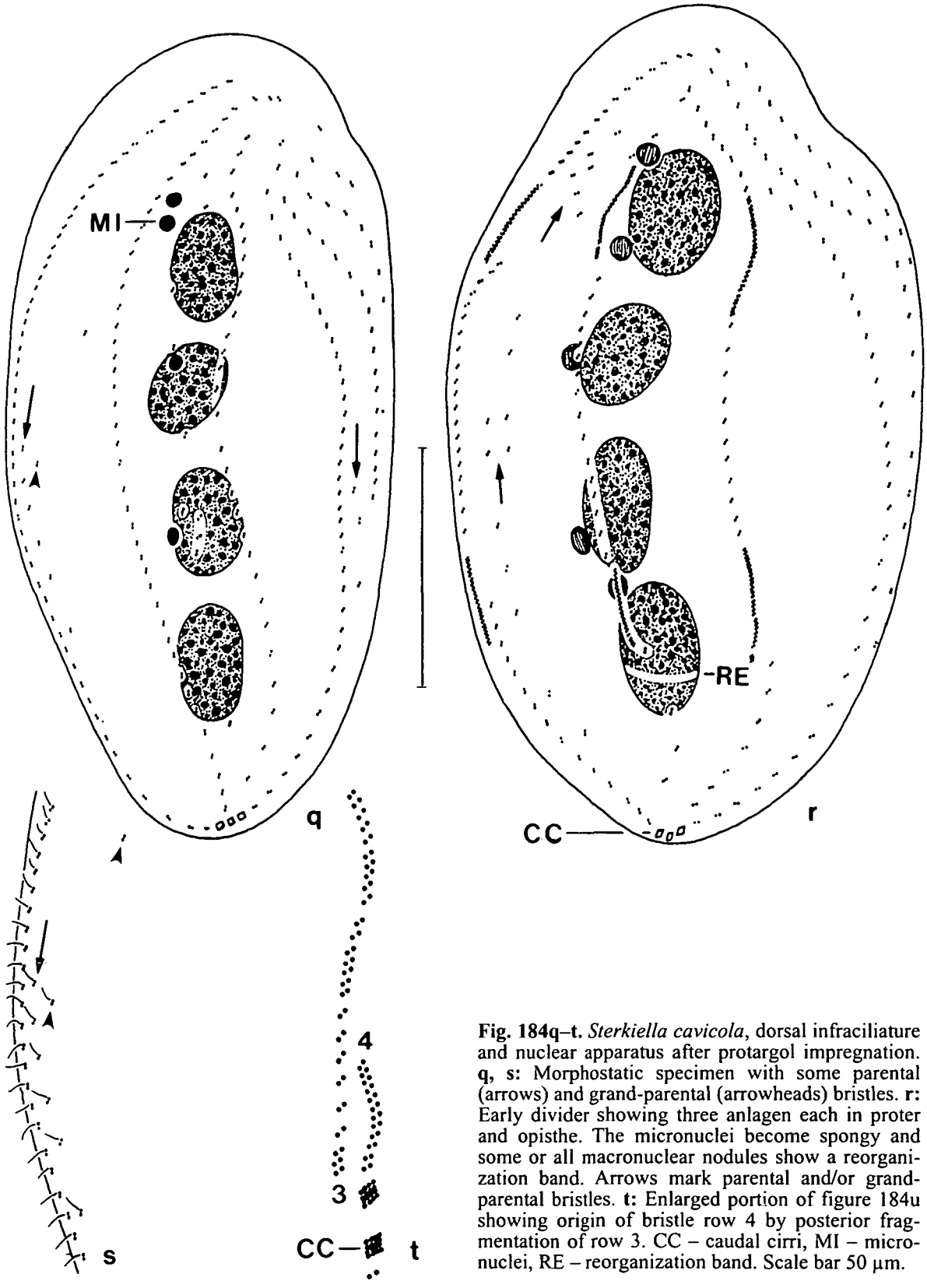

Fig. 184q–t. *Sterkiella cavicola*, dorsal infraciliature and nuclear apparatus after protargol impregnation. **q, s:** Morphostatic specimen with some parental (arrows) and grand-parental (arrowheads) bristles. **r:** Early divider showing three anlagen each in proter and opisthe. The micronuclei become spongy and some or all macronuclear nodules show a reorganization band. Arrows mark parental and/or grand-parental bristles. **t:** Enlarged portion of figure 184u showing origin of bristle row 4 by posterior fragmentation of row 3. CC – caudal cirri, MI – micronuclei, RE – reorganization band. Scale bar 50 μm.

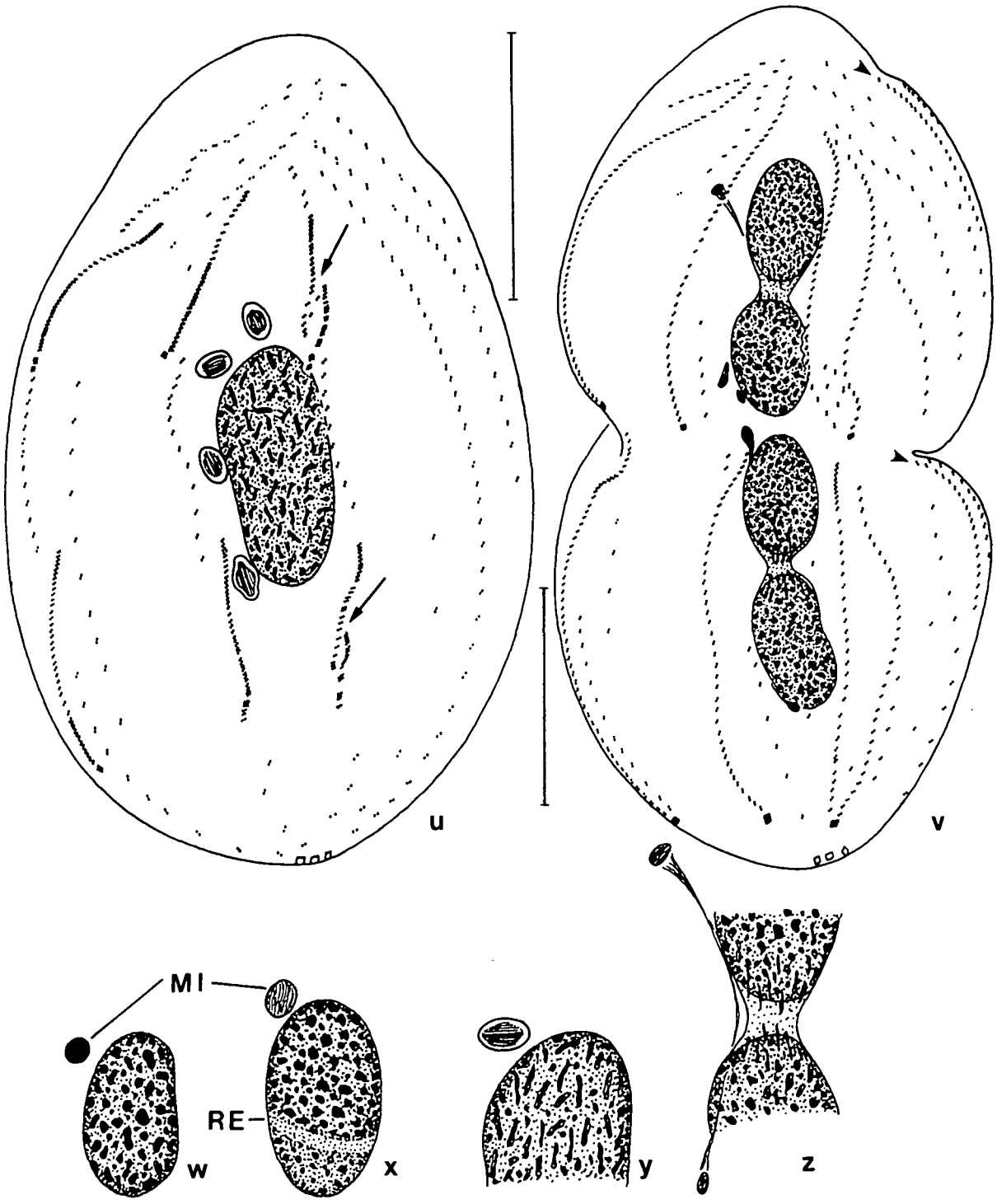

Fig. 184u–z. *Sterkiella cavicola*, dorsal infraciliature and nuclear apparatus after protargol impregnation. **u:** Middle divider with macronuclear nodules condensed to an ellipsoidal mass. Bristle row 4 originates by posterior fragmentation of row 3 (arrows); for a detail, see figure 184t. **v:** Late divider showing that caudal cirri are generated at posterior end of rows 1, 2, and 4. Arrowheads mark dorsomarginal rows produced at anterior end of right marginal rows. The macronuclear nodules are performing a second round of division. **w–z:** Changes in the fine structure of the nuclear apparatus during cell division (x–z); figure (w) shows the morphostatic pattern. MI – micronuclei, RE – reorganization band. Scale bars 50 µm.

Hemisincirra namibiensis nov. spec. (Fig. 185a–p; Table 162)

Diagnosis: Size about 65 × 13 µm in vivo; elongate rectangular. On average 4 macronuclear nodules in series left of midline, 2 micronuclei, 12 adoral membranelles, 20 cirri in right and 24 cirri in left marginal row, 5 cirri in ventral cirral row, 2 frontoterminal cirri, 1 buccal cirrus, 4 transverse cirri, and 2 dorsal kineties.

Type location: Litter around *Stipagrostis* roots in a sand dune between the villages of Aus and Helmeringhausen, Namibia, 26°05'S 16°35'E (site 17 in figure 2 and chapter 2.1.2).

Etymology: Named after the country discovered.

Description: Size 60–80 × 10–15 µm in vivo, usually near 65 × 13 µm, length:width ratio about 5:1 both in vivo and protargol preparations; flexible but acontractile. Outline elongate rectangular because of straight margins and evenly rounded ends; dorsoventrally flattened up to 2:1. Usually four macronuclear nodules forming strand left of cell's midline, nodules sometimes paired with each one micronucleus in between (Fig. 185a, l); individual nodules usually ellipsoidal, rarely globular or irregular, contain many minute nucleoli. Usually two bright, globular micronuclei attached to macronuclear nodules at variable positions, prominent both in vivo and in protargol preparations (Fig. 185a, c–p). No cortical granules. Cytoplasm colourless, with some crystals and food vacuoles.

Cirral pattern rather constant, number of cirri of usual variability (Fig. 185a–d; Table 162). Most cirri about 10 µm long in vivo, fine because usually composed of two or four cilia only. Marginal rows end slightly to distinctly above rear body end, right row begins near posterior end of ventral cirral row, that is, at level of buccal vertex. Buccal cirrus slightly behind anterior end of undulating membranes. Frontal, frontoterminal, and transverse cirri each usually composed of four cilia; right frontal cirrus, as is usual, at distal end of adoral zone. Invariably two frontoterminal cirri right of anterior end of ventral cirral row. Ventral cirral row terminates at 22% of body length, that is, at level of buccal vertex (23%). Transverse cirri near posterior margin of cell and thus distinctly projecting from body proper; usually one or two cirri, each composed of two cilia only, ahead of transverse cirri, likely pretransverse ventral cirri. Dorsal cilia about 3 µm long in vivo, arranged in two rows almost as long as body; bristles in kinety 2 rather widely spaced. No caudal cirri.

Adoral zone occupies about 23% of body length, invariably composed of 12 membranelles of usual shape and structure in the 16 specimens investigated; frontal (distal) four membranelles separated from ventral membranelles by an about one membranelle-wide gap at left anterior corner. Buccal cavity small and flat. Exact structure and arrangement of undulating membranes not clearly recognizable; both almost straight and usually one over the other forming rather thick line. Pharyngeal fibres of ordinary length and structure after protargol impregnation, extend obliquely backwards (Fig. 185a, b, d).

Occurrence and ecology: To date found only at type location, that is, the Namib Escarpment. In eight slides, we found only 20 specimens.

Comparison with related species: As concerns the cirral pattern, *Hemisincirra namibiensis* belongs to the *H. gellerti* group. However, in both *H. gellerti gellerti* (FOISSNER, 1982) FOISSNER, 1984 and *H. gellerti verrucosa* FOISSNER, 2000a, the ventral cirral row is

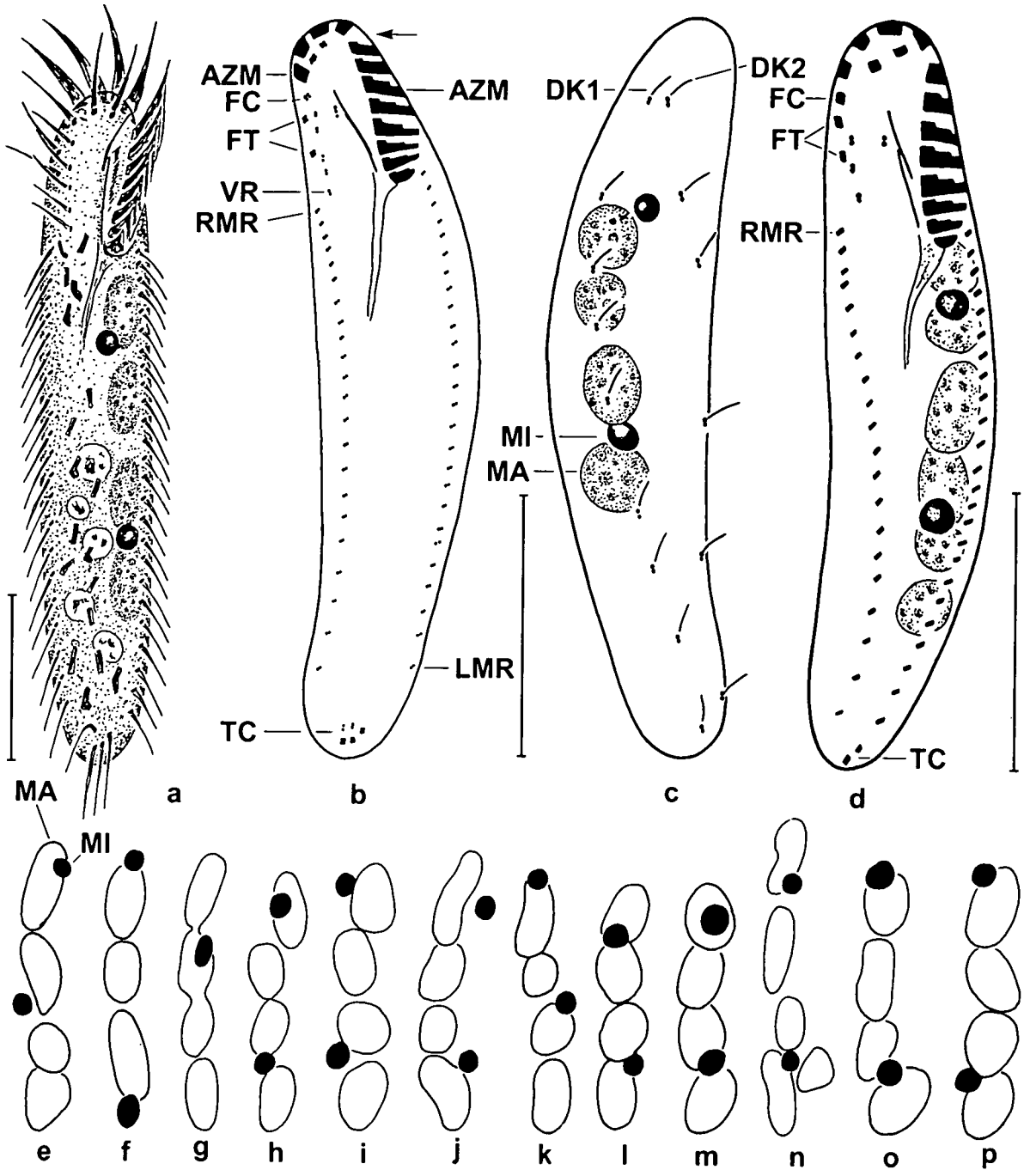

Fig. 185a–p. *Hemisincirra namibiensis* from life (a) and after protargol impregnation (b–p). **a:** Ventral view of a representative specimen. **b, c:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrow marks gap in adoral zone at left anterior corner. **d:** Infraciliature of ventral side of a specimen with six macronuclear nodules and only three minute cirri in the frontoventral row. The transverse cirri are only partially recognizable because the posterior cell portion is twisted. **e–p:** Variability of nuclear apparatus. AZM – adoral zone of membranelles, DK1, 2 – dorsal kineties, FC – right frontal cirrus, FT – frontoterminal cirri, LMR – last cirrus of left marginal row, MA – strand of macronuclear nodules, MI – micronucleus, RMR – first cirrus of right marginal row, TC – transverse cirri, VR – last cirrus of ventral cirral row. Scale bars 20 μm.

Table 162. Morphometric data on *Hemisincirra namibiensis*.

Characteristics[a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	57.7	57.0	5.2	1.3	9.1	48.0	68.0	17
Body, width	11.7	11.5	1.4	0.4	11.8	10.0	14.0	14
Body length:width, ratio	5.0	4.8	0.7	0.2	13.3	4.1	6.5	14
Anterior body end to proximal end of adoral zone, distance	13.6	14.0	1.3	0.3	9.3	11.0	17.0	17
Body length:length of adoral zone, ratio	4.3	4.2	0.6	0.1	13.9	3.5	6.2	17
Anterior body end to end of ventral cirral row, distance	12.9	13.0	1.4	0.4	11.1	10.0	15.0	16
Body length:length of ventral cirral row, ratio	4.5	4.6	0.4	0.1	9.1	3.9	5.3	16
Anterior body end to buccal cirrus, distance	6.4	6.0	0.9	0.2	13.9	5.0	8.0	16
Anterior body end to right marginal row, distance	13.5	14.0	1.9	0.5	13.9	11.0	17.0	17
Anterior body end to nuclear apparatus, distance	13.8	14.0	1.9	0.5	14.0	10.0	18.0	17
Posterior body end to last right marginal cirrus, distance	6.1	6.0	1.7	0.4	28.5	3.0	9.0	16
Posterior body end to last left marginal cirrus, distance	5.7	6.0	2.1	0.5	37.5	2.0	11.0	15
Anterior macronuclear nodule, length	7.4	8.0	1.9	0.5	25.3	3.0	10.0	17
Anterior macronuclear nodule, width	3.7	4.0	0.8	0.2	20.8	3.0	5.0	17
Macronuclear nodules, number[b]	4.1	4.0	0.6	0.1	14.6	3.0	6.0	17
Anterior micronucleus, length	2.2	2.4	–	–	–	1.6	2.4	17
Anterior micronucleus, width	2.1	2.4	–	–	–	1.6	2.4	17
Micronuclei, number[c]	1.9	2.0	–	–	–	1.0	2.0	17
Nuclear figure, length	25.6	25.0	4.1	1.0	15.8	19.0	32.0	17
Adoral membranelles, total number	12.0	12.0	0.0	0.0	0.0	12.0	12.0	16
Frontal adoral membranelles, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	16
Ventral adoral membranelles, number	8.0	8.0	0.0	0.0	0.0	8.0	8.0	16
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	14
Ventral cirral row, number of cirri[d]	5.1	5.0	0.8	0.2	16.3	3.0	7.0	14
Frontoterminal cirri, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	14
Buccal cirri, number[e]	0.9	1.0	–	–	–	0.0	1.0	17
Transverse cirri, number[f]	4.3	4.5	0.8	0.2	18.0	3.0	5.0	12
Right marginal cirri, number	20.7	22.0	3.2	0.8	15.3	15.0	25.0	17
Left marginal cirri, number	24.1	25.0	2.3	0.6	9.4	20.0	27.0	16
Dorsal kineties, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	17

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Of 17 specimens investigated, one specimen each had three (Fig. 185f), five (Fig. 185n), or six (Fig. 185d) macronuclear nodules.

[c] Of 17 specimens investigated, two have one micronucleus.

[d] Of 14 specimens investigated, one specimen each had three (Fig. 185d), six, or seven cirri in this row.

[e] Lacking in 1 out of 17 specimens investigated.

[f] Including presumed pretransverse ventral cirri ahead of transverse cirri.

distinctly longer than the adoral zone (vs. of about same length in *H. namibiensis*) and the right marginal row is only slightly shortened anteriorly (vs. distinctly shortened in *H. namibiensis*). Furthermore, both subspecies have cortical granules and more macronuclear nodules (8–9 on average vs. 4), adoral membranelles (13–17 vs. 12), and dorsal kineties (4 vs. 2) than *H. namibiensis*. *Hemisincirra quadrinucleata* HEMBERGER, 1985, which has the same nuclear pattern, is larger (110–130 µm vs. 60–90 µm) and has more adoral membranelles (15–16 vs. 12) and dorsal kineties (3 vs. 2); furthermore, its undulating membranes are very differently arranged, namely, as in → *Terricirra* BERGER & FOISSNER, 1989a, to which HEMBERGER's species very likely belongs (BERGER & FOISSNER 1989a). In vivo, *Hemisincirra namibiensis* is identified by the following combination of features: 60–80 µm long; body elongate rectangular; four macronuclear nodules with usually two prominent micronuclei; right marginal row anteriorly strongly shortened, commencing at level of buccal vertex.

Hemisincirra inquieta HEMBERGER, 1985 (Fig. 186a–k; 401a–h; Tables 163, 164)

Description of Namibian site (5) population: Size 80–160 × 10–15 µm in vivo, usually about 120 × 15 µm and thus slightly larger than previous populations (80–110 × 10–15 µm). Length:width ratio near to 8:1 on average (Table 163), that is, slender with posterior body half tapering and rear end narrowly rounded or bluntly pointed, often more or less distinctly sigmoidal and slightly twisted about main body axis; dorsoventrally only slightly flattened (about 1.5:1); acontractile but very flexible. Narrowed posterior body portion usually stouter in preparations (Fig. 186a, d). On average 28 ellipsoidal (5 × 3 µm in vivo) macronuclear nodules scattered between oral vertex and posterior fifth of body; nucleoli minute. Usually three inconspicuous micronuclei, 2 × 1.5 µm in size. Contractile vacuole slightly above mid-body at left margin of cell. Cortex thin and flexible, contains a loose lattice of fibres and conspicuous granules between cirral bases and around dorsal bristles. Individual granules brilliant yellowish, compact, ellipsoidal to ovoidal, 1–2 × 0.8–1 µm in size; rarely impregnate with the protargol method used (Fig. 186b, c; 401a, b, d–h). Cytoplasm colourless, contains some square crystals and small food vacuoles with remnants of heterotrophic flagellates (*Polytomella*) and bacteria. Glides moderately fast on microscope slide and on and between soil particles, showing great flexibility.

Cirral pattern and number of cirri of usual variability (Fig. 186a, d, f; Table 163). Cirri about 8 µm long in vivo, most composed of four cilia, buccal cirrus and some cirri of frontoventral row consist of even only two cilia. Both marginal rows extend to posterior body end bearing two transverse cirri and, occasionally, one to three caudal cirri (Fig. 186d, g, h); however, we cannot exclude that the caudal cirri are marginal cirri dislocated by the preparation procedures, which usually broaden the fragile posterior body portion. Right marginal row considerably shortened anteriorly and thus distinctly separate from frontoterminal cirri underneath distal end of adoral zone of membranelles. Frontal cirri in transverse row near anterior body end, not enlarged, first frontal cirrus frequently near gap between frontal and ventral adoral membranelles, third close to uppermost frontoterminal cirrus. Buccal cirrus in corner where paroral and endoral abut, inconspicuous because invariably composed of only two cilia.

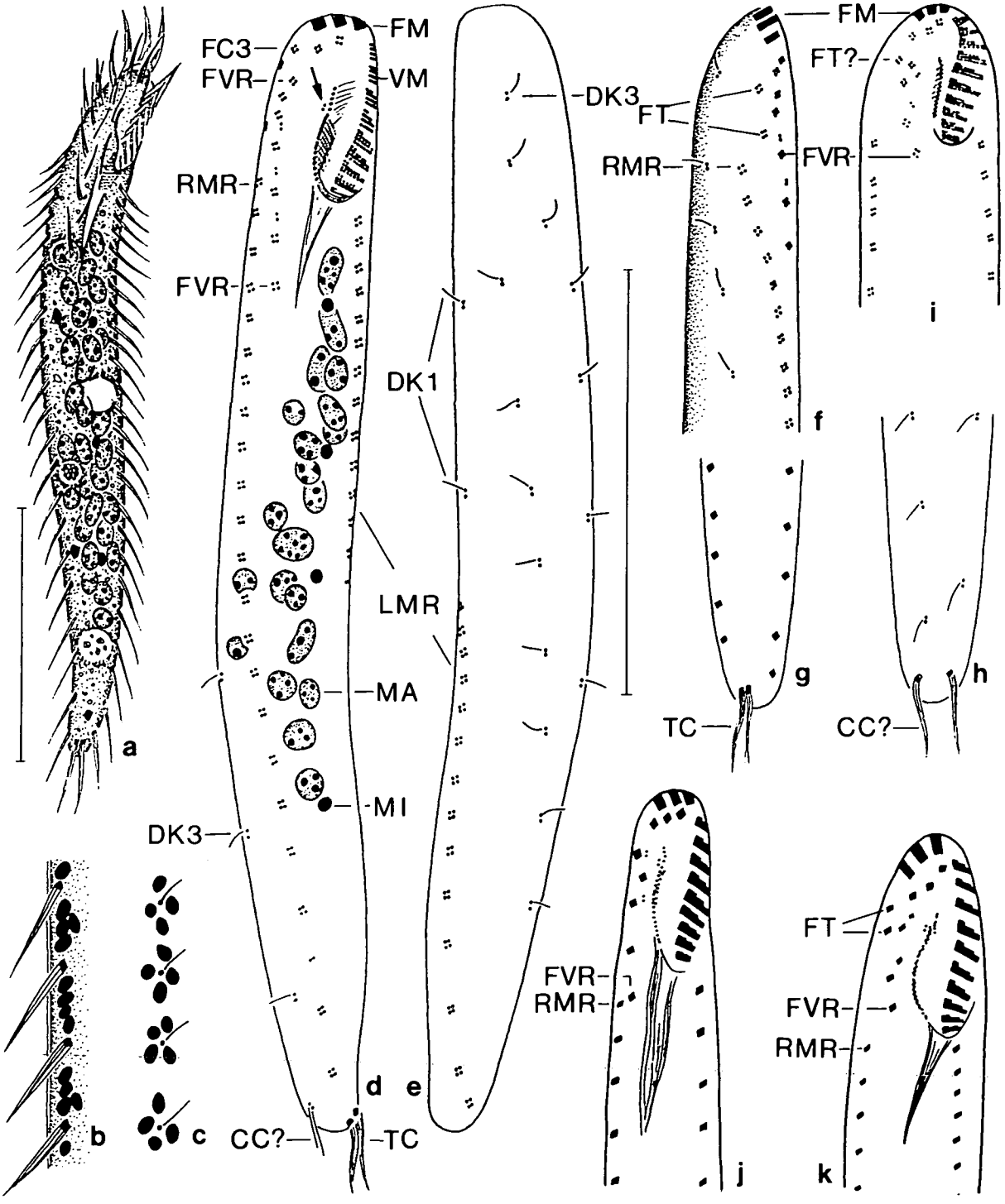

Fig. 186a–k. *Hemisincirra inquieta*, Namibian (a–h) and other (i–k) specimens from life (a–c) and after protargol impregnation (d–k). **a:** Ventral view. **b, c:** Cortical granules are between cirri and around dorsal bristles. **d, e:** Infraciliature of ventral and dorsal side. Arrow marks buccal cirrus. **f:** Dorsolateral view showing relationship between frontoterminal, frontoventral, and marginal cirri. **g, h:** A specimen likely having two caudal cirri. **i–k:** Oral area of type population (HEMBERGER 1982), of a German specimen (BERGER and FOISSNER 1987), and of a specimen from Iceland (BERGER and FOISSNER 1989a). CC? – caudal cirri, DK1, 3 – dorsal kineties, FC3 – third frontal cirrus, FM – frontal membranelles, FT – frontoterminal cirri, FVR – frontoventral row, LMR – left marginal row, MA – macronuclear nodule, MI – micronucleus, RMR – begin of right marginal row, TC – transverse cirri, VM – ventral membranelles. Scale bars 40 µm (a, d, e).

Table 163. Morphometric data on *Hemisincirra inquieta* from Namibian site (5).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	111.8	108.0	16.2	4.5	14.5	77.0	140.0	13
Body, width	14.9	15.0	1.3	0.4	8.6	13.0	17.0	13
Anterior body end to proximal end of adoral zone, distance	18.6	18.0	0.8	0.2	4.1	18.0	20.0	13
Anterior body end to end of frontoventral row, distance	25.7	26.0	2.3	0.6	8.8	22.0	29.0	13
Anterior body end to right marginal row, distance	14.7	15.0	3.0	0.8	20.1	11.0	22.0	13
Anterior body end to paroral membrane, distance	7.8	8.0	1.0	0.3	13.0	6.0	9.0	13
Anterior body end to first macronuclear nodule, distance	21.2	20.0	2.1	0.6	9.6	18.0	25.0	13
Nuclear figure, length	65.5	67.0	12.3	3.4	18.8	38.0	90.0	13
Macronuclear nodules, length	4.4	4.0	1.1	0.3	25.6	3.0	6.0	13
Macronuclear nodules, width	2.2	2.0	–	–	–	2.0	3.0	13
Macronuclear nodules, number	28.3	30.0	4.0	1.1	14.1	19.0	32.0	13
Micronuclei, length	1.9	2.0	–	–	–	1.5	2.0	13
Micronuclei, width	1.5	1.5	–	–	–	1.5	2.0	13
Micronuclei, number	2.8	3.0	0.9	0.3	33.5	1.0	4.0	13
Adoral membranelles, number	13.9	14.0	–	–	–	13.0	14.0	13
Right marginal cirri, number	22.7	23.0	3.0	0.8	13.1	16.0	26.0	13
Left marginal cirri, number	24.3	25.0	4.2	1.2	17.4	16.0	30.0	13
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13
Frontoterminal cirri, number	1.9	2.0	–	–	–	1.0	2.0	13
Frontoventral row, number of cirri	8.2	9.0	1.1	0.3	14.0	7.0	10.0	13
Frontal field, total number of cirri [b]	14.1	14.0	1.1	0.3	7.9	13.0	16.0	13
Transverse cirri, number	1.9	2.0	–	–	–	0.0	2.0	13
Caudal cirri, number [c]	1.5	2.0	0.8	0.2	53.1	0.0	3.0	13
Dorsal kineties, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Frontal cirri, buccal cirrus, frontoterminal cirri, plus cirri of frontoventral row.

[c] Identity of cirri uncertain; see description.

Frontoventral row right of midline, slightly longer than adoral zone of membranelles, composed of an average of eight slightly scattered cirri, of which some consist of only two cilia.

Dorsal bristles about 3 µm long in vivo, invariably arranged in three loosely ciliated kineties; row 1, however, consists of only one to three kinetids in anterior body half. Row 2 distinctly shortened anteriorly (Fig. 186d–f, h).

Adoral zone inconspicuous because occupying only 17% of body length on average, indistinctly bipartite by small gap at left anterior corner, producing 3 frontal and 10–11 ventral membranelles of ordinary structure. Buccal field narrow and flat, buccal lip covers proximal third of adoral zone. Paroral and endoral membrane difficult to distinguish, but

show a characteristic, double curved pattern (Fig. 186d; 401b): a short, slightly curved anterior portion (paroral?) with 5 µm long cilia abuts on a longer and more distinctly curved posterior portion (endoral?); possibly, the short anterior portion overlaps the posterior to some extent. Pharyngeal fibres comparatively conspicuous.

Occurrence and ecology: *Hemisincirra inquieta* is one of the most common soil hypotrichs and has been recorded in a wide variety of terrestrial habitats from all main biogeographic regions, except for Antarctica (FOISSNER 1998a). In Namibia, the species is also frequent (Table 4), but saline habitats are less preferred.

Comparison with previous descriptions and related species: The original description of *H. inquieta* is rather brief and incomplete because HEMBERGER (1982, 1985) provided only limited morphometrics (Table 164), did not describe details of the oral apparatus (Fig. 186i), and did not study live cells, overlooking the highly characteristic cortical granules. Furthermore, he did not give any location (Peru? Germany?). Thus, BERGER & FOISSNER (1987) redefined the species with a German population. The arrangement and colour of the cortical granules of *H. inquieta* is highly characteristic and important. Thus, we provide our original notes (partially unpublished) on six populations: "yellowish granule clusters" (Kenyan population 1, studied 1985); "few orange granules around cirral bases and dorsal bristles" (Kenyan population 2, studied 1985); "brilliant yellowish, compact, 1–2 × 0.8–1 µm-sized, ellipsoidal to ovoidal granules in clusters between cirral bases and around dorsal bristles" (Namibian population described here); "yellowish granules around cirral bases and dorsal bristles" (Austrian population, studied 1981); "brilliant yellow, about 1 µm-sized granules around cirral bases and dorsal bristles" (German population, BERGER & FOISSNER 1987); "orange-yellowish, about 1 µm-sized, ellipsoidal granules around cirral bases and dorsal bristles" (Iceland population, BERGER & FOISSNER 1989a). Obviously, the arrangement of the granules is largely constant, while colour varies considerably from yellowish over yellow to orange.

Basically, the present observations agree with those of HEMBERGER (1982, 1985) and BERGER & FOISSNER (1987, 1989a), although there are rather conspicuous differences in details and morphometrics (Table 164). Most differences concern the illustration and interpretation of the frontoventral cirral row and undulating membranes (Fig. 186i–k). As these minute structures are difficult to analyze, slight differences must not be over-interpreted. The Namibian specimens differ from the other populations mainly by the frontoventral row, which is longer and composed of more cirri; however, the characteristic structure of the row, that is, alternately four and two cilia cirri is the same, indicating conspecificity. This is substantiated by the German specimens, whose frontoventral row also slightly extends beyond the oral vertex (Fig. 186j). Only HEMBERGER's population has distinctly fewer macronuclear nodules (Table 164).

Taking all data together, there is considerable variability in this species, even if some misobservations are assumed. Basically, *H. inquieta* can be defined as follows: Size usually 90–120 × 10-15 µm in vivo, very elongate (7:1) with posterior body portion narrowed or bluntly pointed. Usually about 30 scattered macronuclear nodules. Cortical granules yellowish to orange, about 1 µm in size, found only around cirri and dorsal bristles. Adoral zone indistinctly bipartite, < 20% of body length, composed of 12–14 membranelles. About 11 cirri in frontal field, 20 cirri in right marginal row, and 2 transverse cirri; frontoventral cirral row about as long as adoral zone or slightly longer. Three dorsal kineties with row 1 consisting of only one to three kinetids.

Table 164. Comparison of main morphometrics of four *Hemisincirra inquieta* populations.

Characteristics [a]	Population [b]	$\bar{x}$	M	SD	CV	Min	Max	n
Body, length	TY	?	100.0	?	?	90.0	125.0	100 ?
	GE	78.0	75.0	12.1	15.5	63.0	100.0	10
	IS	84.6	90.0	11.4	13.4	70.0	98.0	7
	NA	111.8	108.0	16.2	14.5	77.0	140.0	13
Body, width	TY	?	15.0	?	?	?	?	100 ?
	GE	10.1	10.0	1.3	12.7	7.0	11.0	10
	IS	12.6	13.0	1.3	10.1	11.0	14.0	7
	NA	14.9	15.0	1.3	8.9	13.0	17.0	13
Anterior body end to proximal end of adoral zone, distance	TY	one sixth of body length (~17 µm)						100 ?
	GE	13.2	13.0	0.8	5.9	12.0	15.0	10
	IS	15.1	15.0	1.4	8.9	13.0	17.0	7
	NA	18.6	18.0	0.8	4.1	18.0	20.0	13
Anterior body end to last cirrus of frontoventral row, distance	TY	about as long as adoral zone						100 ?
	GE	16.2	16.0	2.5	15.6	13.0	21.0	10
	IS	about as long as adoral zone						7
	NA	25.7	26.0	2.3	8.8	22.0	29.0	13
Adoral membranelles, number	TY	?	12.0	?	?	?	?	100 ?
	GE	13.0	13.0	0.5	3.6	12.0	14.0	10
	IS	13.0	13.0	0.7	5.3	12.0	14.0	7
	NA	13.9	14.0	–	–	13.0	14.0	13
Macronuclear nodules, number	TY	?	?	?	?	14.0	17.0	100 ?
	GE	27.7	29.0	3.6	13.2	22.0	32.0	10
	IS	31.7	32.0	2.1	6.7	30.0	36.0	7
	NA	28.3	30.0	4.0	1.1	19.0	32.0	13
Cirri in frontal field, total number [c]	TY	?	11.0	?	?	?	?	100 ?
	GE	11.0	11.0	0.0	0.0	11.0	11.0	10
	IS	about 11						7
	NA	14.1	14.0	1.1	7.9	13.0	16.0	13
Right marginal cirri, number	TY	?	18.0	?	?	16.0	19.0	100 ?
	GE	16.8	17.0	1.9	11.5	13.0	20.0	10
	IS	21.4	21.0	2.3	10.7	18.0	24.0	7
	NA	22.7	23.0	3.0	13.1	16.0	26.0	13
Dorsal kineties, number	TY	3.0	3.0	0.0	0.0	3.0	3.0	100 ?
	GE	3.0	3.0	0.0	0.0	3.0	3.0	10
	IS	3.0	3.0	0.0	0.0	3.0	3.0	7
	NA	3.0	3.0	0.0	0.0	3.0	3.0	13

[a] Data based on protargol-impregnated and randomly selected specimens from raw cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] TY – type population, locality unknown (from HEMBERGER 1982, 1985); GE – German population (from BERGER & FOISSNER 1987); IS – Iceland population (from BERGER & FOISSNER 1989a); NA – Namibian population (from Table 163).

[c] Frontal cirri, buccal cirrus, frontoterminal cirri, plus cirri of frontoventral row.

Thin, medium-sized hypotrichs like *H. inquieta* are difficult to identify. In vivo, it is best determined by body size and shape, the colour and arrangement of the cortical granules, the scattered macronuclear nodules, and the short frontoventral row. This combination of features separates it clearly from, for instance, *H. gracilis* (no cortical granules), *H. gellerti* (cortical granules colourless and in dense rows), and *H. wenzeli*, three soil hypotrichs described by FOISSNER (1982, 1987c). The last mentioned species differs from *H. inquieta* only by the colourless cortical granules and the distinct caudal cirri, a feature weakened by the Namibian specimens. Another species difficult to distinguish from *H. inquieta* is *Holostichides terricola* FOISSNER, 1988a. This species also has yellow cortical granules which, however, are scattered, that is, not restricted to cirral and dorsal bristle bases. Furthermore, the macronuclear nodules form a strand left of midline and the frontoventral cirral row extends to mid-body. Several → *Urosomoida* and → *Erimophrya* species are also rather similar, but have only two macronuclear nodules.

Hemisincirra rariseta nov. spec. (Fig. 187a–g; Table 165)

Diagnosis: Size about 170 × 14 µm in vivo; vermiform. Usually 16 macronuclear nodules in series left of midline. On average 26 right and 25 left marginal cirri, 2 frontoterminal cirri, and 7 frontoventral cirri in a row ending near level of buccal vertex. Invariably 2 bipolar dorsal kineties. Adoral zone bipartited into 3 frontal and 13 ventral membranelles, occupies about 16% of body length.

Type location: Soil from the *Aloe dichotoma* forest near the Gariganus Guest Farm, Namibia, 26°30'S 18°25'E (site 5 in figure 2 and chapter 2.1.2).

Etymology: Composite of the Greek words *rara* (few) and *saeta* (bristle ~ cirrus), referring to the sparse frontoventral ciliature.

Description: Size 120–200 × 10–20 µm in vivo, usually about 170 × 14 µm, length: width ratio invariably ≥ 8:1, on average near 10:1 (Table 165). Vermiform with anterior portion slightly and posterior conspicuously narrowed, a tail, however, is not formed; frequently distinctly twisted about main body axis and serpentine with posterior portion usually straight or slightly curved; flattened only in oral area, acontractile (Fig. 187a, b). Nuclear apparatus in central quarters of cell, macronuclear nodules in series left of midline, rarely in two indistinct overlapping strands; individual nodules globular to elongate ellipsoidal, on average ellipsoidal, nucleoli minute. Usually one broadly ellipsoidal micronucleus each near anterior and posterior quarter of macronuclear strand. Contractile vacuole slightly above mid-body. Cortex thin and very flexible, destitute of specific granules. Cytoplasm colourless, contains many granules and food vacuoles with bacteria and fungal spores. Moves moderately fast and serpentinely on microscope slide and between soil particles, showing great flexibility.

Cirral pattern and number of cirri of usual variability, except for the strongly varying number of frontoventral cirri (Fig. 187a, b, d–f; Table 165). Cirri about 12 µm long and fine, consist of two rows with only two (posterior third of marginal rows, frontoterminal cirri, rear cirri of frontoventral row) or three (anterior thirds of marginal and frontoventral rows) cilia each. Both marginal rows extend to posterior body end bearing two to three spread (likely caudal)

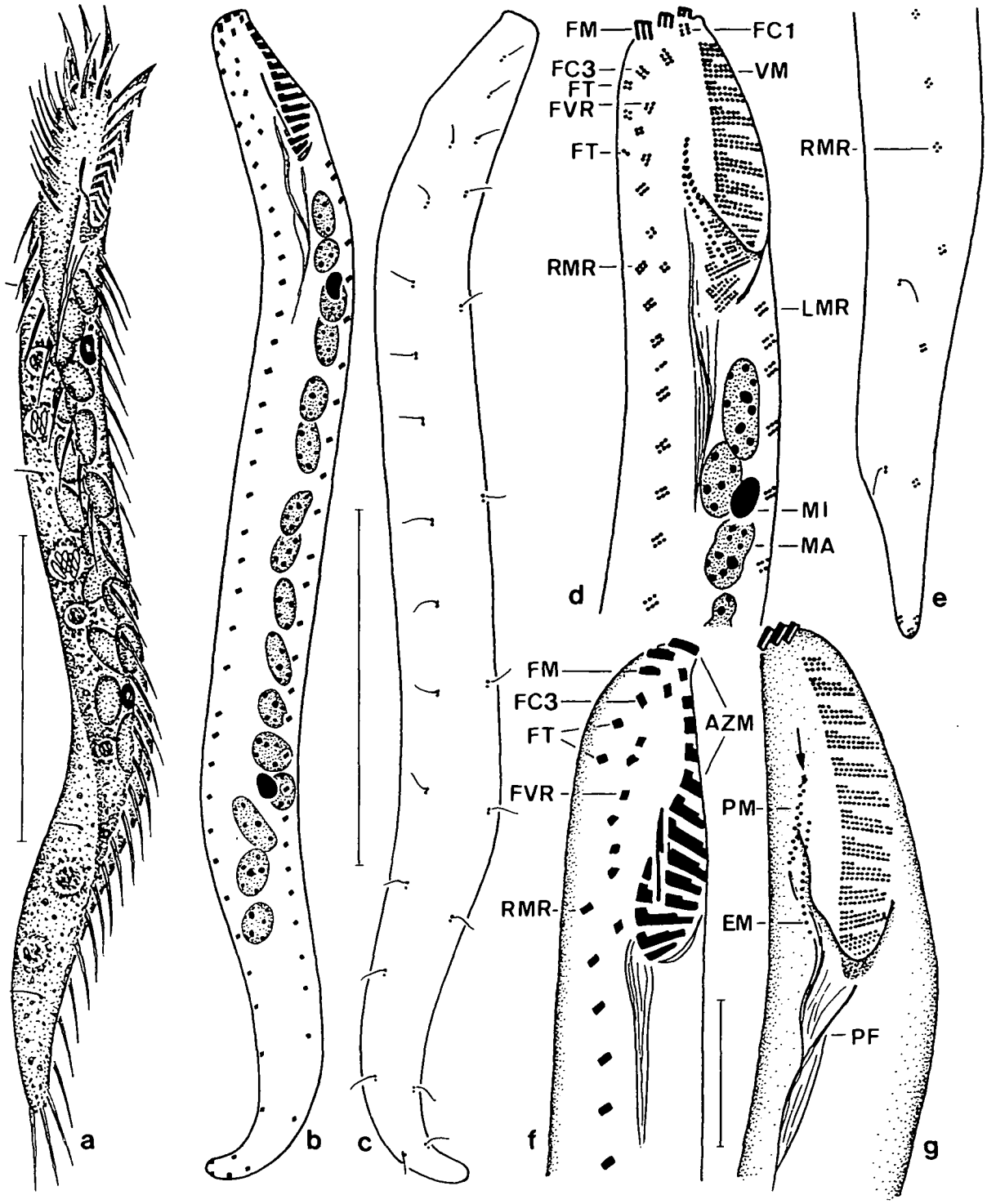

Fig. 187a–g. *Hemisincirra rariseta* from life (a) and after protargol impregnation (b–g). **a:** Ventral view of a twisted specimen. **b, c:** Infraciliature of ventral and dorsal side of holotype specimen. **d, f, g:** Details of infraciliature in ventral (d), dorsolateral (f) and ventrolateral (g) view. Arrow in (g) marks enlarged granule at end of paroral membrane, possibly a vestigial buccal cirrus. **e:** Posterior portion of specimen shown in (d). The marginal cirri consist of only four cilia. AZM – adoral zone, EM – endoral membrane, FC1, 3 – frontal cirri, FM – frontal membranelles, FT – frontoterminal cirri, FVR – frontoventral row, MA – macronuclear nodule, MI – micronucleus, LMR – left marginal row, PF – pharyngeal fibres, PM – paroral membrane, RMR – right marginal row, VM – ventral membranelles. Scale bars 50 µm (a–c) and 10 µm (d–g).

cirri; right marginal row shortened anteriorly by about 15 µm and thus distinctly separated from frontoterminal cirri at distal end of adoral zone. Frontal cirri in subapical, oblique row, first cirrus invariably in gap between frontal and ventral adoral membranelles. Frontoventral row right of midline, ends slightly above oral vertex, composed of an average of seven cirri forming indistinct pairs; anteriormost cirrus of row invariably shifted slightly leftwards. Buccal cirrus very likely lacking or very close to anterior end of paroral membrane, where a slightly enlarged granule is recognizable in some specimens.

Dorsal bristles about 5 µm long in vivo, arranged in two rows extending to posterior body end, left row slightly shortened anteriorly; bristles of right row more loosely spaced than those of left, except in oral portion (Fig. 187c).

Adoral zone inconspicuous because occupying only 16% of body length, bipartited into 3 frontal and 13 ventral membranelles of ordinary fine structure by a distinct gap at left anterior body corner; anteriormost ventral membranelle composed of three basal body rows only.

Table 165. Morphometric data on *Hemisincirra rariseta*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	143.2	140.0	17.6	4.0	12.3	115.0	170.0	19
Body, width	13.9	13.0	1.1	0.3	7.9	13.0	16.0	19
Anterior body end to proximal end of adoral zone, distance	22.6	22.0	1.5	0.3	6.7	20.0	25.0	19
Anterior body end to paroral membrane, distance	9.4	9.0	1.1	0.3	11.9	7.0	11.0	19
Paroral membrane, length	5.2	5.0	0.6	0.1	11.7	4.0	6.0	19
Anterior body end to right marginal row, distance	15.8	16.0	2.0	0.5	12.8	13.0	20.0	19
Anterior body end to frontoventral cirral row, distance	5.7	6.0	1.2	0.3	21.2	3.0	7.0	19
Anterior body end to end of frontoventral cirral row, distance	20.5	20.0	3.3	0.8	16.0	15.0	26.0	19
Anterior body end to first macronuclear nodule, distance	24.7	25.0	3.0	0.7	12.0	17.0	29.0	19
Nuclear figure, length	83.8	85.0	14.5	3.3	17.3	59.0	108.0	19
Macronuclear nodules, length	6.8	7.0	1.1	0.3	16.0	5.0	8.0	19
Macronuclear nodules, width	4.0	4.0	0.6	0.1	14.6	3.0	5.0	19
Macronuclear nodules, number	14.9	16.0	2.4	0.5	15.8	7.0	18.0	19
Micronuclei, length	3.6	4.0	–	–	–	3.0	4.0	19
Micronuclei, width	2.5	3.0	–	–	–	2.0	3.0	19
Micronuclei, number	1.9	2.0	0.8	0.2	42.7	1.0	4.0	19
Frontal adoral membranelles, number	3.1	3.0	–	–	–	3.0	4.0	19
Ventral adoral membranelles, number	12.9	13.0	0.8	0.2	6.3	12.0	14.0	19
Adoral membranelles, total number	15.9	16.0	0.8	0.2	5.1	15.0	17.0	19
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
Frontoterminal cirri, number	2.2	2.0	–	–	–	2.0	3.0	19
Frontoventral cirri, number	7.0	7.0	1.7	0.4	23.7	5.0	11.0	19
Right marginal cirri, number	26.6	26.0	3.5	0.8	13.0	21.0	36.0	19
Left marginal cirri, number	25.1	25.0	2.3	0.5	9.3	21.0	29.0	19
Dorsal kineties, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Buccal field narrow and flat, buccal lip covers posteriormost adoral membranelles. Paroral and endoral membrane close together and staggered, paroral likely composed of dikinetids. Pharyngeal fibres conspicuous (Fig. 187a, b, d, f, g).

Occurrence and ecology: To date found only at type location, where it was rather abundant. The species is well adapted to the sandy habitat by its slender shape.

Comparison with related species: This species highly resembles *Vermioxytricha muelleri* (FOISSNER, 1986) and → *V. arenicola* in body size and shape as well as number of macronuclear nodules and adoral membranelles. The main difference is the buccal cirrus which is very likely lacking in *H. rariseta*. A further important difference concerns the right dorsal kinety, which is reduced to a few anterior dikinetids in *V. muelleri* and → *V. arenicola*. There are also several significant morphometric differences, viz., the number of right (43–46 vs. 26) and left (39 vs. 25) marginal cirri and the total number of cirri (frontal, frontoterminal, frontoventral, buccal) in the frontal field (8 vs. 12). Furthermore, → *V. arenicola* has cortical granules.

There are several other similar species which, however, have three dorsal kineties, viz., *Hemisincirra kahli* (BUITKAMP, 1977b) and *Circinella vettersi* (BERGER & FOISSNER, 1989a), or only one dorsal kinety, namely, *Hemisincirra interrupta* (FOISSNER, 1982), *Hemisincirra vermiculare* HEMBERGER, 1985, and *Circinella filiformis* (FOISSNER, 1982). Certainly, these species differ from *H. rariseta* also in other characteristics, but the number of dorsal kineties, which is very constant in the group, is the easiest feature recognizable also on careful live observation. Generally, all species mentioned above are difficult to distinguish in vivo, and thus identification should be checked in protargol preparations. Furthermore, there are likely many other, as yet undescribed, similar species.

Terricirra matsusakai BERGER & FOISSNER, 1989a (Fig. 381v, 388f, g)

This species, which is rare in Namibia (Table 4) and world-wide, is mentioned to confirm two main genus features, viz., the dark-green cortical granules and the ellipsoidal food vacuoles. Both are highly conspicuous but require observation at magnifications of ≥ ×100.

Euplotopsis incisa nov. spec. (Fig. 188a–h; 402a–e; Table 166)[30]

Diagnosis: Size about 40 × 30 µm in vivo. Ovoidal with sharp subterminal indentation at right body margin, where ventral and dorsal cortical ridges overlap. Macronucleus inverted C-

[30] *Euplotopsis* is feminine gender (Article 30.1.2 of the ICZN 1999), which was obviously overlooked by BORROR & HILL (1995). Thus, the following species names have to be emended (see BORROR & HILL 1995 for literature on the species concerned): *Euplotopsis apsheronica* (AGAMALIEV, 1966) BORROR & HILL, 1995 nom. corr.; *E. bisulcata* (KAHL, 1932) BORROR & HILL, 1995 nom. corr.; *E. encystica* (YONEZAWA, 1985) BORROR & HILL, 1995 nom. corr.; *E. lata* (KAHL, 1932) BORROR & HILL, 1995 nom. corr.; *E. tegulata* (TUFFRAU, 1960) BORROR & HILL, 1995 nom. corr.; *E. labiata* (RUINEN, 1938) nov. comb. (redescription in BLATTERER & FOISSNER 1988).

shaped. 9 frontoventral cirri (cirrus VI/2 lacking) and 9 dorsomarginal ciliary rows. On average 19 adoral membranelles. Dorsal silverline system of double-eurystomus type.

Type location: Slightly saline coastal soil from Dugi Otok, a small island at the Adriatic sea coast of Croatia, 44°N 15°E.

Etymology: The Latin participle *incisa* (cut deeply and sharply) refers to the distinct subterminal indentation.

Description: Size 30–45 × 25–35 µm in vivo. Ovoid to slightly rhomboidal with sharp subterminal indentation at right body margin, where ventral and dorsal cortical ridges overlap (Fig. 188a–e; 402a); distinctiveness of indentation slightly variable, usually well-recognizable even in protargol-impregnated specimens (Fig. 188g, h). Anterior right ventral surface with two flat ridges extending to mid-body; buccal ridge slightly curved and thickened, without peculiarities. Dorsal side convex, extends onto ventral side posteriorly producing hook-like indentation (Fig. 188d); with three to four more or less prominent furrows (Fig. 188c), rarely almost smooth. Nuclear apparatus and contractile vacuole without peculiarities; micronucleus only lightly impregnated with protargol. Cortex bright, rigid, colourless, sculptured by various ridges and furrows, as described above. Food vacuoles with bacterial remnants, concentrated in middle third of cell. Creeps hurriedly on microscope slide and organic debris, sometimes resting for a few seconds.

Cirri about 20 µm long and fine, invariably arranged as shown in figure 188g. Transverse cirri usually conspicuously subterminal at level of cytostome (Table 166). Only 3 caudal cirri. Eight to ten kinetids each in central dorsal kineties. Silverline system very regular, of double-eurystomus type (Fig. 188f, h; 402b–e; for terminology, see CURDS 1975). Oral apparatus without peculiarities, adoral zone of membranelles occupies 64% of body length on average, right half covered by hyaline lip (Fig. 188a, b; 402a).

Occurrence and ecology: The sample from the type location was collected by Dr. Wolfgang PETZ 2–3 m inshore of the Adriatic sea coast on 27.08.1987. It was a mixture of the top 3 cm sand and litter layer and had pH 6.3. Although from near the sea, the material was only slightly saline and contained a typical terrestrial ciliate community with 39 species. In Namibia, we found *E. incisa* in two highly saline soil samples from the Etosha National Park (sites 59, 61). *Euplotopsis incisa* occurred also in a highly saline coastal soil sample (mainly litter and dark humus; pH 8.1; collected by Dr. Maria WALDHÖR on 28.02.1993) from Curaçao (12°N 69°W), a small island at the north coast of Venezuela. These data indicate that *E. incisa* is a halophile cosmopolitan.

Generic classification and comparison with related species: Our population belongs to *Euplotopsis* BORROR & HILL, 1995 because it lacks cirrus VI/2. *Euplotopsis incisa* is unique in that it has a distinct subterminal indentation, which is caused by a specific arrangement of the ventral and dorsal cortical ridges (Fig. 188a, b, g, h; 402a). Admittedly, this is a rather sophisticated feature, which might even have been overlooked in some other species. It is, however, present in populations of several saline soils from widely separated geographical regions (see "occurrence and ecology"). Considering the indentation, the soil habitat, and the rather unique combination of some ciliary features (9 dorsal kineties in spite of small body size, 3 caudal cirri only, transverse cirri distinctly subterminal), species status seems justified for such populations at the present state of knowledge.

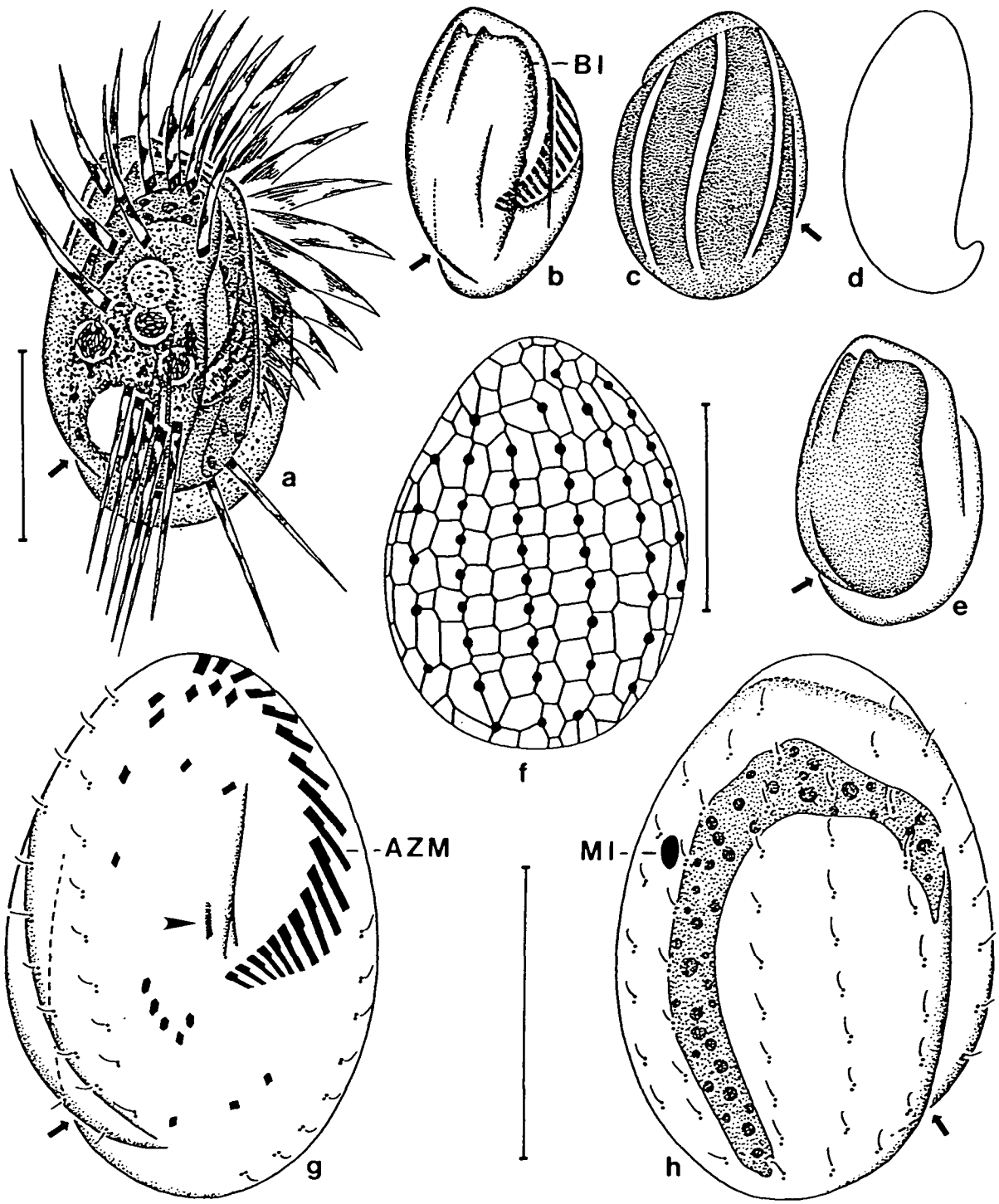

Fig. 188a–h. *Euplotopsis incisa* from life (a–e), after CHATTON-LWOFF silver nitrate impregnation (f), and after protargol impregnation (g, h). Arrows mark the main species feature, that is, the sharp subterminal indentation. **a:** Ventral view of a representative specimen. **b, c, e:** Shape variability and cortical pattern of ventral (b, e) and dorsal (c) side. **d:** Right lateral view. **f:** Ciliary and silverline pattern of dorsal side. **g, h:** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrowhead marks paroral membrane. AZM – adoral zone of membranelles, BI – buccal ridge, MI – micronucleus. Scale bars 20 μm.

Except for the subterminal indentation, *Euplotopsis incisa* is rather similar to other small species of the genus with a silverline system of the double-eurystomus type (see BORROR & HILL 1995 and CURDS 1975 for literature on the species mentioned in the following comparison): *Euplotopsis affinis* (6–9, usually 7–8 dorsal kineties, 4 caudal cirri, usually 40–70 µm long; FOISSNER et al. 1991), *E. bisulcata* (8 dorsal kineties, 4 caudal cirri, different cortical pattern), *E. finki* (7 dorsal kineties, transverse cirri in two groups, 4 caudal cirri, very conspicuous cortical ridges), *E. labiata* (8 dorsal kineties, 4 caudal cirri, with prominent postoral process; redescription in BLATTERER & FOISSNER 1988), *E. parkei* (4 caudal cirri, usually only 8 frontoventral cirri).

Very recently, we found a similar, or the same, species in a slightly acidic (pH 6.0) and saline (8 ‰) soil sample (yellowish sand with patches of iron concretions mixed with many roots and litter mainly from legumes planted for desalinization) from the Al-Hassa Oasis in Saudi Arabia. This population matches the cells from Croatia in every respect, except for cirrus VI/2, which is present (Fig. 402b-e). Thus, it has 10 frontoventral cirri and would belong to *Euplotes* (BORROR & HILL 1995).

Table 166. Morphometric data on *Euplotopsis incisa*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	35.4	36.0	3.5	1.1	10.0	26.0	40.0	11
Body, width	25.3	25.0	2.4	0.7	9.5	20.0	30.0	11
Anterior body end to proximal end of adoral zone, distance	22.6	23.0	1.4	0.4	6.0	20.0	24.0	11
Anterior body end to distalmost transverse cirrus, distance	23.0	25.0	4.3	1.3	18.8	13.0	27.0	11
Macronucleus, length [b]	28.3	29.0	3.2	1.0	11.2	20.0	31.0	11
Macronucleus, width	4.2	4.0	0.8	0.2	17.8	3.0	5.0	11
Adoral membranelles, number	19.4	20.0	1.0	0.3	5.3	18.0	21.0	11
Frontoventral cirri, number	9.0	9.0	0.0	0.0	0.0	9.0	9.0	11
Transverse cirri, number	5.0	5.0	0.0	0.0	0.0	5.0	5.0	11
Caudal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
Dorsal kineties, number	8.8	9.0	–	–	–	8.0	9.0	11

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Measured as distance between anterior curve and posterior end of nucleus.

HETEROTRICHIDA

Of the 643 soil ciliate species known globally, only 24 (4.1 %) are heterotrichs, and possibly only *Phacodinium metchnicoffi* (CERTES) and *Balantidioides* are confined to terrestrial habitats (FOISSNER 1998a). Likely, some → *Blepharisma* and → *Condylostomides* species also prefer soil environments. Interestingly, anaerobic heterotrichs of the genus *Metopus* occur rather frequently, especially in occasionally flooded soils, such as floodplains and marshes. Thus, they can serve as bioindicators for soil anaerobity (FOISSNER 1999e). In contrast, anaerobic caenomorphids (e.g., *Caenomorpha*) and odontostomatids (e.g., *Epalxella*) are lacking in soil, supporting recent ontogenetic data showing that they are quite different from metopids (FOISSNER & AGATHA 1999).

Blepharisma bimicronucleatum VILLENEUVE-BRACHON, 1940, bluish variant (Fig. 189a–e; 403a–c; Table 167)

Material: Specimens from grassland soil (pH 6.6) taken at the bank of a stream in the surroundings of the Keekoro Lodge, Masai Mara National Reserve, Kenya, 01°25'S 35°10'E.

Description: Size 60–110 × 20–35 µm in vivo, usually about 85 × 30 µm, 2:1 flattened laterally. Lanceolate, anterior end bluntly pointed, posterior broadly rounded and somewhat irregular due to the contractile vacuole, ventral side slightly concave along adoral zone, dorsal moderately convex (Fig. 189a, b; 403a–c; Table 167). Macronucleus in centre of cell, ellipsoidal in 37 specimens and reniform to elongate reniform in 24 out of 61 cells investigated; contains many minute nucleoli. Micronuclei minute, that is, about 1.5 µm across and surrounded by a distinct membrane in protargol preparations; three dividers show two dividing micronuclei each. Contractile vacuole in posterior body end, surrounded by "feeder vacuoles" during systole. Cortex very flexible, distinctly furrowed by ciliary rows, contains about 10 rows of pigment granules between each two kineties. Individual pigment granules about 0.5 µm across, blue-grey to blue-green, cells appear like a pale *Stentor coeruleus*, that is, light blue-grey with or without a reddish shimmer (Fig. 189b). Cytoplasm colourless and foamy due to many vacuoles containing only some granules. Glides slowly on microscope slide and between soil particles.

Somatic and oral ciliary pattern as in congeners (Fig. 189a, c–e; 403a–c). Thus, only some details will be reported. Cilia 12 µm long in vivo, about half of the dikinetids has only the anterior basal body ciliated. One shortened, loosely ciliated kinety right of undulating membrane. Postoral secant system indistinct. Adoral zone of membranelles J-shaped, that is, only indistinctly spiralized proximally, individual bases up to 4 µm wide in vivo and of different fine structure in various regions of the zone (Fig. 189c): composed of two long and one shortened row in anterior two thirds of zone; followed by about 10 membranelles each composed of three basal body rows of equal length; the last four to six membranelles are composed of only two basal body rows of equal length. Zigzagging portion of paroral membrane short, that is, about one third of entire length.

Occurrence and ecology: Found in Kenya, as described above, in Namibia (Table 4), and in a variety of soils globally (FOISSNER, unpubl.), indicating a wide ecological range and cosmopolitan distribution. Rarely, the pink and bluish variety occurred together.

Comparison with literature data and related species: We consider our bluish *Blepharisma* as conspecific with the pink to red *B. bimicronucleatum*, as redescribed by FOISSNER (1989), because the colour of the pigment can be changed from red to blue by light and oxygen (for an excellent review, see GIESE 1973). Furthermore, morphology and morphometry match well (Table 167). The identity of *B. bimicronucleatum* is still somewhat doubtful and carefully discussed in FOISSNER (1989). HIRSHFIELD et al. (1973) consider *B. bimicronucleatum* as a variety of *B. lateritium*, which was disproved by FOISSNER (1989). The present investigations emphasize the stability of this form and thus suggest that it is a distinct species. *Blepharisma bimicronucleatum* is rather similar to *B. hyalinum*, as redescribed by FOISSNER (1989) and AESCHT & FOISSNER (1998), which, however, has colourless cortical granules and only one micronucleus.

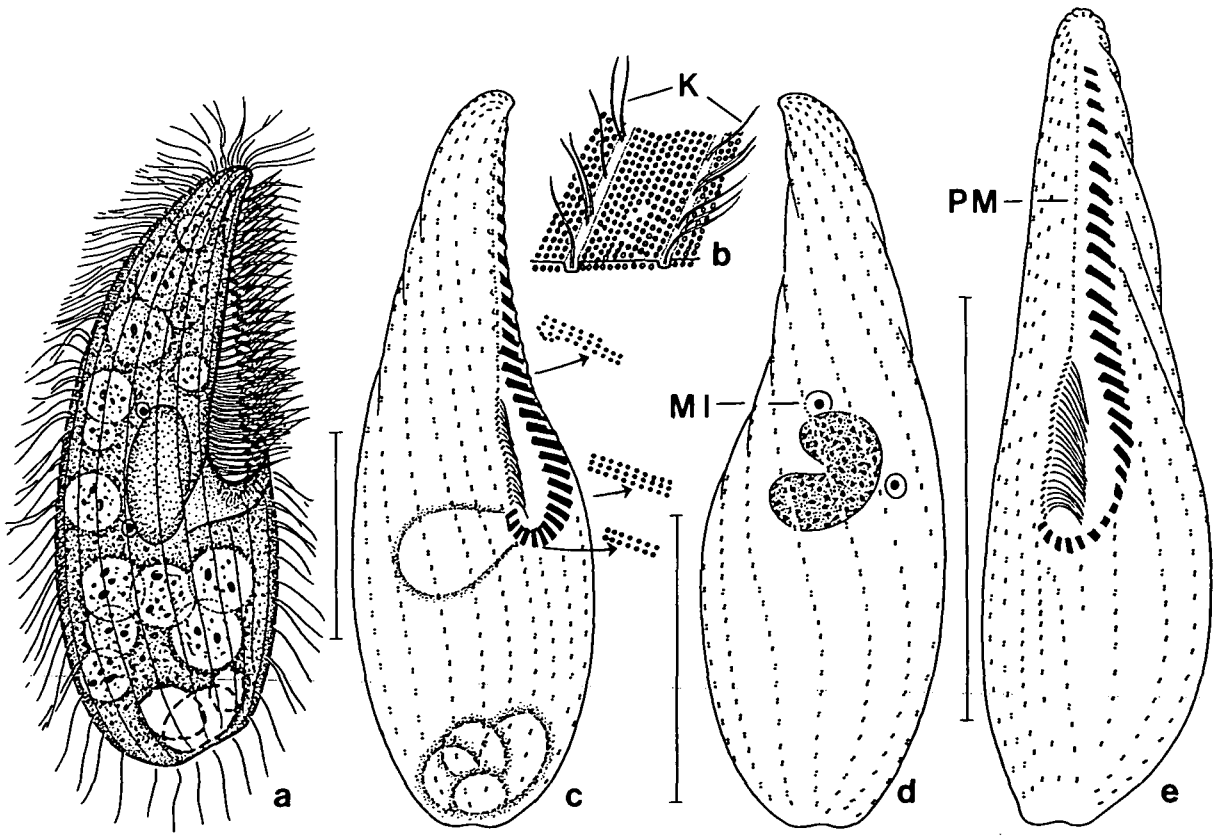

Fig. 189a–e. *Blepharisma bimicronucleatum*, bluish variant from life (a, b) and after protargol impregnation (c–e). **a:** Right side view of a representative specimen with an ellipsoidal macronucleus and many food vacuoles with loose content. **b:** Surface view showing rows of bluish cortical granules between the kineties. **c, d:** Infraciliature of right and left side of a specimen with reniform macronucleus. Note different fine structure of adoral membranelles in certain regions of the zone. **e:** Infraciliature of ventral side. The paroral membrane consists of two portions: in the anterior two thirds it is composed of widely spaced, longitudinally orientated dikinetids, while the posterior third consists of closely spaced, zigzagging basal bodies associated with distinct fibres. K – somatic kineties, MI – micronucleus, PM – paroral membrane. Scale bars 30 µm.

It is still doubtful whether the bluish blepharismas described in the literature are valid species or variants of red ones. In any case, none of the blue or grey-blue species matches our population better than *B. bimicronucleatum*: *B. coeruleum* GAJEVSKAJA, 1927 is blue to grey-blue and has symbiotic green algae; *B. violaceae* TUCOLESCO, 1962 is violet to red-violet, pointed at both ends, 200 µm long, and has only 10 ciliary rows; *B. falcatum* GELEI, 1954 is dirty grey in colour and has 45 ciliary rows and 60 adoral membranelles; and *B. lentis* GELEI, 1954 is grey-blue and has 60–70 ciliary rows and 100 adoral membranelles. HIRSHFIELD et al. (1973) mention a bluish-red to blue "*B. lateritium* v. *steini* KAHL, 1932" in their review. We were unable to locate this variety in the literature cited by HIRSHFIELD et al. (1973).

Generally, *Blepharisma* species are not easily identified, and the genus is in urgent need of a solid revision. Doubtlessly, there are quite a lot of distinct species in limnetic, marine, and terrestrial habitats. But many of the "old species" lack sufficient details and need redescription.

Table 167. Morphometric data on the bluish (upper line) and pink (lower line; from FOISSNER 1989) variety of *Blepharisma bimicronucleatum*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	75.5	77.0	15.2	4.2	20.1	50.0	98.0	13
	59.3	56.0	9.7	3.1	16.4	49.0	77.0	10
Body, width	27.3	25.0	5.9	1.6	21.6	19.0	35.0	13
	29.4	29.0	3.9	1.2	13.3	25.0	35.0	10
Anterior body end to deepest proximal point of adoral zone of membranelles, distance	41.0	45.0	5.1	1.4	12.6	31.0	46.0	13
	35.9	36.0	3.7	1.2	10.2	31.0	42.0	10
Anterior body end to macronucleus, distance	28.8	28.0	3.7	1.0	12.9	24.0	35.0	13
	17.8	17.0	3.6	1.1	20.3	14.0	24.0	10
Wide of widest adoral membranelle	3.4	3.5	–	–	–	3.0	4.0	13
	3.5	3.2	–	–	–	3.0	4.0	7
Macronucleus, length	18.7	18.0	4.6	1.3	24.5	13.0	28.0	13
	18.7	18.0	3.1	1.0	16.5	14.0	22.0	10
Macronucleus, width	8.2	8.0	1.5	0.4	18.0	6.0	11.0	13
	7.4	7.0	1.1	0.3	14.5	6.0	10.0	10
Micronucleus, largest diameter	1.4	1.4	–	–	–	1.2	1.4	13
	1.4	1.4	–	–	–	1.3	1.6	10
Ciliary rows, postoral number	15.7	16.0	1.2	0.3	7.5	14.0	19.0	13
	19.9	20.0	1.6	0.5	8.0	18.0	23.0	10
Dikinetids in a right side kinety, number	51.5	50.0	12.1	3.4	23.5	37.0	75.0	13
	54.0	53.0	11.3	3.6	20.8	35.0	80.0	10
Adoral membranelles, number	32.8	33.0	2.3	0.6	6.9	28.0	36.0	13
	37.6	38.0	2.1	0.7	5.5	35.0	40.0	10
Macronuclei, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Metopus gibbus KAHL, 1927 (Fig. 190a–s; 404a–o; Table 168)

Neotype material: Neotypified from Corsican population, according to reasons 1, 3, 4, 6 given in chapter 2.4.2. Three populations were studied (see "occurrence and ecology"). They are quite similar, in spite of the large geographical distance, not only in morphology but also in main morphometrics (Table 168). Thus, the improved diagnosis and the redescription summarize all data.

Synonymy: JANKOWSKI (1964b) and ESTEBAN et al. (1995) synonymized *M. gibbus* with *M. striatus* MCMURRICH, 1884. However, this is not justified because, according to the original description and several redescriptions of *M. striatus* (FOISSNER 1980c; FOISSNER et al. 1992, Fig. 88–93 on p. 417; KAHL 1932), both differ significantly in body shape (cp. figures 190a–c with figure 404d), body size (30–55 µm vs. 80–170 µm), location and shape of macronucleus (preoral vs. postoral and reniform vs. globular), cortical granules [small (0.7 × 0.4 µm) vs. rod-shaped forming distinct fringe (Fig. 404d, f); thus MCMURRICH named the organism *striatus*!], ratio of body length to length of caudal cilia (about 1–2:1 vs. about 3–8:1 as estimated from figures in literature cited above), and length of perizonal ciliary stripe (terminating on dorsal side vs. on right body margin as estimated from figures in literature cited above). The species named *M. striatus* by ESTEBAN et al. (1995) is completely different from KAHL's and our *M. gibbus* and thus misidentified because it is distinctly smaller (38–71 µm) than the populations found by MCMURRICH (1884; 80–170 µm), KAHL (1932; 80–120 µm), and FOISSNER (1980c; 80–110 µm). Unfortunately, ESTEBAN et al. (1995) did not provide detailed data about variation and infraciliature.

Improved diagnosis: Size about 40 × 25 µm in vivo. Pyriform due to hemispherical preoral dome and obconical postoral body portion. Macronucleus in preoral dome, reniform. Cortical granules about 0.7 × 0.4 µm, colourless, closely spaced. Five perizonal and usually 13 somatic ciliary rows, of which two to three extend onto preoral dome. About 13 dikinetids with two elongated cilia each produce an equal number of syncilia in anterior portion of dome kinety 1. About 6 ciliated dikinetids form an equal number of distinctly elongated, synciliary caudal cilia. Adoral zone slightly shorter than perizonal ciliary stripe, terminates on ventral side right of midline near posterior third of cell, composed of about 16 membranelles.

Redescription: Size 30–55 × 18–35 µm in vivo, as calculated from measurements of live specimens and values shown in table 168, assuming a shrinkage of 10–20% due to the preparation procedures; average values of populations rather close (30–39 × 18–27 µm). Average length:width ratio (1.5–1.7:1) and ratio of preoral:postoral body portion (1.3–1.8:1) very similar among populations, extreme values, however, rather wide (1.3–1.9:1; 1.0–2.4:1; Table 168). Overall shape pyriform to ellipsoidal, dorsoventrally flattened up to 2:1. Preoral dome conspicuous because occupying about 1/3 of body length in ventral view, projects slightly above ventral and left lateral surface, traverses ventral side almost perpendicularly and merges smoothly into right dorsal surface near posterior third of cell; central dome portion hemispherical, broadly sigmoidal in top view due to curved and slightly bulged dome margin, which forms obtuse angle with ventral surface and merges into anterior left margin of dorsal side (Fig. 190m–o). Postoral body portion slightly obconical to cylindroidal with rear end bluntly pointed to evenly rounded. Macronucleus invariably in anterior body half, usually in preoral dome, reniform, rarely ellipsoidal, about 20–25 × 8 µm in vivo, becomes stouter

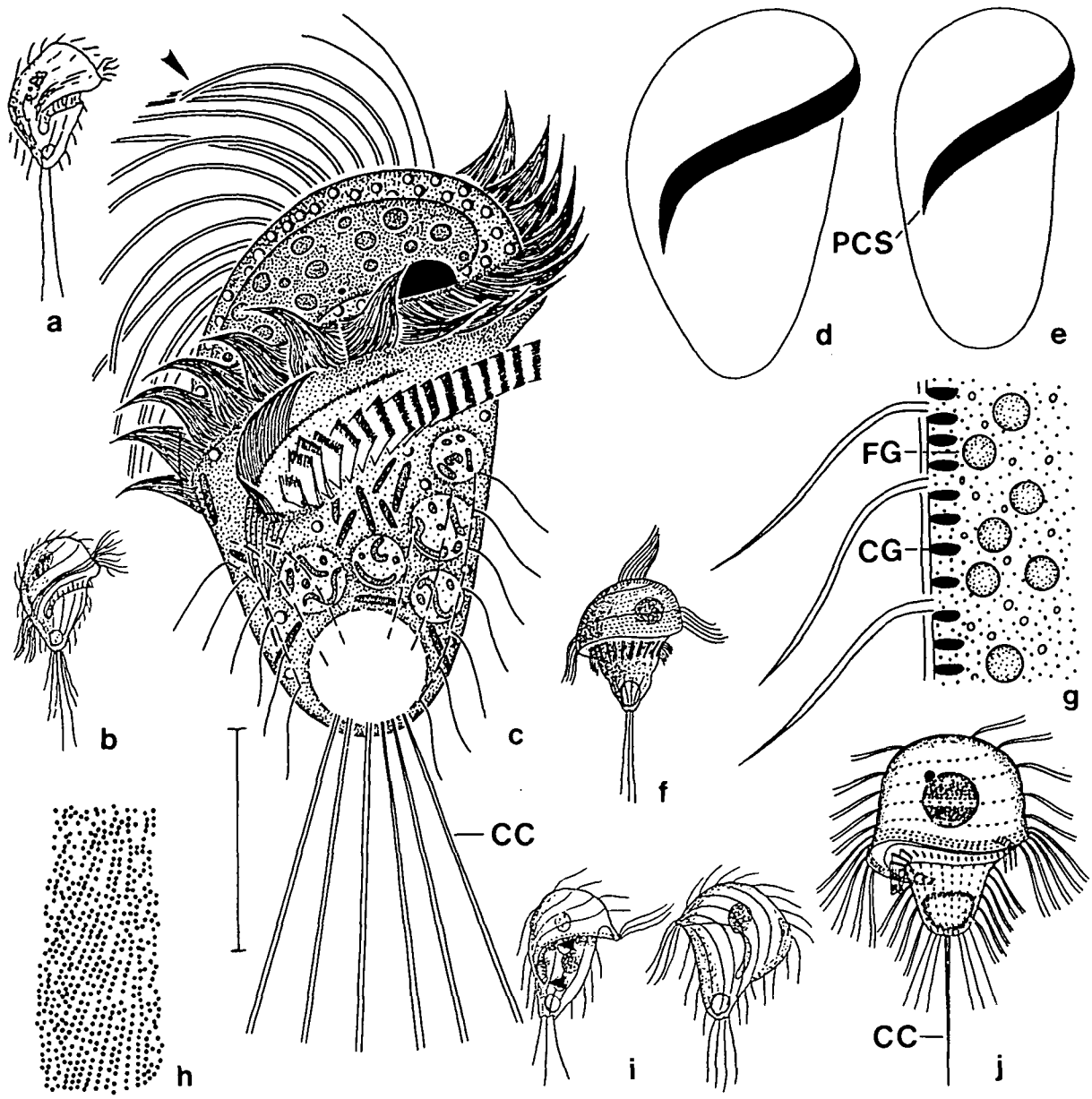

Fig. 190a–j. *Metopus gibbus* (a–e, g, h) and similar species (f, i, j) from life (a–g, i, j) and after silver carbonate impregnation (h). **a:** Ventral view of a specimen from German type population (from KAHL 1927a), length about 30 µm (20–25 µm in KAHL 1927a due to calibration error). **b:** Ventral view of a specimen from another (?) German population, length 30 µm (from KAHL 1932). **c:** Ventral view of a representative specimen from Corsican neotype population showing rod-shaped bacteria in the cytoplasm. The postoral ventral ciliature is sparse, except at the posterior end, where elongated, synciliary and thus rather conspicuous caudal cilia occur. About 13 elongated syncilia occur on the preoral dome (arrowhead). Note that only the proximal third of the paroral is ciliated. **d, e:** Common body shapes of specimens from Brazilian population. **f:** *Cirranter mobilis* (PENARD, 1922) JANKOWSKI, 1964b (syn. *Trochella mobilis*), which is similar to *M. gibbus* in body shape, size (length 40 µm), location of macronucleus, caudal cilia, and syncilia on preoral dome (from KAHL, 1932); it lacks, however, other somatic ciliature and thus belongs to the armophorids. **g, h:** Optical section and surface view of cell periphery showing lipid droplets about 1 µm across and highly refractive, colourless cortical granules with a size of 0.5–1 × 0.4 µm. **i:** *Metopus fastigatus* KAHL, 1927a (length 50 µm) differs from *M. gibbus* in that the adoral zone (delimited by arrows) is much shorter than the perizonal stripe and composed of distinctly fewer membranelles (7–8 vs. 13–19). **j:** *Brachonella caenomorphoides* FOISSNER, 1980c (length 30–40 µm) possesses, like *M. gibbus*, synciliary caudal cilia. CC – synciliary caudal cilia, CG – cortical granules, FG – fat globules, PCS – perizonal ciliary stripe. Scale bar 20 µm.

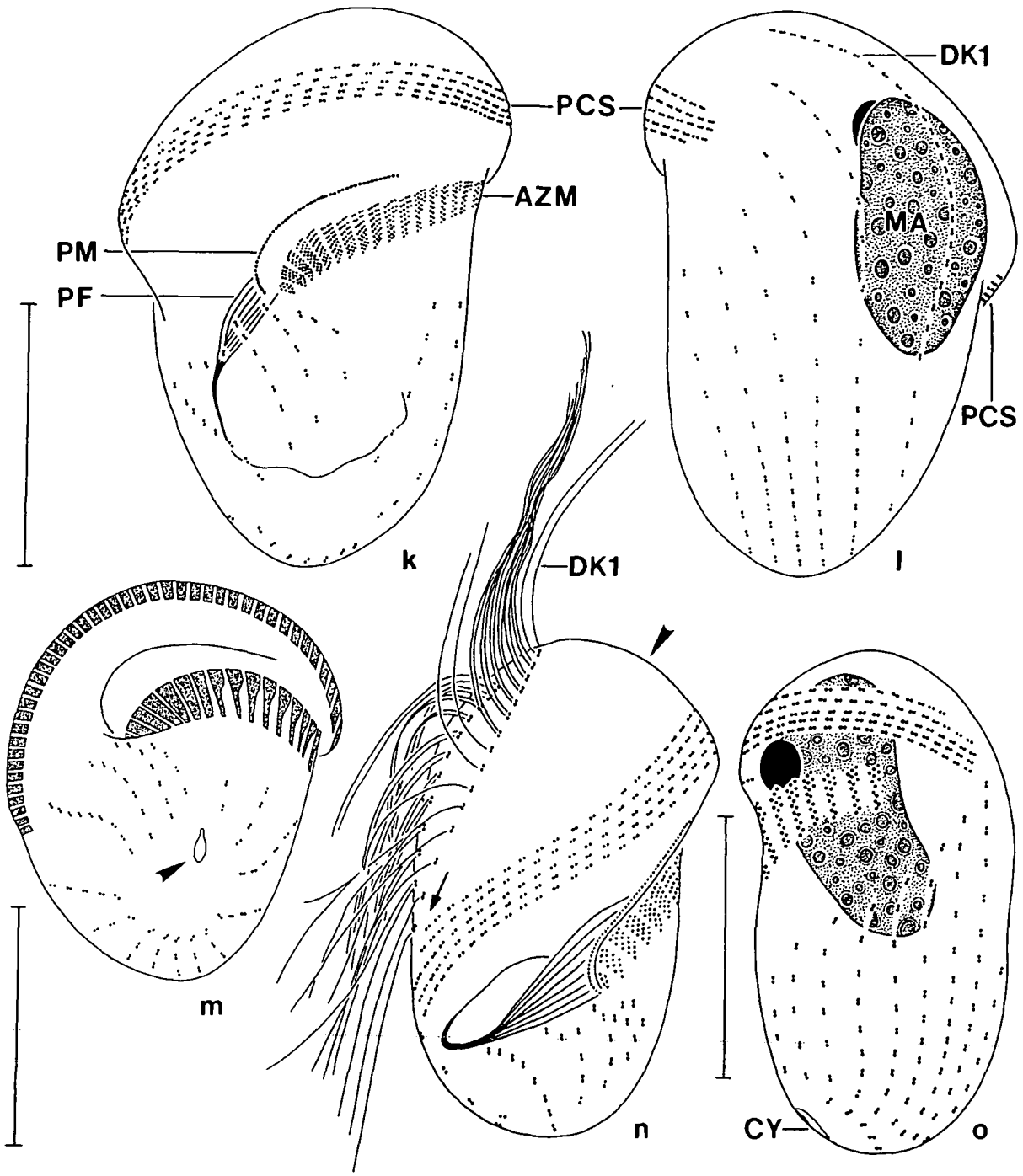

Fig. 190k–o. *Metopus gibbus*, infraciliature after protargol impregnation. **k, l:** Ventral and dorsal view of a specimen with a short perizonal stripe from Corsican neotype population. **m:** Oblique posterior polar view of a Namibian specimen showing the subterminal, blank circular area containing the cytopyge (arrowhead). **n, o:** Right and left side of a Namibian specimen showing cilia of dome (dorsal) kineties. Note glabrous ventral dome portion (arrowhead) due to the dorsally situated dome kinety 1. In this cell, the perizonal stripe extends to posterior body third, as is usual for this species and most Corsican specimens (Table 168). Arrow marks posterior end of perizonal ciliary rows 1 and 2. AZM – adoral zone of membranelles, CY – cytopyge, DK1 – dome (dorsal) kinety 1, MA – macronucleus, PCS – perizonal ciliary stripe, PF – pharyngeal fibres, PM – paroral membrane. Scale bars 20 μm.

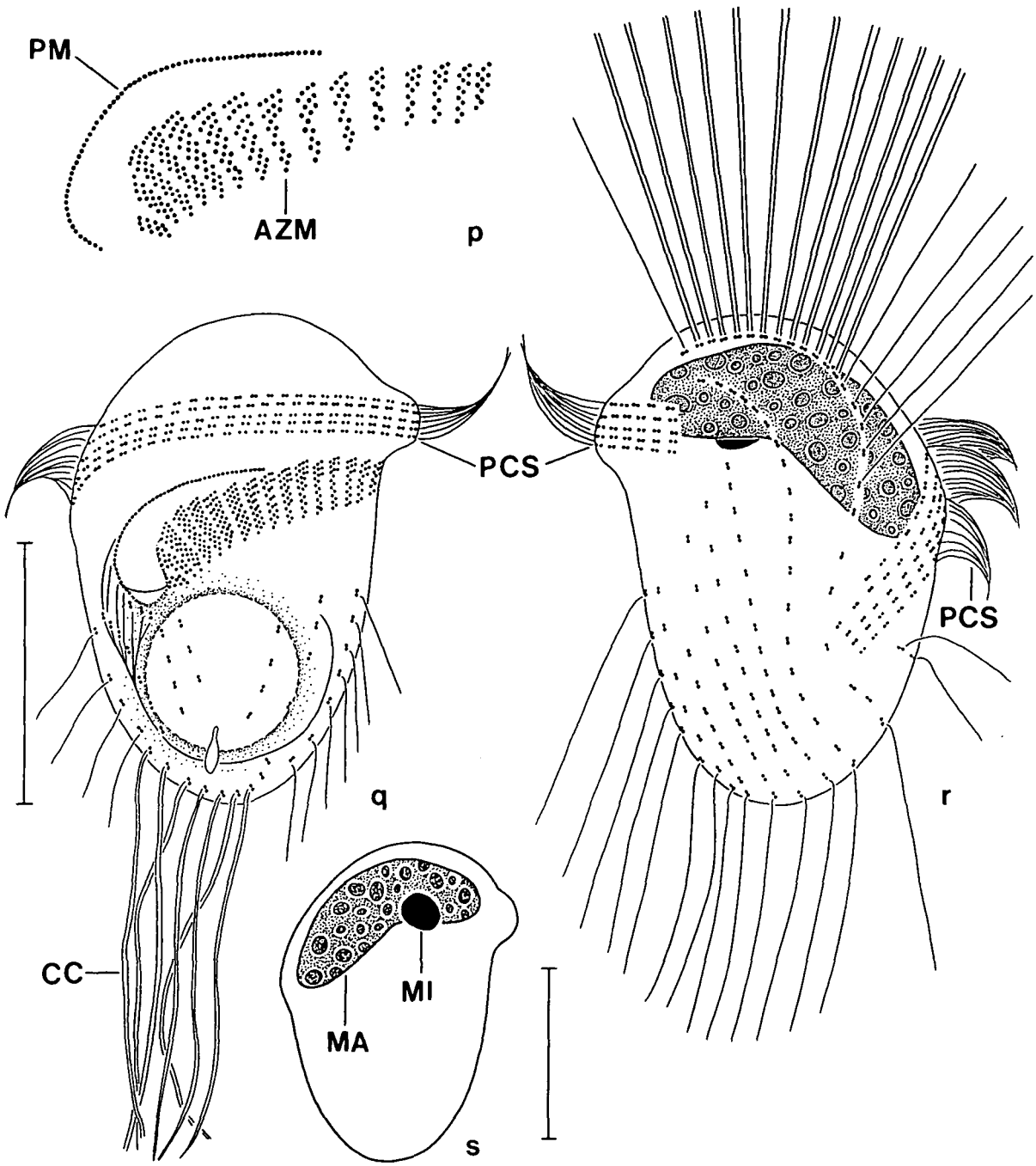

Fig. 190p–s. *Metopus gibbus*, infraciliature and nuclear apparatus of Namibian specimens after protargol impregnation. **p:** Adoral zone and paroral membrane. Membranelle structure depends on zone region: one buccal membranelle composed of three fairly short rows of basal bodies; membranelles of mid-ventral portion consist of four rows of basal bodies producing short, curved kineties (cp. figure 404n); membranelles at left body margin composed of two long rows of zigzagging basal bodies, to which a short row is attached anteriorly. **q–s:** Ventral and dorsal view and nuclear apparatus of same specimen. The last dikinetid of each dorsal kinety has a synciliary caudal cilium on ventral side; the dikinetids of the anterior portion of dome kinety 1 are also synciliar. Note that somatic cilia are distinctly shorter ventrally than dorsally. The macronucleus is in the preoral dome with the micronucleus at its ventral anterior end. AZM – adoral zone of membranelles, CC – caudal cilia, MA – macronucleus, MI – micronucleus, PCS – perizonal ciliary stripe, PM – paroral membrane. Scale bars 20 µm.

(shrinks) under cover glass pressure and in prepared cells; contains numerous nucleoli and is frequently infested by bacteria in Brazilian specimens (Fig. 404e). Micronucleus usually near or attached to ventral anterior end of macronucleus, about 6 × 4 µm in vivo. Cytopyge subterminal on ventral side, slit-like (Fig. 190m, q), likely also serving as discharge device for the contractile vacuole because no excretory pore could be found. Cortical granules, possibly mucocysts, about 0.5–1 × 0.4 µm in vivo, colourless but highly refractive, orientated perpendicularly to cell surface and closely spaced in about 10–20 rows between each two kineties (Fig. 190h; 404a–c, o); stain reddish with methyl green-pyronin and black with silver carbonate, but are not extruded. Cytoplasm colourless to slightly yellowish, contains lipid droplets about 1 µm across mainly in preoral dome and numerous, about 5 × 0.5 µm-sized, rod-shaped bacteria (Fig. 404k–m); no specific granule accumulation in preoral dome. Food vacuoles about 5–10 µm across, contain residues of bacteria and their spores. Swims rather rapidly and slightly swaying.

Somatic ciliature composed of dikinetids and complex due to the occurrence of dikinetids with packed cilia, so-called syncilia (CORLISS 1979, KAHL 1932) or "cirri" (JANKOWSKI 1964b), whose proximal portion is slightly thickened in protargol preparations (Fig. 404 l): ventral cilia about 8 µm long, originate from posterior basal body of dikinetids; perizonal stripe composed of ciliated dikinetids with about 10 µm long cilia; lateral and dorsal cilia up to 20 µm long, most originate from posterior basal body, except in anterior and posterior region, where ciliated dikinetids occur, namely, 10–16 ($\bar{x}$ = 13, n = 11) about 25 µm long syncilia in anterior region of dome kinety 1[31] (except for 1–2 isolated cilia at the anterior end), ordinary pairs at anterior end of dome kineties 2 and 3, and 30–35 µm long synciliary caudal cilia at posterior end of 5–7 dorsal kineties (Fig. 190c, n, q, r; 404c, h, l, m). Ciliary rows meridionally arranged, except for distinctly curved postcytostomial kineties and some scattered dikinetids underneath buccal vertex; ventrally slightly more widely spaced than dorsally; dikinetids orientated parallel or slightly oblique to kinety axis, except for last, distinctly inclined caudal cilia bearing dorsal dikinetids (Fig. 190k, m, n; 404k). Post-cytostomial and ventrolateral kineties separated by rather broad glabrous stripe, distinctly apart from adoral zone of membranelles, slightly shortened posteriorly to leave blank a small, roughly circular excretion area containing the opening for the cytopyge and contractile vacuole (Fig. 190k, m, q; 404a, c). Dorsal kineties decrease in distance and become shortened in preoral dome area from right to left, while slightly elongated posteriorly and thus extending across pole to blank excretion area; two to three dorsal kineties extend onto preoral dome, rightmost kinety (dome kinety 1) widely separate from perizonal ciliary stripe, compared to well-studied congeners, ventral dome area thus glabrous (Fig. 190k–o, q, r; 404h, i). Perizonal ciliary stripe commences at left margin of dorsal side, follows curvature of bulged ventral dome margin and terminates on right margin of dorsal side in last third of cell (Table 168); about 4 µm wide, composed of five very closely spaced kineties[32], of which kineties 4 and 5 are often slightly shortened anteriorly and posteriorly and slightly apart from and more widely spaced than kineties 1–3. Perizonal dikinetids of rows 1–3 form 38–50 short, straight ("false") kineties usually slightly staggered from dikinetids of kineties 4 and 5.

Adoral zone of membranelles slightly sigmoidal, extends in flat, broad corner formed by preoral dome and ventral surface, commences at left side and extends obliquely to right body

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[31] numbered from anterior to posterior

[32] numbered from ventrally to dorsally

margin, performs slight clockwise rotation on plunging into very shallow buccal cavity slightly below mid-body. Membranelles with about 5 µm long cilia, bases up to 5 µm long and cuneate, structure depends on zone region (Fig. 190p; 404n): one buccal membranelle composed of three fairly short rows of basal bodies; membranelles of mid-ventral portion consist of four rows of basal bodies producing short, curved kineties; membranelles at left body margin composed of two long rows of zigzagging basal bodies, to which a short row is attached at right anterior end. Paroral membrane in corner formed by preoral dome and ventral surface, commences near midline of cell and curves to proximal end of buccal vertex, composed of basal bodies in single line, bears 10 µm long cilia only in proximal third of row. Pharyngeal fibres extend postero-laterally and curve back almost to oral cavity as a long, narrow funnel.

Table 168. Morphometric data on three populations of *Metopus gibbus*: MB – Brazil, MC – Corsica, MN – Namibia.

Characteristics [a]	Pop [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	MB	34.8	35.0	4.0	0.9	11.4	29.0	44.0	19
	MC	38.4	39.0	4.8	1.4	12.4	28.0	45.0	11
	MN	30.9	30.0	3.0	0.8	9.8	26.0	38.0	15
Body, total width [b]	MB	22.1	23.0	2.9	0.7	13.1	16.0	28.0	19
	MC	25.8	27.0	3.3	1.0	12.8	18.0	31.0	11
	MN	18.4	18.0	1.6	0.4	8.7	16.0	21.0	15
Body length:total width, ratio [b]	MB	1.6	1.6	0.1	0.0	8.3	1.4	1.8	19
	MC	1.5	1.5	0.1	0.1	7.9	1.3	1.7	11
	MN	1.7	1.6	0.1	0.1	8.4	1.5	1.9	15
Body, preoral:postoral portion, ratio	MB	1.8	1.8	0.3	0.1	19.0	1.3	2.4	13
	MC	1.3	1.2	0.3	0.1	21.3	1.0	1.8	11
	MN	1.4	1.3	0.2	0.1	13.9	1.1	1.8	15
Paroral membrane, length [c, d]	MC	13.5	14.0	1.0	0.3	7.7	12.0	15.0	11
	MN	17.3	18.0	1.6	0.4	9.4	14.0	19.0	15
Anterior body end to posterior end of perizonal stripe, distance	MB	23.0	23.5	1.7	0.7	7.3	21.0	25.0	6
	MC	22.6	23.0	2.0	0.6	8.6	18.0	25.0	12
	MN	22.5	23.0	1.8	0.5	7.9	19.0	26.0	15
Anterior body end to proximal end of adoral zone of membranelles, distance	MB	22.5	24.0	3.5	1.0	15.6	18.0	30.0	13
	MC	21.4	21.0	2.3	0.7	10.7	18.0	26.0	11
	MN	18.8	19.0	1.6	0.4	8.3	16.0	21.0	15
Distance anterior body end to end of perizonal stripe:body length, ratio in %	MB	69.1	67.7	4.3	1.7	6.2	65.7	77.4	6
	MC	63.4	63.9	7.4	2.1	11.6	50.0	77.4	12
	MN	69.0	69.7	5.2	1.4	7.6	60.0	77.4	15
Distance anterior body end to end of adoral zone of membranelles: body length, ratio in %	MB	63.9	64.1	4.5	1.2	7.0	55.6	70.6	13
	MC	56.0	55.3	5.1	1.5	9.1	50.0	64.3	11
	MN	57.7	55.9	3.2	0.8	5.6	53.3	64.3	15
Macronucleus, length	MB	17.5	18.0	2.5	0.7	14.5	13.0	21.0	13
	MC	18.6	18.0	2.4	0.7	12.8	14.0	22.0	11
	MN	18.4	18.0	2.1	0.6	11.6	16.0	25.0	15
Macronucleus, width	MB	7.1	6.0	1.8	0.5	24.8	5.0	11.0	13
	MC	8.3	8.0	1.8	0.5	21.7	5.0	10.0	11
	MN	6.7	6.0	1.1	0.3	16.3	5.0	8.0	15

(continued)

Characteristics [a]	Pop [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Anterior body end to posterior end of macronucleus, distance	MB	19.6	19.0	4.2	1.0	21.4	13.0	28.0	17
	MC	21.4	22.0	4.1	1.2	19.0	16.0	29.0	11
	MN	15.7	16.0	1.5	0.4	9.6	13.0	18.0	15
Micronucleus, length	MB	4.6	5.0	–	–	–	3.0	5.0	13
	MC	4.0	4.0	–	–	–	3.0	5.0	11
	MN	3.3	3.0	–	–	–	3.0	4.0	15
Micronucleus, width	MB	4.3	5.0	–	–	–	3.0	5.0	13
	MC	3.5	3.0	–	–	–	3.0	4.0	11
	MN	3.1	3.0	–	–	–	3.0	4.0	15
Macronucleus, number	MB	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
	MC	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
	MN	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Micronucleus, number	MB	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13
	MC	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
	MN	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Somatic ciliary rows, number [c]	MC	12.7	13.0	0.7	0.2	5.1	12.0	14.0	11
	MN	14.5	14.0	–	–	–	14.0	15.0	15
Caudal cilia, number [c]	MC	12.6	12.0	2.0	0.3	7.7	12.0	14.0	10
	MN	12.3	12.0	1.0	0.3	8.4	10.0	14.0	15
Adoral membranelles, number	MB	15.8	15.0	1.8	0.7	11.6	13.0	19.0	8
	MC	16.7	16.0	1.3	0.4	8.0	15.0	19.0	10
	MN	17.3	17.0	0.7	0.2	4.1	16.0	18.0	15
Perizonal ciliary rows, number	MB	5.0	5.0	0.0	0.0	0.0	5.0	5.0	19
	MC	5.0	5.0	0.0	0.0	0.0	5.0	5.0	11
	MN	5.0	5.0	0.0	0.0	0.0	5.0	5.0	15
Perizonal ciliary rows, number of "false" kineties [c, e]	MC	45.6	45.0	3.4	1.5	7.4	42.0	50.0	5
	MN	43.7	44.0	2.8	0.7	6.5	38.0	47.0	15

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, Pop – population, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Total width = including projecting anterior portion of preoral dome. Cells were not selected for a particular orientation.

[c] Specimens of Brazilian population were too poorly impregnated to estimate this feature.

[d] Measured as chord of curve formed by the organelle.

[e] See description of species.

Occurrence and ecology: *Metopus gibbus* was discovered in a sapropelic pond in northern Germany (KAHL 1927a). We found *M. gibbus* in soil from Corsica and Namibia, and in material from a termite hill in Brazil, indicating that it is cosmopolitan. Corsica (neotype population, collected by Dr. Bruno GANNER, Salzburg, in September 1985): bank of a stream flowing into a reservoir near the village of Ajaccio (41°N 08°E), soil sandy with grass remnants, pH 4.1; Namibia: sites 4, 30, 49, 66, 73; Brazil: remnants of a termite hill from the Amazon floodplain near Manaus (04°S 60°W; for details see MARTIUS 1994, who provided the sample in 1995).

Comparison with original description and similar species: Our populations match the original description (KAHL 1927a), which KAHL (1932) later improved, in size, shape, location of nuclear apparatus, caudal cilia forming syncilia (definitely mentioned in KAHL 1932), and a perizonal ciliary stripe commencing and terminating dorsally (as estimated from figure 190b). However, there are some differences, namely the frontal syncilia and the unciliated ventral dome portion, which KAHL (1927a, 1932) did not describe. Possibly, KAHL overlooked these features because he found only few and very fragile specimens, two attributes which were not obvious in our populations. Furthermore, the glabrous ventral dome portion is difficult to recognize without silver impregnation; and even the syncilia at the anterior end of dome kinety 1 rarely appear as conspicuously as shown in our illustrations because they easily separate and loose metachrony under cover glass pressure.

Metopus fastigatus KAHL, 1927a is the only congener with a similar size (40–50 µm), body shape (broadly pyriform), ratio of body length to length of caudal cilia (1–2:1, as estimated from Fig. 190i), and location of the macronucleus. However, the species differ significantly in the number of adoral membranelles (7–8 vs. 13–19), and especially, in that the adoral zone of membranelles is much shorter than the perizonal stripe in *M. fastigatus*, which KAHL (1927a, 1932) thus classified in a distinct group. Accordingly, synonymization of *M. fastigatus* with *M. striatus*, as performed by ESTEBAN et al. (1995), must be rejected; in fact, it is curious because ESTEBAN et al. (1995) found 45 membranelles in their *M. striatus*, while KAHL (1927a, 1932) definitely mentioned only 7–8 in *M. fastigatus*. KAHL, who was a very experienced observer, certainly is above such an error, especially since he found three species with this peculiar feature.

The syncilia on the anterior and posterior pole area, the blank ventral dome portion, the location of the macronucleus, and the pyriform body shape give *M. gibbus* a *Cirranter*-like appearance (cp. figure 190c with figure 190f; DECAMP & WARREN 1997, KAHL 1932, PENARD 1922). *Cirranter* belongs to the armophorids, according to the reduced somatic ciliature, the structure of the perizonal ciliary stripe, and the occurrence of syncilia (DECAMP & WARREN 1997, FERNANDEZ-GALIANO & FERNANDEZ-LEBORANS 1980, JANKOWSKI 1964a, b, SOLA et al. 1990, 1992). Our data show that syncilia occur in a typical *Metopus* species, and FOISSNER (1980c) described *Brachonella caenomorphoides*, which possesses a cirrus-like bundle of caudal cilia (Fig. 190j). Thus, syncilia are not unique to the armophorids, indicating that caenomorphids and metopids could belong to the same group. However, ontogenesis is distinctly different, suggesting that both metopids and armophorids should have the same (ordinal) rank (FOISSNER & AGATHA 1999).

Metopus minor KAHL, 1927 (Fig. 191a–d, g–k; 405a–f; Table 169)

1927 *Metopus setosus* var. *minor* KAHL, Arch. Protistenk., 57: 145.

1932 *Metopus setosus* var. *minor* KAHL, 1927 – KAHL, Tierw. Dtl., 25: 420 (revision).

1980 *Metopus minor* KAHL, 1927 – FOISSNER, Ber. Nat.-Med. Ver. Salzburg, 5: 79 (redescription from life and elevation to species status).

Material: This species is difficult to study because the cortical granules impregnate and hide the infraciliature. Thus, observations from three populations are combined and no

neotype is fixed because the preparations are too mediocre. The first population, from which protargol-impregnated voucher slides have been deposited, is from Iceland, Landmannarlaugar, where it occurred in soil and litter from an acidic (pH 4.9) moorland grown with *Carex* spp., *Sphagnum* and other mosses, and some shrubs, such as *Eriophorum scheuchzeri* and *E. angustifolium* (sample kindly provided by Dr. Wolfgang VETTERS, Salzburg University, 1985). The second population is from Namibian site (66), where excellent silver carbonate impregnations were obtained (Fig. 405a–f). The third population is a single, excellently impregnated specimen from Kenya, Africa (Fig. 191g, h). Unfortunately, we did not properly designate the slide and could not find it again.

Description: The in vivo observations are from the Iceland specimens, which are highly similar to those illustrated by KAHL and FOISSNER (Fig. 191a–d). Thus only a schematic figure is provided (Fig. 191i). Size 30–40 × 12–15 µm in vivo, length:width ratio 2.2–3.3:1, on average 2.5:1 in protargol preparations; inconspicuously flattened dorsoventrally. Oblong with distinctly projecting preoral dome providing cells with typical *Metopus* shape; ratio of preoral:postoral body portion 2.3:1 on average (Fig. 191i, j, k; Table 169). Macronucleus usually at level of adoral zone of membranelles, globular to slightly ellipsoidal; nucleoli conspicuous, globular. Micronucleus 3–4 µm across and thus large compared to size of cell, usually near anterior end of macronucleus. Contractile vacuole in posterior body end. Cortex flexible, studded with rows of minute (< 0.5 µm) granules hardly recognizable in vivo, but staining red with methyl green-pyronin and dark with protargol (Fig. 191k; 405f). Cytoplasm colourless, without granule accumulation in preoral dome and bacterial symbionts; the latter occur, however, in the Namibian specimens (Fig. 405a, b). Food vacuoles about 5 µm across, contain many refractive granules about 1 µm across, likely bacterial spores. Swims rather rapidly by rotation about main body axis.

Somatic and oral infraciliature studied in the three populations mentioned above and basically as in congeners (→ *M. gibbus* and FOISSNER & AGATHA 1999). Thus, only some remarkable details will be mentioned (Fig. 191g, h, j, k; 405a–e): (i) ordinary somatic cilia about 10 µm long in vivo, caudal cilia 30–50 µm long and thus very conspicuous; (ii) paired cilia occur mainly on ventral half of preoral dome, while the other dikinetids have only the posterior basal body ciliated; (iii) all populations have about 8–10 somatic kineties plus 5 perizonal ciliary rows forming 12–15 short, "false" kineties; (iv) the adoral zone of membranelles and the paroral membrane appear more conspicuous in vivo than protargol preparations, likely due to the strongly curved and overhanging preoral dome; (v) adoral zone composed of only 6–9 membranelles in all populations.

Occurrence and ecology: KAHL (1927a) discovered *M. minor* in sapropelic ponds near Hamburg, Germany. FOISSNER (1980c) recorded it from a similar habitat in the Austrian Central Alps at about 1800 m above sea-level. The sites of the populations investigated in the present study are mentioned in the Material section above. Two of them are semiedaphic habitats, viz., moorland and mud from rock pools. This indicates that *M. minor* prefers limnetic environments, specifically the microaerobic or anaerobic sapropel. We found *M. minor* also in Venezuela, indicating a cosmopolitan distribution.

Comparison with previous descriptions: *Metopus minor* is a very distinct species due to the small body size and long caudal cilia. These features, as well as similar numbers of ciliary rows and adoral membranelles, are present in all populations investigated in the present study and by KAHL (1927a, 1932) and FOISSNER (1980c); thus conspecificity is

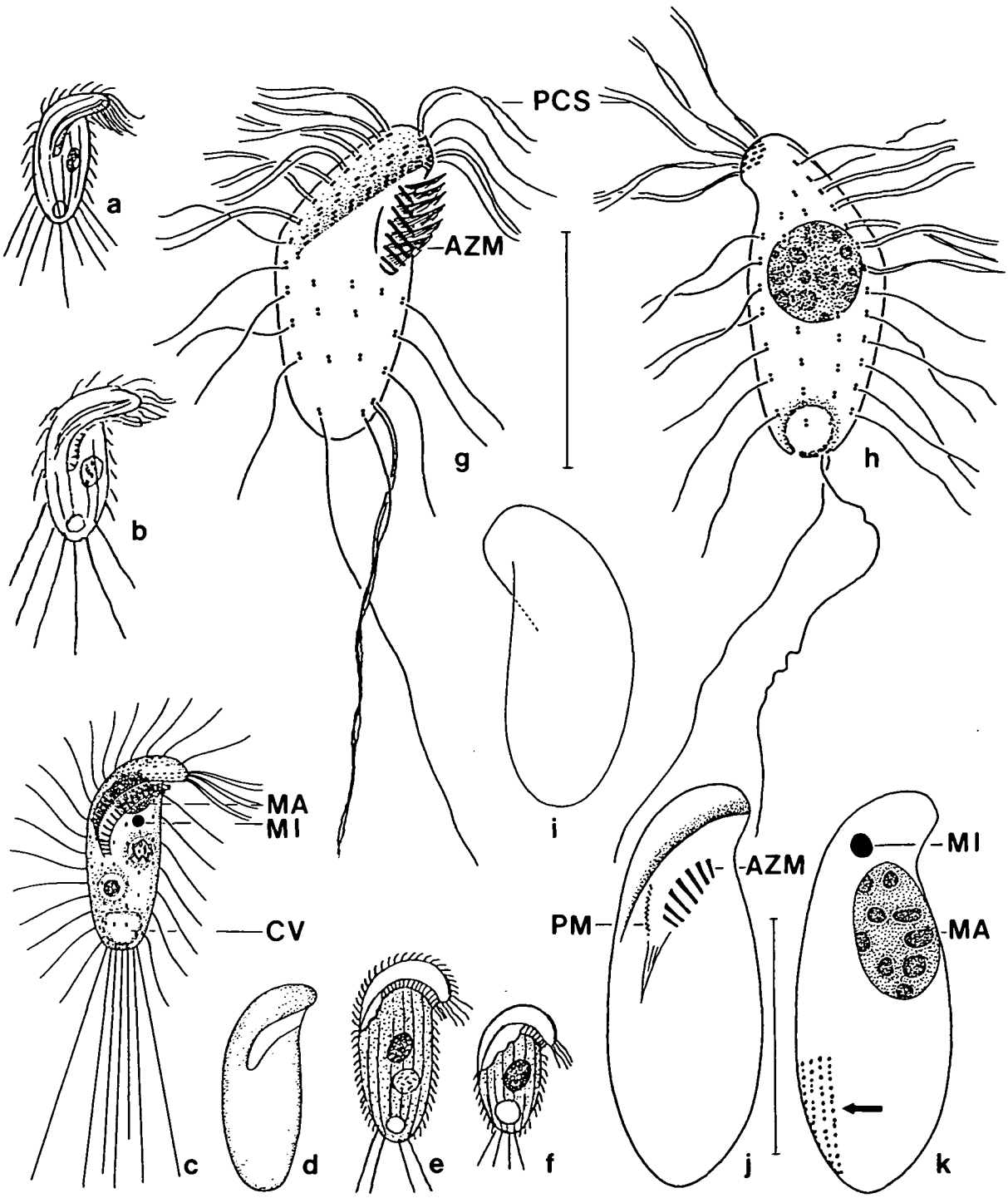


Fig. 191a–k. *Metopus minor* and its supposed synonym, *M. recurvatus* (e, f) from life (a–f, i) and after protargol impregnation (g, h, j, k). **a, b:** Original figures, length about 40 µm (from KAHL 1927a, 1932). **c, d:** Austrian specimens, 30–35 µm (from FOISSNER 1980c). Adoral zone of membranelles likely figured too large. **e, f:** Ventral view of *M. recurvatus* (length 40 µm) and *M. recurvatus* var. *pusillus* (length 25 µm), synonyms of *M. minor* (from VUXANOVICI 1962b). **g, h:** Ventrolateral and dorsolateral view of a Kenyan specimen with excellently impregnated infraciliature. **i:** Dorsal view of a specimens from Iceland. **j, k:** Oral infraciliature and nuclear apparatus of a specimen from Iceland, in which the somatic ciliary pattern is hidden by cortical granules (arrow). AZM – adoral zone of membranelles, CV – contractile vacuole, MA – macronucleus, MI – micronucleus, PCS – perizonal ciliary stripe, PM – paroral membrane. Scale bars 20 µm.

beyond reasonable doubt. KAHL (1927a, 1932) already mentioned the stability of this "variety", which is emphasized by our investigations and supports the species status given by FOISSNER (1980c).

FOISSNER (1980c) suggested *M. recurvatus* and *M. recurvatus* var. *pusillus*, both rather superficially described by VUXANOVICI (1962b), as junior synonyms of *M. minor* (Fig. 191e, f). ESTEBAN et al. (1995) obviously synonymize *M. setifer* KAHL, 1932 with *M. setosus* and *M. setosus* var. *minor*. We disagree, at least for the "variety" *minor*, because *M. setifer* is distinctly larger, viz. 60–90 µm long and has a much longer adoral zone of membranelles.

Table 169. Morphometric data on *Metopus minor*, Iceland population.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	30.6	31.0	2.2	0.7	7.1	28.0	35.0	10
Body, width	12.5	13.0	0.7	0.2	5.7	11.0	13.0	10
Body length:width, ratio	2.5	2.4	0.3	0.1	10.8	2.2	3.2	10
Anterior body end to proximal end of adoral zone of membranelles, distance	13.5	13.5	1.2	0.4	8.7	12.0	16.0	10
Body length: distance anterior body end to proximal end of adoral zone, ratio	2.3	2.3	0.2	0.1	9.5	1.9	2.6	10
Macronucleus, length	10.5	10.0	1.4	0.4	12.9	8.0	13.0	10
Macronucleus, width	8.4	8.5	1.0	0.3	11.5	7.0	10.0	10
Macronuclei, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10
Micronucleus, maximum diameter	3.0	3.0	–	–	–	2.5	3.5	10
Micronuclei, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	10
Adoral membranelles, number	6.3	6.0	–	–	–	6.0	7.0	10

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Metopus palaeformis KAHL, 1927 (Fig. 192a–i, m–o; 405g, h; Table 170)

1927 *Metopus palaeformis* KAHL, Arch. Protistenk., 57: 132.

1932 *Metopus palaeformis* KAHL, 1927 – KAHL, Tierwelt Dtl., 25: 410 (revision and description of the formae *ovalis* and *attenuata*).

1995 *Metopus palaeformis* KAHL, 1927 – ESTEBAN, FENCHEL & FINLAY, Arch. Protistenk., 146: 155 (redescription from life; no silver impregnation, no detailed morphometrics).

Neotype material: Neotypified from Madagascan population, according to reasons 1, 3, 4, 6 given in chapter 2.4.2. Site description, see → *Bryophyllum penardi*.

Improved diagnosis: Size about 100 × 25 µm. Elongate ellipsoidal, hardly spiralized, preoral dome inconspicuous because only slightly curved and flat. Macronucleus postoral in

middle body third, oblong. Cortical granules in loosely spaced rows, minute, strongly refractive. All somatic cilia of similar length, arranged in an average of 18 meridional rows, 5 modified to a perizonal stripe about half as long as adoral zone composed of 20 membranelles on average.

Description of Madagascan neotype population: Size 80–120 × 15–30 µm in vivo, in other populations 70–200 × 8–31 µm (ESTEBAN et al. 1995); length:width ratio 3.7–5.6:1, on average 4.3:1 in vivo and protargol preparations (Table 170). Shape inconspicuous, that is, elongate ellipsoidal and only indistinctly spiralized and flattened, preoral dome comparatively inconspicuous because only slightly curved and flat (Fig. 192a, m, o).

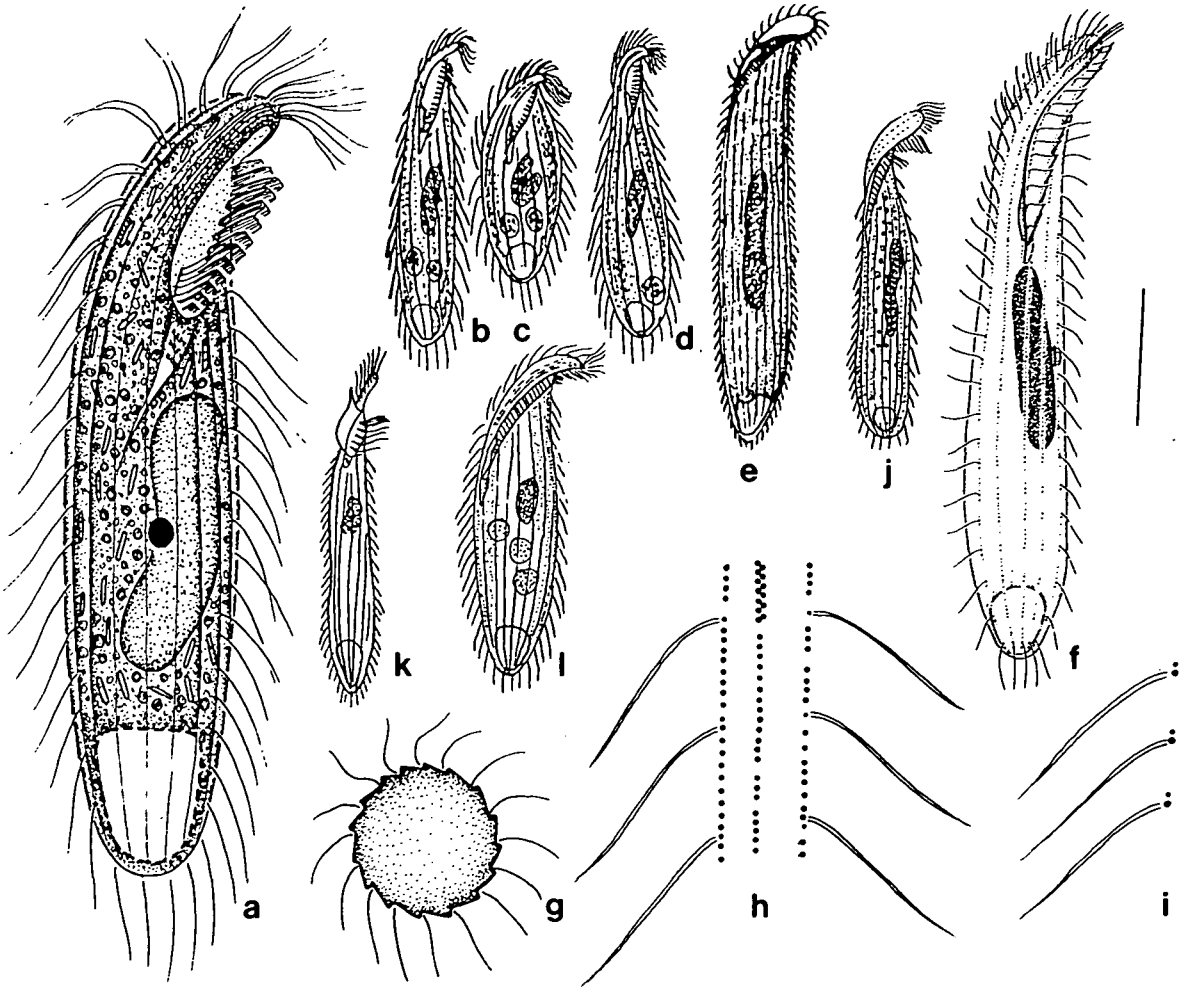


Fig. 192a–l. *Metopus palaeformis*, Madagascan (a, g–i) and other (b–f) populations, and supposed synonyms (j–l) from life (a–h, j–l) and after protargol impregnation (i). **a:** Ventrolateral view of a representative specimen, length 90 µm. Note methanogenic bacterial rods in the cytoplasm. **b–d:** *Metopus palaeformis* forma *typica* (80 µm), forma *ovalis* (70 µm), and forma *attenuatus* (80 µm); from KAHL (1932). **e:** *Metopus palaeformis* f. *typica* (80 µm); from VUXANOVICI (1961b). **f:** *Metopus palaeformis*, bar 20 µm (from ESTEBAN et al. 1995). **g:** Transverse view in mid-body. **h:** Cortical granulation. **i:** Part of a postoral kinety. The anterior, barren basal body is smaller than the posterior, ciliated one. **j:** *Metopus hyalinus*, 130 µm (from KAHL 1932). **k:** *Metopus tenuis*, 110 µm (from KAHL 1932). **l:** *Metopus rostratus*, 100 µm (from KAHL 1932).

Macronucleus postoral in middle third of cell, globular to very oblong (6:1) and more or less distinctly tortuous. Micronucleus attached to macronucleus at varying positions, about 4 µm across in vivo (Fig. 192a, m, o; 405h). Contractile vacuole in posterior body end, excretory pore not recognizable. Cortex distinctly ribbed along ciliary rows (Fig. 192g); cortical granules conspicuous, although colourless and only 0.2–0.3 µm across, because strongly refractive and in distinct, occasionally zigzagging rows within and between kineties (Fig. 192h; 405g). Cytoplasm colourless, packed with granules 1–2 µm across and 3–5 µm long rods,

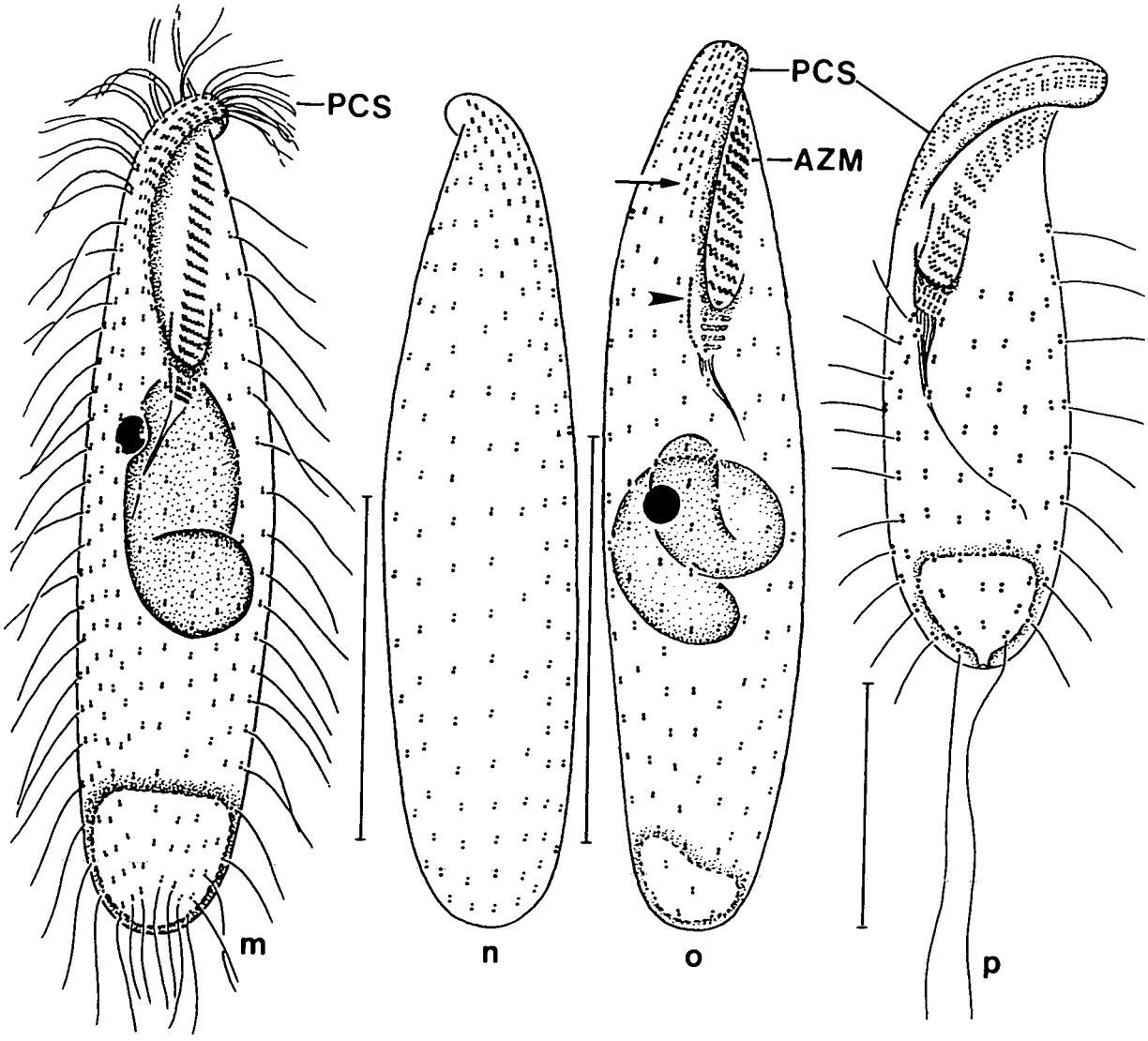


Fig. 192m–o. *Metopus palaeformis*, somatic and oral ciliary pattern of Madagascan specimens after protargol impregnation. **m, n:** Ventral and dorsal view of neotype specimen. **o:** Ventrolateral view of another specimen. Note the short perizonal stripe (posterior end marked by arrow) and the inconspicuous paroral membrane (arrowhead). AZM – adoral zone of membranelles, PCS – perizonal ciliary stripe. Scale bars 30 µm.

Fig. 192p. *Metopus hasei*, ventral somatic and oral ciliary pattern of a Namibian specimen after protargol impregnation (from FOISSNER & AGATHA 1999). Note the long caudal cilia, the main difference to *M. palaeformis*. Scale bar 30 µm.

likely methanogenic bacteria (for details, see ESTEBAN et al. 1995), which intensely impregnate with protargol. Likely feeds on bacteria. Movement inconspicuous.

Cilia about 12 µm long in vivo, no elongated caudal cilia, paired only in dome area, anterior basal body of dikinetids barren and slightly smaller in other regions; arranged in an average of 18 equidistant, almost meridional rows, leaving blank posterior pole centre. Perizonal ciliary stripe of usual structure, short, that is, about half as long as adoral zone of membranelles (Fig. 192a, m–o; Table 170).

Adoral zone inconspicuous because occupying merely one third of body length, only slightly spiralized, and membranellar bases only 4 µm long. Zone fine structure as in *M. hasei* (FOISSNER & AGATHA 1999). Paroral membrane short and inconspicuous.

Table 170. Morphometric data on *Metopus palaeformis*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	81.7	81.0	9.1	2.7	11.1	70.0	100.0	11
Body, width	19.3	20.0	2.8	0.9	14.7	13.0	23.0	11
Body length:width, ratio	4.3	4.4	0.6	0.2	12.9	3.7	5.6	11
Anterior body end to proximal end of adoral zone, distance	27.8	28.0	3.0	0.9	10.9	23.0	35.0	11
Macronucleus, length (spread)	32.6	35.0	–	–	–	17.0	50.0	11
Macronucleus, width	10.3	10.0	2.3	0.7	22.7	6.0	15.0	11
Micronucleus, length	3.6	3.5	–	–	–	3.0	4.0	11
Micronucleus, width	3.1	3.0	–	–	–	3.0	3.5	11
Somatic kineties, number	17.6	18.0	1.4	0.4	7.8	15.0	20.0	11
Adoral membranelles, number	19.9	20.0	2.2	0.7	10.9	17.0	24.0	11

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Occurrence and ecology: *Metopus palaeformis* is a common freshwater ciliate and rare in terrestrial habitats, where *M. hasei* is much more frequent. It is an obligate anaerobe lacking conventional mitochondria, like the congeners (ESTEBAN et. al. 1995). Reliable records are known from Europe (ESTEBAN et. al. 1995, KAHL 1932), Namibia (Table 4), and Madagascar (Fig. 192a).

Identification and comparison with related species: Our observations match the original description (KAHL 1927a, 1932) and add significant data on the infraciliature. Thus, identification is beyond reasonable doubts, and the population can serve as a neotype.

Metopus palaeformis is highly similar to *M. hasei*, as redescribed by FOISSNER & AGATHA (1999), except for the lacking caudal cilia. Indeed, this is the sole reliable difference, especially when the considerable variation both species exhibit is taken into account (ESTEBAN et al. 1995, FOISSNER & AGATHA 1999). A minor difference concerns the preoral

dome, which is more distinctly curved in *M. hasei* than in *M. palaeformis* (Fig. 192m, p).

Metopus palaeformis has been kept in culture and studied ecologically for several years by FINLAY and co-workers (for a brief review, see ESTEBAN et al. 1995). Detailed morphological data were not provided, although ESTEBAN et al. (1995) documented various cytological features and the morphological variation by excellent micrographs. The strong variation was not seen in the specimens from the non-flooded Petri dish culture and seems to be related mainly to starvation. However, KAHL (1932) observed similar variation in nature and distinguished a forma *typica*, *ovalis,* and *attenuatus* (Fig. 192b–c). Based on the data available, ESTEBAN et al. (1995) suggest the following synonymy, with which we largely agree: *M. hyalinus* KAHL, 1927a (Fig. 192j); *M. rostratus* KAHL, 1927a (Fig. 192 l); *M. tenuis* KAHL, 1927a (Fig. 192k; synonymy doubtful in our opinion); and *Tesnospira alba* JANKOWSKI, 1964b (Fig. 192k; synonymy doubtful in our opinion).

Metopus contortus (QUENNERSTEDT, 1867) KAHL, 1932 (Fig. 193a–r; 405i–k; Tables 171, 172)

Material: Namibian site (49), where it occurred two weeks after rewetting the sample.

Identification: *Metopus contortus* has been studied by several authors, although in varying detail (Table 172). While the number of adoral membranelles is fairly similar in the populations investigated, body size and number of ciliary rows are not. These features indicate two groups, one with a size around 100 µm and about 30 ciliary rows, and another with a size near 150 µm and 40–50 ciliary rows. The Namibian specimens and *M. jankowskii* DRAGESCO, 1968 obviously belong to the second group.

Of the redescriptions listed in Table 172, only that of DRAGESCO (1996) is detailed enough to be compared with our data. His specimens match the original description in size, but are more slender, while our specimens match the original description in shape, but are considerably larger. Further, the number of ciliary rows is significantly different ($\bar{x}$ = 48 vs. 31), which causes a rather different general appearance of the populations (Fig. 193i, o). Another difference concerns the caudal cilia, which are 23–50 ($\bar{x}$ = 40 µm) long in our specimens, while only 16–23 µm in those of DRAGESCO. The macronucleus is more anterior in the French than the Namibian specimens (15% vs. 27% distant from anterior body end).

These and the above mentioned differences indicate that *M. contortus* consists of two species or subspecies, as already proposed by KAHL (1932), who distinguished a forma *major* and a forma *pellitus* (Fig. 193d, e). However, data are still too incomplete for a reliable conclusion. Thus, and because our population is from a limnetic habitat, it is not used as a neotype.

Observations on Namibian specimens: The somatic and oral ciliary pattern of the Namibian *M. contortus* is highly similar to that of congeners, for instance, → *M. gibbus* and *M. inversus*, as redescribed by FOISSNER & AGATHA (1999). Thus, the reader is referred to these descriptions, the detailed figures, figure explanations, and morphometrics (Table 171). The following items list some additional observations: (i) Body only indistinctly spiralized and highly variable in size and shape, viz., 107–175 × 40–75 µm and widened or narrowed subterminally in protargol preparations (Fig. 193i, m; 405i); (ii) Preoral dome thinner

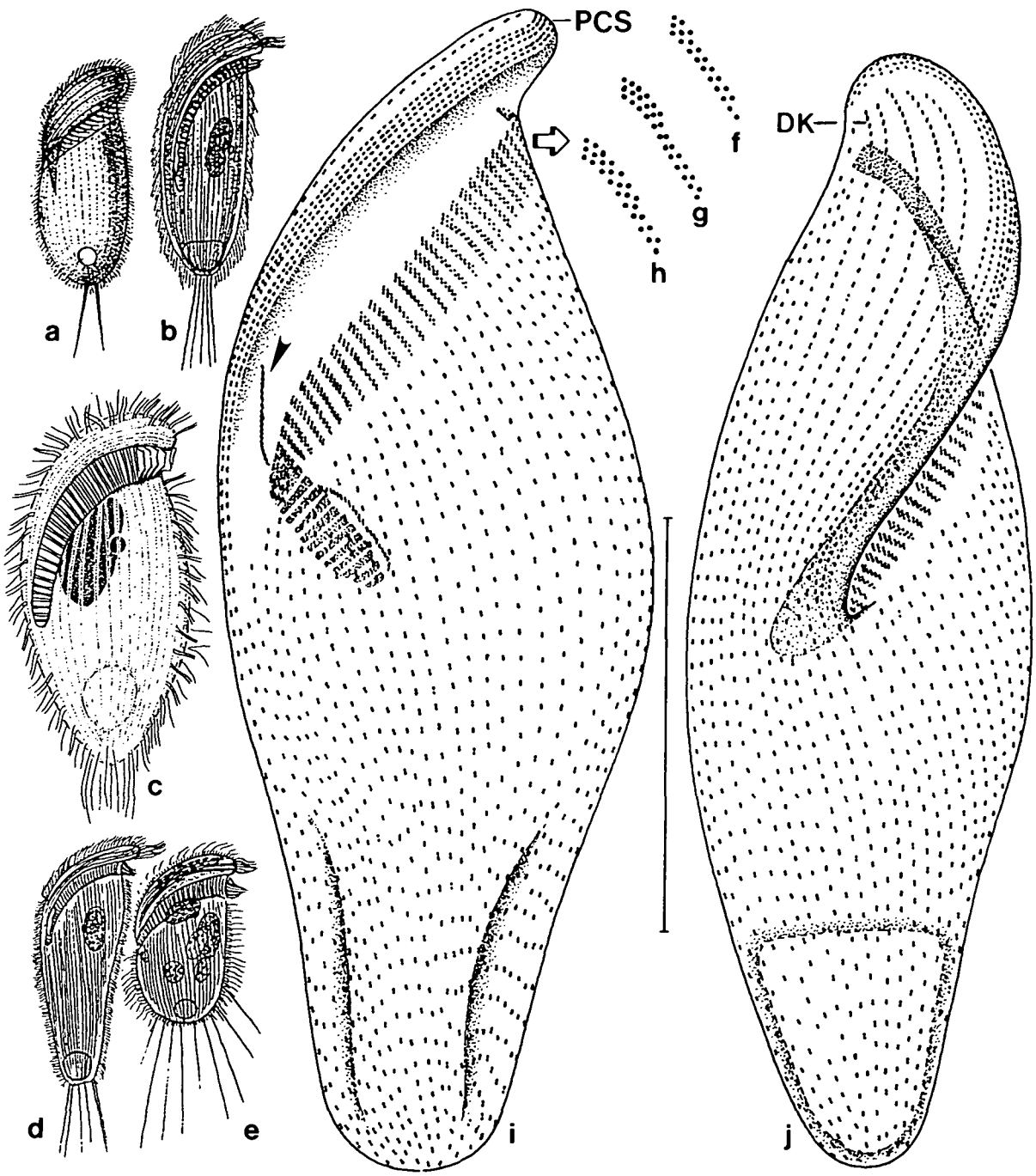


Fig. 193a–j. Various populations of *Metopus contortus* from life (a–e) and after protargol impregnation (i, j). **a:** Ventral view of holotype specimen, length 100 µm (from KENT 1882 after QUENNERSTEDT 1867). **b:** Ventral view, length 130 µm (from KAHL 1932). **c:** Ventral view, composite (?) of in vivo and protargol observations, length 70 µm (89–165 µm according to text). **d, e:** Ventral view of forma *major* (length 230 µm) and forma *pellitus* (length 90 µm); from KAHL (1932). **f–h:** Fine structure of membranelles in distal, middle and proximal region of adoral zone of Namibian specimens. **i, j:** Somatic and oral ciliary pattern of ventral and right side of Namibian specimens. Arrowhead marks undulating membrane. For details on perizonal stripe, see figures 193k, l. DK – dome (dorsal) kineties, PCS – perizonal ciliary stripe. Scale bar 50 µm.

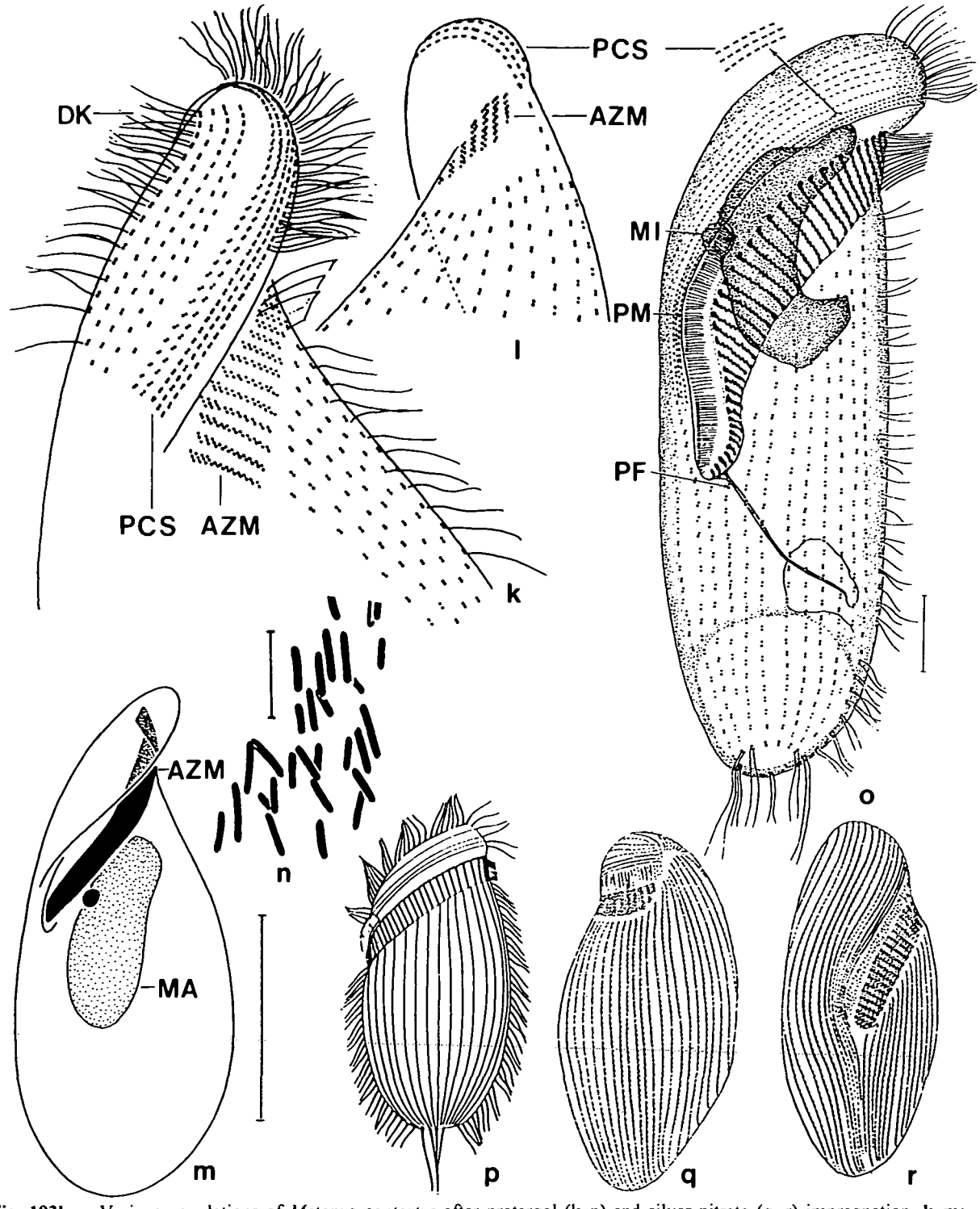


Fig. 193k–r. Various populations of *Metopus contortus* after protargol (k–n) and silver nitrate (q, r) impregnation. **k–m:** Overview (m) and details of ciliary pattern in anterior body region of a Namibian specimen. Scale bar 50 µm. **n:** Subcortical, methanogenic bacteria of a Namibian specimen. Scale bar 10 µm. **o:** Ciliary pattern of ventral side and nuclear apparatus of a French specimen (from DRAGESCO 1996). Scale bar 10 µm. **p:** Ventral view of a North American specimen, length 100 µm (from BORROR 1963). **q, r:** Ciliary pattern of left and right side of French specimens (from VILLENEUVE-BRACHON 1940), length 200–250 µm. AZM – adoral zone of membranelles, DK – dorsal (dome) kineties, MA – macronucleus, MI – micronucleus, PCS – perizonal ciliary stripe, PF – pharyngeal fibres, PM – paroral membrane.

than in type and DRAGESCO's specimens, similar as in KAHL's forma *major* (Fig. 193d, i, m; 405i); (iii) About 2:1 flattened dorsoventrally; (iv) Macronucleus in anterior ventral body half, likely fragile because strongly distorted in most specimens (Fig. 193m); (v) Cortical granules not studied in vivo and not recognizable in the protargol preparations; (vi) Packed with methanogenic bacteria, as first described by ESTEBAN et al. (1995), most of which impregnate with protargol and are located in an about 5 µm thick, cortical layer (Fig. 193n; 405j, k); (vii) Somatic ciliature conspicuous due to the many narrowly spaced ciliary rows (Fig. 193i, j), similar to the populations of KAHL (1932) and VILLENEUVE-BRACHON (1940; Fig. 193b, d, e, q, r); (ix) Somatic cilia 15 µm, caudal cilia 40 µm long on average in protargol-impregnated specimens. Only the posterior basal body of the dikinetids is ciliated, except of the perizonal stripe and the anterior region of the dome kineties, which have ciliated both basal bodies (Fig. 193k); (x) Perizonal stripe of ordinary structure (Fig. 193k, l; FOISSNER & AGATHA 1999); (xi) Adoral zone of membranelles of ordinary shape and structure, ends more or less distinctly curved, depending on orientation of cell (Fig. 193i–l; 405i, k). Individual membranelles of slightly different fine structure in distal, middle, and proximal portion of zone, as shown in figures 193f–h. (xii) Paroral membrane inconspicuous, 23 µm long on average (n = 5).

Table 171. Morphometric data on *Metopus contortus* from Namibian site (49).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	131.5	128.0	18.2	4.2	13.9	107.0	175.0	19
Body, width	52.0	51.0	10.1	2.3	19.4	40.0	75.0	19
Body length:width, ratio	2.6	2.6	0.4	0.1	14.8	2.1	3.3	19
Anterior body end to adoral zone, distance	9.4	9.0	1.9	0.4	20.1	5.0	12.0	19
Anterior body end to end of adoral zone, distance	67.6	65.0	9.3	2.1	13.7	55.0	90.0	19
Anterior body end to macronucleus, distance	34.9	36.0	7.3	1.7	21.0	22.0	50.0	19
Macronucleus, length	44.6	44.0	6.1	1.4	13.6	38.0	65.0	19
Macronucleus, width	20.7	20.0	2.8	0.6	13.3	14.0	25.0	19
Micronucleus, length	5.6	6.0	0.8	0.2	15.0	4.0	7.0	19
Micronucleus, width	4.7	5.0	0.7	0.2	13.8	4.0	6.0	19
Somatic cilia, length	15.2	15.0	2.8	0.6	18.6	10.0	20.0	19
Caudal cilia, length	38.9	40.0	7.0	1.8	18.0	23.0	50.0	16
Ventral adoral membranelles, length	8.0	8.0	0.9	0.2	11.5	7.0	10.0	19
Cytoplasmic bacteria, length	5.3	4.0	2.4	0.5	44.7	3.0	11.0	19
Ciliary rows, number	47.6	48.0	3.6	0.8	7.5	40.0	55.0	19
Kinetids in a left side kinety, number	45.3	45.0	6.5	1.5	14.4	35.0	60.0	19
Adoral membranelles, number	41.4	42.5	4.3	1.0	10.4	33.0	50.0	18

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Table 172. Comparison of *Metopus contortus* populations.

Authors	Size in vivo (µm)	Caudal cilia	Nucleus location	Numbers		Habitat
				ciliary rows	adoral membranelles	
QUENNERSTEDT (1867)	100× 40	present	?	?	?	marine
KAHL (1932)	100–160× 30–55	present	trunk	narrowly striated	?	marine & brackish
VILLENEUVE-BRACHON (1940)	200–250 × 70–90	present	?	40–50	?	brackish
BORROR (1963)	100–112 × 42–56	present	trunk	35	38	marine
CZAPIK & JORDAN (1976a)	100–110	present	trunk	30–34	?	brackish
ESTEBAN et al. (1995) [a]	89–165 × 26–51	present	trunk	40	35–50	marine
DRAGESCO (1996) [b]	110–130	present	trunk	27–34	38–46	marine
Namibian site (49)	120–200 × 45–80	present	trunk	40–55	33–50	limnetic
JANKOWSKI (1964b) [c]	150× 57	absent	trunk	30	?	limnetic

[a] Up to 70 µm, according to Fig. 9 in ESTEBAN's paper, here reproduced as figure 193c.

[b] DRAGESCO (1996) illustrates the perizonal stripe to be composed of only three kineties. However, a reinvestigation showed that it is of ordinary structure, that is, composed of five rows (slides kindly provided by Prof. DRAGESCO).

[c] An obvious misidentification, as shown by the lack of caudal cilia.

Condylostomides etoschensis nov. spec. (Fig. 194a–n; 406a–u, 407a–f, j; Table 173)

Diagnosis: Size about 240 × 110 µm in vivo. Conspicuously yellowish due to bright, citrine cortical granules 0.4 µm across and arranged in closely spaced rows. On average 8 macronuclear beads in moniliform pattern, 37 somatic kineties, and 56 adoral membranelles. Frontal membranelles conspicuous, extend along anterior third of paroral membrane.

Type location: Highly saline soil from an ephemeral pool at the margin of the Etosha Pan, Namibia, 18°55'S 16°25'E (site 65 in figures 2, 3 and chapter 2.1.2).

Etymology: Named after the area discovered.

Description: We studied two populations of this species. Both are from subtropical Africa and fairly similar. Thus, the description comprises both, but morphometric data are kept separate, and the formal diagnosis contains only the Namibian type population, which could be cultivated for some weeks in local soil percolate enriched with squashed wheat grains to stimulate growth of indigenous protists, the preferred food of *C. etoschensis*.

Size 160–300 × 70–150 µm in vivo, usually about 240 × 110 µm. Very flexible and slightly contractile in anterior half. Overall shape ellipsoidal, hungry specimens laterally flattened up to 2:1, usually widest slightly above mid-body where adoral zone of membranelles enters buccal cavity, often narrowed posteriorly, dorsal side more or less distinctly convex, ventral straight and slightly receding along adoral zone of membranelles, posterior end broadly rounded, anterior bluntly pointed and slightly projecting above ventral surface (Fig. 194a, b,

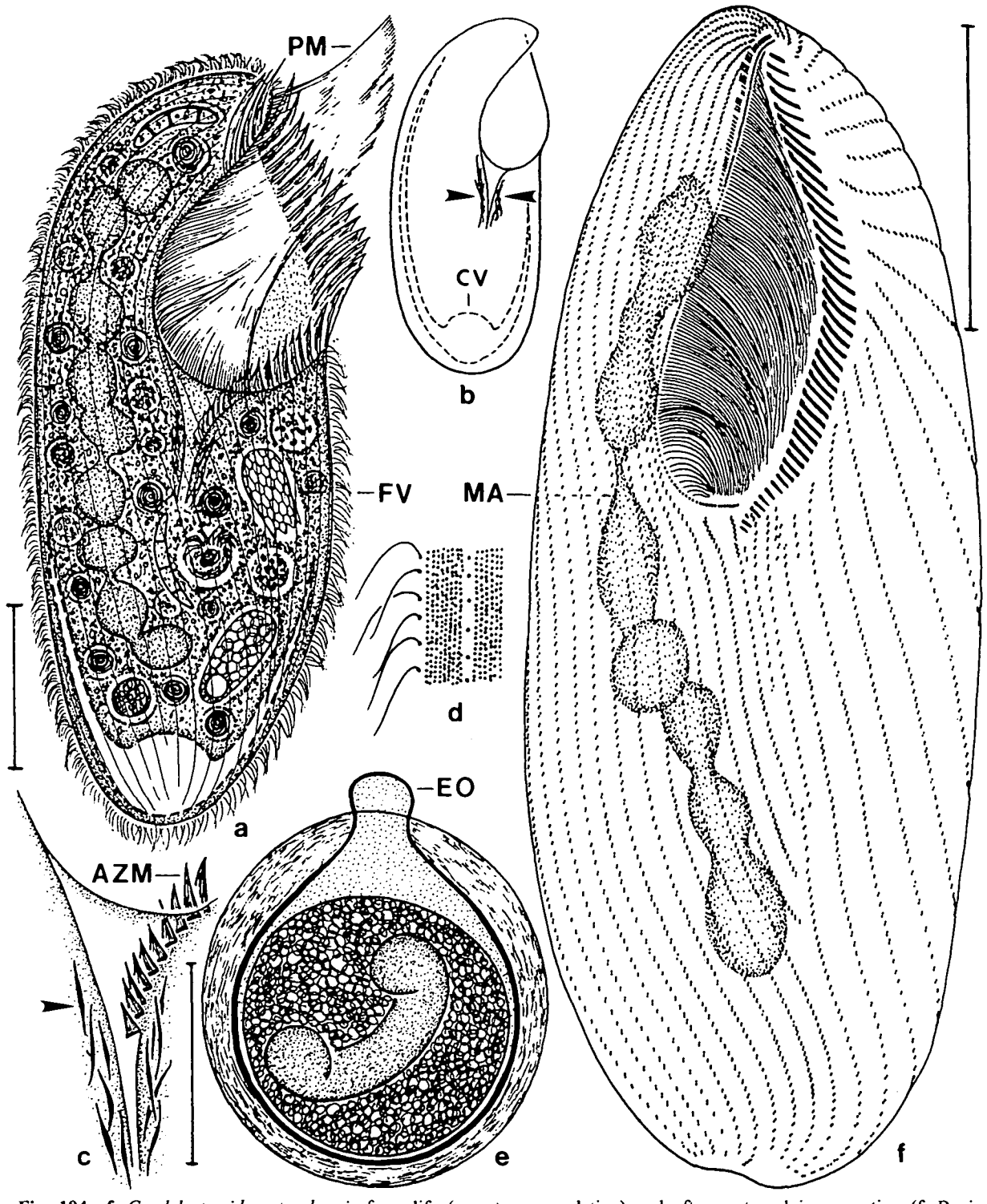
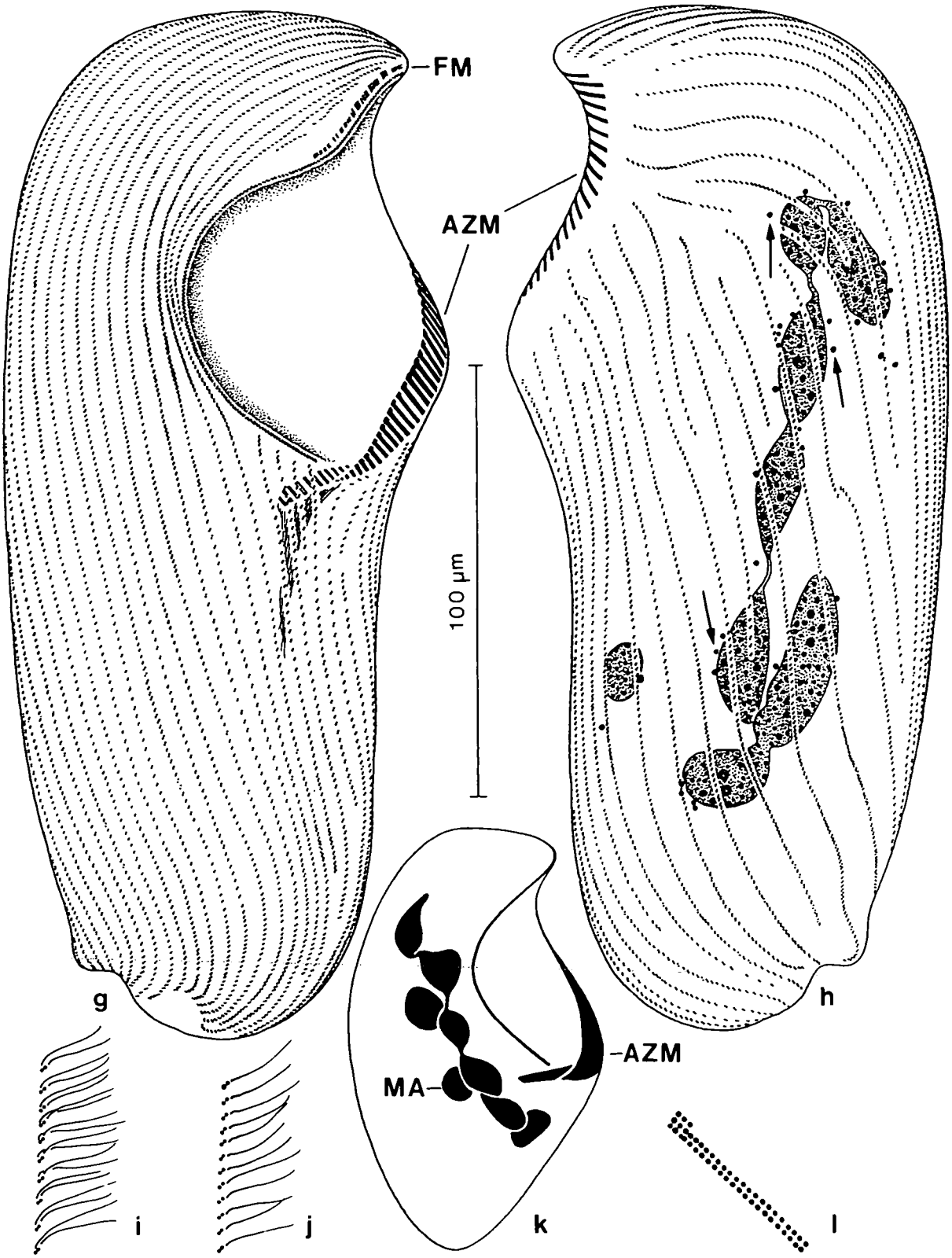


Fig. 194a–f. *Condylostomides etoschensis* from life (a–e, type population) and after protargol impregnation (f, Benin population). **a:** Right lateral view of a representative specimen. **b, c:** Shape variant. Arrowheads mark fusiform structures, very likely membrane reservoirs, surrounding the short cytopharynx. **d:** Surface view showing rows of citrine cortical granules between the ciliary rows. **e:** Resting cyst. **f:** Infraciliature of ventral side. For details, see figure 194m. AZM – adoral zone of membranelles, CV – contractile vacuole, EO – emergence pore, FV – food vacuole with a testate amoeba, MA – moniliform macronucleus, PM – paroral membrane. Scale bars 50 µm (a, f) and 20 µm (e).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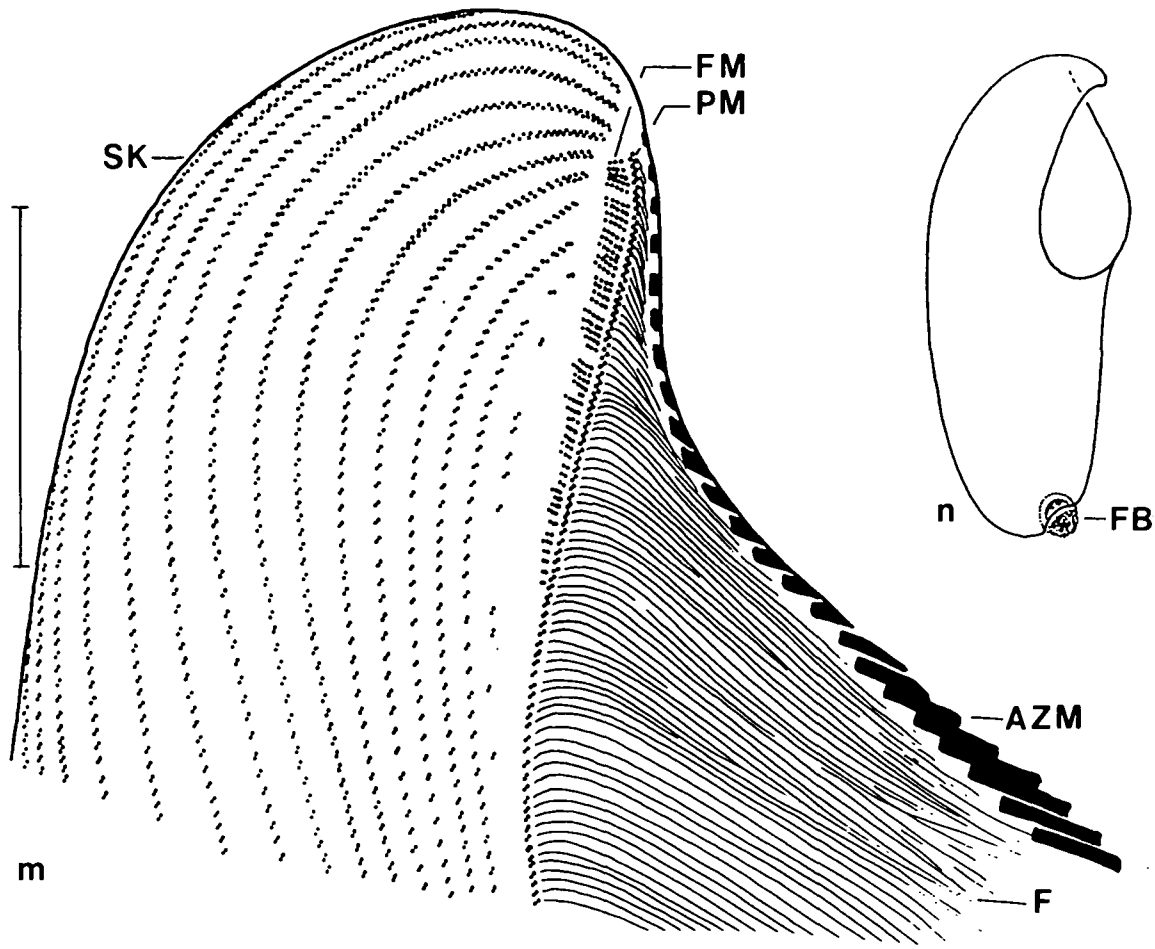

Fig. 194m, n. *Condylostomides etoschensis* from life (n) and after protargol impregnation (m). **m:** Infraciliature of anterior right side. **n:** Shape variant expelling a faecal bale. AZM – adoral zone of membranelles, F – fibres originating from paroral dikinetids, FB – faecal bale, FM – frontal membranelles, PM – paroral membrane, SK – somatic kineties. Scale bar 25 μm.

g, n; 406b, c, f, h, i; Table 173). Macronucleus in dorsal half of cell, moniliform, beads globular to ellipsoidal and of highly variable size, distinctly or indistinctly separate from each other, some usually scattered in cytoplasm or side by side forming two indistinct rows; nucleoli minute and numerous. Micronuclei near or attached to macronuclear beads, small (≤2 μm) and numerous (Fig. 194a, f, h, k; 406n; Table 173). Contractile vacuole in posterior end, large and occasionally deforming cell when completely filled, possesses two long collecting canals extending to level of buccal cavity, vacuole and canals stand out as bright areas from opaque cytoplasm in well-fed specimens. Cytopyge subterminally on ventral side

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Fig. 194g–l. *Condylostomides etoschensis* after protargol impregnation. **g, h:** Infraciliature of right and left side and nuclear apparatus of Namibian holotype specimen. Arrows mark some of the numerous micronuclei. **i, j:** Ciliary rows. **k:** Small (143 μm), stout specimen. **l:** Fine structures of an adoral membranelle. AZM – adoral zone of membranelles, FM – frontal membranelles, MA – macronucleus.

(Fig. 194a, b, n; 406a, d). Cortical granules 0.3–0.4 µm across, citrine and thus providing cells with yellowish colour, arranged in closely spaced rows between somatic kineties and in buccal cortex, release fluid content when extruded and produce yellowish zone around cell, impregnate well with silver carbonate and protargol (Fig. 194d; 406m, s, u, 407d). Cytoplasm colourless in Namibian type population, yellowish in Benin specimens, usually contains many food vacuoles with fungal conidia, heterotrophic flagellates (*Peranema* sp., *Polytoma* sp.), ciliates (*Tetrahymena rostrata*, *Halteria grandinella*, *Cyrtolophosis mucicola*), and testate amoebae (*Trinema lineare*, *Euglypha* sp.). Glides slowly on microscope slide and between soil particles showing great flexibility.

Somatic cilia about 10 µm long, arranged in slightly oblique rows leaving blank small, circular area on posterior pole; very closely spaced, especially in anterior region of right and dorsal side. Kineties composed of obliquely oriented dikinetids usually having only the anterior basal body ciliated, Benin specimens with ciliated dikinetids throughout or at least on postoral and left lateral surface; about twice as widely spaced on left as on right side, some kinety fragments occur right of paroral membrane and on postoral right and ventral side, where kineties form an indistinct suture (Fig. 194a, f–j, m; 406k, l, n, q, t).

Oral apparatus conspicuous, occupies about 36% (Benin population) to 48% (Namibian type population) of body length, that is, extends from ventral anterior end to near mid-body (Fig. 194a, f, g, k, m; 406a–i, k, l, n, t). Buccal cavity large but only slightly concave and contractile, thus always widely open, even in preserved specimens; buccal wall lined by long microtubule ribbons originating from paroral dikinetids, stripes of microtubule ribbons separated by rows of minute, non-extrusive, conical organelles which stain with protargol like basal bodies (Fig. 407a, c, d). Pharynx small, obconical, contains narrowed posterior portion of adoral zone of membranelles, surrounded by many fusiform structures, likely membrane reservoirs for food vacuole formation (Fig. 194a–c, g).

Paroral membrane conspicuous, emerges from small cleft at right margin of buccal cavity, commences apically and extends to midline of proximal buccal vertex, composed of dikinetids having 50–60 µm (!) long cilia producing giant velum. Frontal membranelles form distinct stripe along right anterior third of paroral, composed of closely spaced, about 20 µm long cilia, indistinctly separate from each other, decrease in size from anterior to posterior. Along left margin of paroral membrane minute, claviform structures (Fig. 194a, f, g, m; 406c, e–i, k, l, n, r, t, 407f).

Adoral zone of membranelles conspicuous, extends in wide spiral from anterior left margin of buccal cavity to near mid-body, where it curves right and to body centre; number of membranelles distinctly higher in Namibian (46–67, $\bar{x}$ = 55.6) than Benin (33–44, $\bar{x}$ = 38.2) specimens (Table 173). Individual membranelles decrease in size at ends of zone, composed of two up to 12 µm long rows with about 20 µm long cilia and, at left inner end, a very short row with cilia only 5 µm long (Fig. 194a, f, g, h, l; 406o, 407e).

Resting cysts slightly to distinctly ellipsoidal (length with emergence pore: 37–52 µm, $\bar{x}$ = 44 µm, SD = 4.3 µm, CV = 9.8%, n = 11; width: 33–42 µm, $\bar{x}$ = 37.6 µm, SD = 3.0 µm, CV = 8.0%, n = 11), contain semicircular macronuclear mass and many fat globules. Ectocyst membranous and hyaline, about 5 µm thick, citrine like cortical granules, usually covered with bacteria and organic debris. Endocyst compact, about 1.5 µm thick, yellowish, forms globular emergence pore (Fig. 194e; 406j, p).

Occurrence and ecology: Found in several soil samples from the Etosha Pan region

(Table 4) and in a sample from Benin (surroundings of Cotonou University; red, very sandy, litter-poor soil and mud from fields and desiccated ponds, pH 7.3; sample kindly provided by Prof. Dr. Jean DRAGESCO; voucher slide deposited). The Etosha samples were heavily saline, and the Benin sample contained material from the margin of a shallow lagoon. This indicates that *C. etoschensis* is a semiterrestrial species living on the bottom of saline inland ponds.

Table 173. Morphometric data on *Condylostomides etoschensis*.

Characteristics [a]	Population [b]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	NT	228.3	230.0	33.9	10.2	14.9	148.0	275.0	11
	BF	205.9	205.0	23.7	7.1	11.5	160.0	250.0	11
	BW	232.3	225.0	32.4	9.8	13.9	190.0	290.0	11
Body, width	NT	108.5	105.0	18.8	5.7	17.2	90.0	155.0	11
	BF	88.7	87.0	11.8	3.5	13.2	67.0	105.0	11
	BW	125.6	125.0	17.8	5.4	14.2	90.0	157.0	11
Anterior body end to proximal end	NT	109.4	110.0	18.8	5.7	17.2	80.0	135.0	11
of adoral zone, distance	BF	70.8	72.0	7.4	2.2	10.5	55.0	80.0	11
	BW	87.6	87.0	7.3	2.2	8.3	76.0	100.0	11
Macronuclear figure, length	NT	128.4	130.0	25.7	7.8	20.0	92.0	180.0	11
	BF	131.6	130.0	15.7	4.7	11.9	105.0	155.0	11
	BW	147.5	155.0	28.8	8.7	19.5	87.0	185.0	11
Macronuclear nodules, length	NT	23.7	22.0	6.7	2.0	28.2	15.0	35.0	11
	BF	24.0	23.0	7.2	2.2	29.8	15.0	36.0	11
	BW	27.6	22.0	9.7	2.9	35.1	17.0	43.0	11
Macronuclear nodules, width	NT	12.1	12.0	2.3	0.7	19.4	8.0	15.0	11
	BF	11.2	11.0	0.8	0.2	6.7	10.0	12.0	11
	BW	14.6	15.0	2.4	0.7	16.4	11.0	19.0	11
Macronuclear nodules, number	NT	8.6	8.0	2.0	0.6	23.3	5.0	12.0	11
	BF	6.8	7.0	1.2	0.2	17.2	5.0	9.0	30
	BW	6.0	6.0	1.1	0.3	18.3	4.0	7.0	11
Micronuclei, largest diameter	NT	1.7	1.5	–	–	–	1.5	2.0	11
	BF	1.5	1.5	–	–	–	1.2	2.0	11
Micronuclei, number	NT	21.2	21.0	5.0	1.5	23.4	15.0	30.0	11
	BF	11.6	11.0	3.8	1.2	32.9	5.0	18.0	11
Somatic ciliary rows, number in	NT	36.7	37.0	3.9	1.2	10.6	30.0	42.0	11
mid-body	BF	32.3	32.0	–	–	–	32.0	33.0	3
	BW	30.3	31.0	2.5	0.8	8.2	25.0	34.0	11
Dikinetids in a dorsal kinety,	NT	213.6	210.0	23.7	7.1	11.1	180.0	260.0	11
number	BW	138.6	140.0	18.8	5.7	13.6	105.0	165.0	11
Adoral membranelles, number	NT	55.6	56.0	5.8	1.8	10.5	46.0	67.0	11
	BW	38.2	38.0	3.7	1.1	9.8	33.0	44.0	11

[a] Data based on silver-impregnated (methods, see following footnote) specimens. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] NT – Namibian type population, wheat grain culture, impregnated with the DRAGESCO-TUFFRAU protargol method; BF – Benin population, material as obtained with the non-flooded Petri dish method, impregnated with FOISSNER's protargol technique; BW – Benin population, wheat grain culture, impregnated with WILBERT's protargol method.

Generic classification and comparison with related species: *Condylostomides* was established by SILVA NETO (1994), with *C. grolieri* as type species (by monotypy), who discovered it in a calcium carbonate-rich mineral spring in France. He characterized the genus as follows: "Le genre *Condylostomides* est représenté par des ciliés d'assez grande taille (250–400 µm) depourvu de myonèmes, aux cinéties relativement serrées dont quelques postorales, à la cavité péristomienne triangulaire occupant le 1/3 antérieur de la longueur du corps, prolongée en un court infundibulum. La frange adorale d'organelles est semicirculaire peu spiralée à son extrémité posterieure. L'organelle paroral est une double rangée de cinétosomes, antérieurement doublée sur sa droite par de courts segments de cinéties formant paquets ciliaires distincts". We basically agree with this definition, emphasizing the acontractile and ventrally located buccal cavity and the paroral membrane, which is at the right mouth margin in *Condylostomides* and deep into the buccal cavity in *Condylostoma*. Furthermore, the buccal entrance is acontractile and ventral in *Condylostomides*, while contractile and mainly at the anterior end in *Condylostoma*. Thus, these genera look quite different in the scanning electron microscope (cp. figures 406h, i and figure 407j with figure 407g, h).

Condylostomides is probably the nearest relative of *Linostomella* (for a detailed description of this genus, see FOISSNER et al. 1999), a planktonic freshwater condylostomid which differs from *Condylostomides* only by the lack of frontal membranelles (Fig. 407f).

SILVA NETO (1994) did not compare his new species with older descriptions of similar taxa. Specifically, he did not provide any feature that would separate *Condylostomides grolieri* from *Condylostoma tardum* PENARD, 1922. Both have the same general organisation, a similar size and shape, and, more important, three macronuclear beads. Thus, they are very likely synonymous. In our opinion, the following taxa need to be combined with *Condylostomides* and compared with *C. etoschensis*: *Condylostomides tardus* (PENARD, 1922) nov. comb. (basionym: *Condylostoma tardum* PENARD, 1922) differs from *C. etoschensis* mainly by the macronucleus, which consists of three isolated beads; *Condylostomides luteus* (KAHL, 1932) nov. comb. (basionym: *Condylostoma luteum* KAHL, 1932) is considerably smaller than *C. etoschensis* (length 100–130 µm vs. 160–300 µm) and has only two macronuclear beads; and *Condylostomides terricola* (FOISSNER, 1995) nov. comb. (basionym: *Condylostoma terricola* FOISSNER, 1995), which differs from *C. etoschensis* in size (90–140 × 30–60 µm vs. 160–300 × 70–150 µm), number of somatic kineties (15–18 vs. 25–42, $\bar{x}$: 17 vs. 33) and adoral membranelles (33–40 vs. 33–67, $\bar{x}$: 36 vs. 47), cortical granulation (sparse vs. many closely spaced rows), and in the frontal membranelles (more numerous in *C. etoschensis*).

Condylostomides trinucleatus nov. spec. (Fig. 195a–l; 408a–k; Table 174)

Diagnosis: Size about 250 × 125 µm in vivo; ellipsoidal to bursiform. Conspicuously yellowish due to brilliant, citrine cortical granule rows. Invariably 3 macronuclear beads, and an average of 35 adoral membranelles and 30 ciliary rows. A conspicuous, disk-shaped accumulation of rod-shaped structures near proximal end of adoral zone.

Type location: Soil from Murray River floodplain near the town of Albury at the land side of Ryans road, Australia, 37°S 147°E.

Etymology: Composite of the Latin words *tri* (three) and *nucleus* (nucleus), referring to a main feature of the species, viz., the three macronuclear beads.

Description: Culture trials failed, and abundances were low in the non-flooded Petri dish cultures from both the Australian and Namibian sample. Furthermore, the species is fragile and thus most specimens are heavily distorted in the protargol preparations. Accordingly, the type slides are of poor quality and only meristic features can be reliably measured. Nevertheless, all details necessary for a solid description could be collected by combining in vivo observations, protargol impregnation, morphometry, and scanning electron microscopy. Furthermore, some excellently prepared Namibian specimens round up the observations (Fig. 195k, l).

Size 170–270 × 100–135 µm in vivo, usually near 250 × 125 µm; very flexible and slightly contractile in anterior half. Overall shape ellipsoidal to bursiform with anterior end bluntly pointed and posterior broadly rounded; subapically a conspicuous bay, where the adoral zone turns onto left side; laterally up to 2:1 flattened (Fig. 195a–c; 408a). Nuclear apparatus usually slightly underneath mid-body, invariably composed of three obliquely arranged, broadly ellipsoidal to globular macronuclear nodules connected by a strand of argyrophilic material; nucleoli minute and numerous. Micronuclei attached and near to macronuclear beads, minute (1–2 µm across) and numerous (Fig. 195a, b; 408j, k). Contractile vacuole not recognizable. Cytopyge in posterior pole area. Cortical granules about 1 µm across, brilliant citrine and thus providing cells with yellowish appearance, arranged in rows between somatic kineties and in buccal cortex, impregnate with the protargol method used and thus hide the ciliary pattern; granules may distinctly decrease in number under suboptimal growth conditions (Fig. 195d). Cytoplasm colourless and foamy, usually packed with lipid droplets 1–5 µm across, countless lenticular crystals with a size of about 2 × 1 µm, and many small and large food vacuoles making cells dark at low magnification (≤ ×100). Feeds on heterotrophic flagellates (*Polytomella* sp.), ciliates (*Plagiocampa rouxi*, *Leptopharynx costatus*, *Cyrtolophosis mucicola*, *Metopus* sp., *Dexiotricha* sp., *Colpoda* sp.), green algae (*Eudorina*), and fungal conidia. Glides rather rapidly on microscope slide.

Somatic and oral ciliary pattern as described in → *C. etoschensis* and shown in figures 195a, e, h–j; 408a–k. Thus, only some deviating and/or interesting features will be described. Somatic ciliature composed of dikinetids having ciliated only the anterior basal body with 18 µm (!) long, rather stiff and widely spaced cilia. Likely 25–40 ciliary rows, exact number not recognizable in the protargol preparations. Cilia of adoral membranelles about 30 µm long, those of frontal membranelles near 40 µm, and those of paroral membrane even 50 µm long. Adoral fibre system as shown in figure 195j, connected with that of frontal membranelles. At or near proximal end of adoral zone a conspicuous, disc-shaped accumulation of hundreds of rod-shaped structures, likely a membrane reservoir for the food vacuoles; accumulation 20–30 µm across and strongly refractive (anisotropic?) under interference contrast illumination, individual components rod-shaped to acicular, about 12 × 1 µm in size, become inflated and globular (3–4 µm across) when artificially removed or in dead specimens (Fig. 195a, f, g; 408e–g, j, k).

Observations on Namibian site (49) specimens (Fig. 195k, l): The Namibian specimens, which are distinctly inflated in the protargol preparations, are considerably smaller than those from Australia, at least partially because they were not fully developed, as indicated by the very low abundance. All other features, especially the citrine cortical granules,

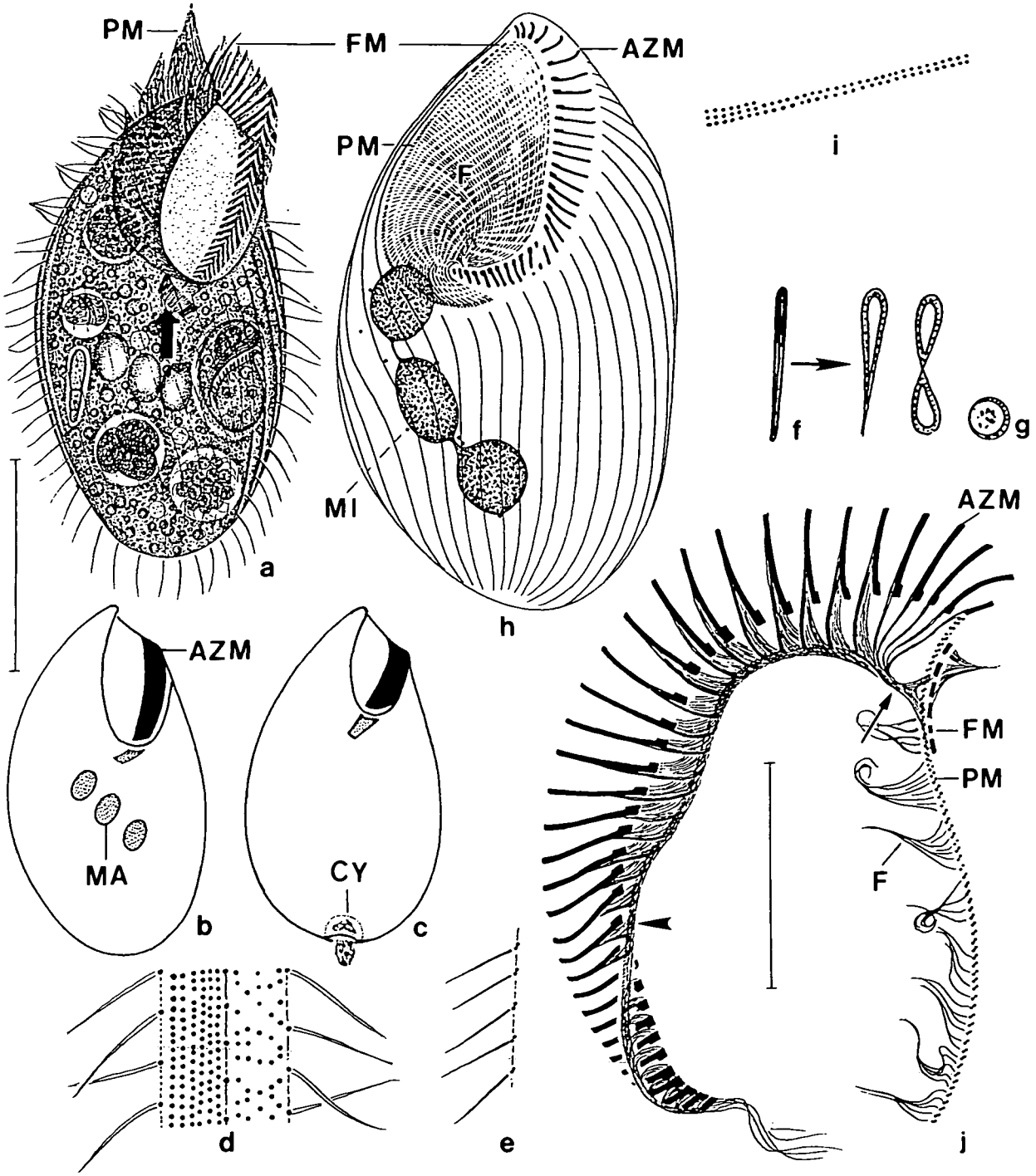


Fig. 195a–j. *Condylostomides trinucleatus* from life (a–d, f, g) and after protargol impregnation (e, h–j). **a:** Right side view. The arrow marks a disc-shaped accumulation of rod-shaped structures. **b, c:** Bursiform shape variants. **d:** Surface view showing rows of citrine cortical granules, left in an ordinary specimen, right in a cell grown suboptimally. **e:** Kineties are composed of dikinetids, but only the anterior basal body is ciliated. **f, g:** The rod-shaped structures near the proximal end of the adoral zone (a, f) degenerate to 4 µm-sized globules in dying specimens (g). **h:** Infraciliature of ventral side (composite). **i:** Fine structure of an adoral organelle. **j:** Oral fibre system seen from inside the cell. Arrow marks fibre connecting adoral and frontal membranelles. Arrowhead denotes thick fibre formed by thin fibres originating from adoral membranelles. AZM – adoral zone of membranelles, CY – cytopyge, FM – frontal membranelles, MA – macronuclear nodules, MI – micronucleus, PM – paroral membrane. Scale bars 100 µm (a, h) and 30 µm (j).

match well. Three of the four specimens found have three macronuclear beads, while one has only two. The oral and somatic ciliary pattern was excellently impregnated and is as in congeners. Only the anterior basal body of the dikinetids is ciliated, even in the oral area.

Occurrence and ecology: *Condylostomides trinucleatus* was discovered in soil from the Murray River floodplain in Australia. In Namibia, it occurred at sites (4) and (49), that is, the floodplain of the Bukaos River and road puddles in the Bambatsi Guest Farm. This indicates that *C. trinucleatus* occurs in both limnetic and terrestrial habitats. Interestingly, all terrestrial condylostomids as yet have been found only in Africa, Australia, and Venezuela (a further undescribed species under investigation).

Condylostomides tardus, *C. grolieri*, and *C. luteus* were discovered in sapropelic habitats, where they occurred together with typically anaerobic inhabitants, such as *Metopus* and *Caenomorpha*. Basically, this applies also to *C. trinucleatus*, which occurred together with *Metopus* spp. in the non-flooded Petri dish culture. On the other hand, it survived for days in oxygenated culture medium (but did not reproduce), and → *C. etoschensis* could be grown for months under aerobic conditions, indicating that condylostomids are not strictly anaerobic.

Generic classification and comparison with related species: For generic classification, see → *Condylostomides etoschensis*. As concerns the species, we adopt the concept used in the relative *Stentor*, that is, we consider the colour of the cortical granules

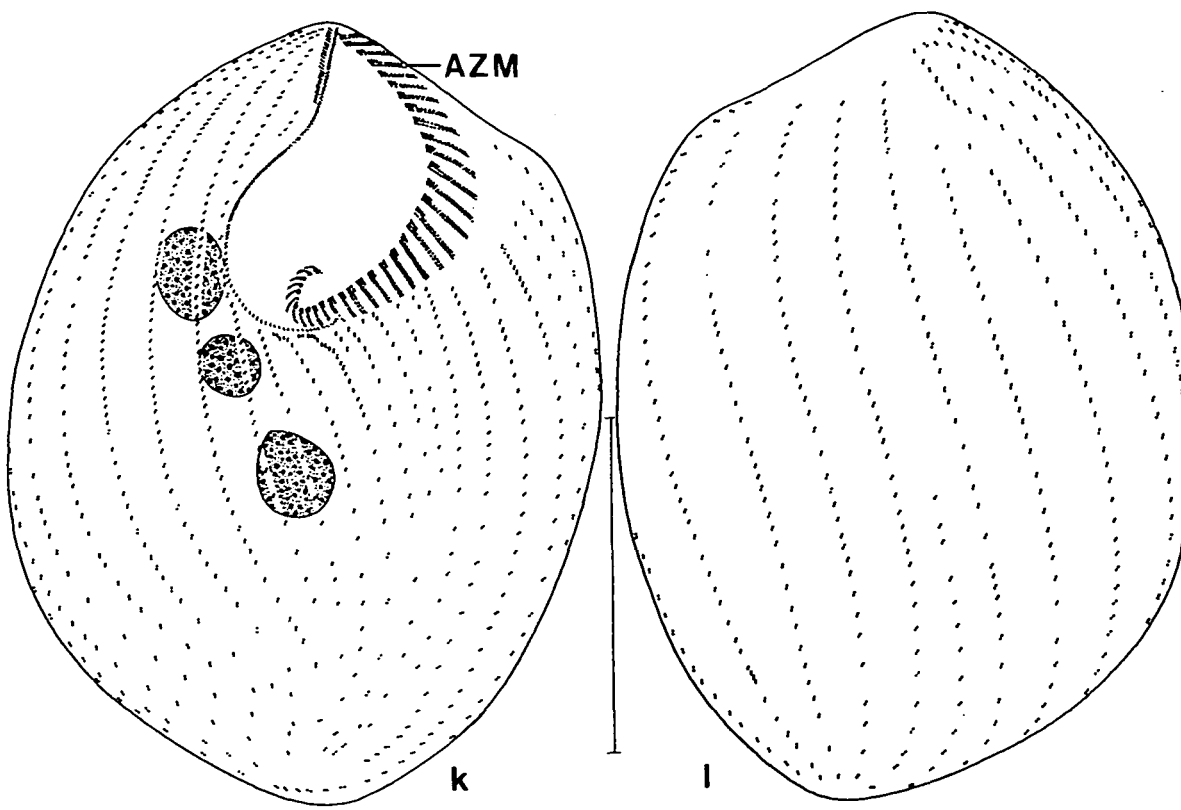


Fig. 195k, l. *Condylostomides trinucleatus*, somatic and oral ciliary pattern and nuclear apparatus of a specimen from Namibian site (49) after protargol impregnation. AZM – adoral zone of membranelles. Scale bar 50 µm.

and the nuclear pattern as main species features. The nuclear pattern, three obliquely arranged nodules, distinguishes *C. trinucleatus* clearly from the other terrestrial condylostomids, viz., *C. terricola* (FOISSNER, 1995) and → *C. etoschensis*, which have a moniliform macronuclear strand. Furthermore, body shape (oblong, that is 3:1 in *C. terricola* and *C. etoschensis* vs. ellipsoidal, that is 2:1 in *C. trinucleatus*), body size (near 110 × 35 µm in *C. terricola* vs. near

Table 174. Morphometric data on Australian (upper line) and Namibian site 49 (lower line) population of *Condylostomides trinucleatus*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length in vivo	235.7	250.0	30.6	11.6	13.0	175.0	270.0	7
	–	–	–	–	–	–	–	–
Body, width in vivo	122.9	125.0	10.8	4.1	8.8	100.0	135.0	7
	–	–	–	–	–	–	–	–
Body, length [b]	161.1	170.0	28.1	7.5	17.4	100.0	200.0	14
	113.5	118.5	18.5	9.3	16.3	87.0	130.0	4
Body, width [b]	107.5	110.0	23.2	6.2	21.6	40.0	130.0	14
	68.8	72.5	21.0	10.5	30.5	40.0	90.0	4
Anterior body end to proximal end of adoral zone, distance [b]	65.9	68.0	13.0	4.1	19.8	35.0	82.0	10
	39.8	39.5	5.7	2.9	14.4	33.0	47.0	4
Macronuclear figure, length	57.5	55.0	12.9	3.5	22.5	35.0	85.0	14
	40.7	41.0	9.5	5.5	23.4	31.0	50.0	3
Macronuclear nodules, length	18.8	19.0	2.7	0.7	14.5	13.0	25.0	14
	14.5	13.5	5.6	2.8	38.4	9.0	22.0	4
Macronuclear nodules, width	15.2	15.0	1.9	0.5	12.7	13.0	18.0	14
	10.5	10.5	1.3	0.7	12.3	9.0	12.0	4
Macronuclear nodules, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	26
	2.8	3.0	–	–	–	2.0	3.0	4
Micronuclei, length	1.4	1.3	–	–	–	1.2	2.0	9
	1.4	1.5	–	–	–	1.3	1.5	3
Micronuclei, width	1.4	1.3	–	–	–	1.2	2.0	9
	1.4	1.5	–	–	–	1.3	1.5	3
Micronuclei, number [c]	7.2	7.0	–	–	–	5.0	10.0	6
	5.0	4.0	–	–	–	4.0	7.0	3
Adoral membranelles, number	35.1	35.0	3.5	0.9	10.0	27.0	40.0	15
	29.0	28.5	3.9	2.0	13.5	25.0	34.0	4
Basis of a left side adoral organelle, length	14.2	14.0	1.3	0.4	9.2	12.0	17.0	14
	8.5	8.5	1.3	0.7	15.2	7.0	10.0	4
Ciliary rows, number	–	–	–	–	–	–	–	–
	18.5	16.5	5.9	3.0	32.0	14.0	27.0	4

[a] Data based, if not otherwise stated, on mounted, protargol-impregnated (FOISSNER's method), selected (inflated and/or heavily distorted cells excluded) specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Values hardly useable because specimens are heavily distorted.

[c] Values uncertain because some likely hidden by macronuclear nodules.

250 × 120 in *C. etoschensis* and *C. trinucleatus*), number of ciliary rows (about 17 in *C. terricola* vs. 30–35 in *C. etoschensis* and *C. trinucleatus*), and number of adoral membranelles (about 35 in *C. terricola* and *C. trinucleatus* vs. 56 in *C. etoschensis*) are conspicuously different. Additionally, only *C. trinucleatus* has a conspicuous, disk-shaped accumulation of pharyngeal organelles, while they are rather scattered in → *C. etoschensis* and inconspicuous or lacking in *C. terricola* (FOISSNER, 1995); however, in *C. tardus* (PENARD, 1922) and *C. luteus* (KAHL, 1932), they seem to be as conspicuous as in *C. trinucleatus*.

As concerns the nuclear pattern, *C. trinucleatus* matches *C. tardus* (PENARD, 1922) and its proposed junior synonym, *C. grolieri* SILVA NETO, 1994 (see *C. etoschensis*). Indeed, these species are highly similar to each other, differing mainly in the colour of the cortical granules: brilliant citrine in *C. trinucleatus*, while colourless in *C. tardus*. As *C. tardus* was studied also by KAHL (1932), there hardly can be any doubt that the granules are colourless. *Condylostomides grolieri* is said to have a "coloration sombre", but the colour of the cortical granules, recognizable in figure 2 of SILVA NETO's paper, is not specified. Thus, this species cannot be identified and is best considered as a junior synonym of *C. tardus*. *Condylostomides luteus* (KAHL, 1932), which has citrine cortical granules like *C. trinucleatus*, is much smaller than *C. trinucleatus* (100–130 µm vs. 170–270 µm) and has only two (vs. three) macronuclear beads.

COLPODEA

The Colpodea were extensively reviewed by FOISSNER (1993c). He recognized 55 genera with a total of 170 species. Since then, nine new species and seven new genera were described: *Corticocolpoda* FOISSNER, 1993a; *Idiocolpoda* FOISSNER, 1993b; *Pentahymena* FOISSNER, 1994b; *Dapedophrya* FOISSNER, 1995; *Mykophagophrys* FOISSNER, 1995; *Hackenbergia* FOISSNER, 1997b; *Fungiphrya* FOISSNER, 1999a. In the present monograph, four new genera and 17 new species will be described, and some poorly known species redescribed, raising the colpodids to roughly 190 reliable species. This shows that the diversity of the colpodids is by no means exhausted. Indeed, the rate at which we find new genera and species has not dropped since 1993, showing that a considerable portion of the colpodids is still undiscovered.

Although morphological investigations (FOISSNER & KREUTZ 1998) and gene sequence data (LYNN et al., 1999) confirmed and refined some of the proposed relationships among colpodid orders, others remain doubtful, and evolution within orders is largely speculative. Unfortunately, the new taxa discovered since 1993 hardly make clearer evolutionary relationships; on the contrary, the bewildering diversity of the oral structures and silverline systems confuse them more and more. This is emphasized by the genera → *Platyophryides* and → *Ottowphrya* described in the present monograph.

Colpoda formisanoi nov. spec. (Fig. 196b–o; 409a–g; Table 175)

Diagnosis: Size about 35 × 22 µm in vivo. Slenderly to broadly sigmoidal with wide anterior and tail-like narrowed posterior end. On average 12 somatic ciliary rows, of which two are strongly shortened on left side. Left oral polykinetid elongate square, consists of an average of 9 minute kineties.

Type location: Bark of a *Colophospermum mopane* tree at the Bambatsi Guest Farm, Namibia, 20°10'S 15°25'E (site 51 in figure 2 and chapter 2.1.2).

Dedication: We dedicate this species to Dott. Mario FORMISANO (Italy), who illustrated it in 1957, but did not name it.

Description: Size 30–40 × 15–30 µm in vivo, usually about 35 × 22 µm, length:width ratio 1.2–1.9:1, on average 1.4:1; laterally flattened up to 2:1. Shape highly characteristic, that is, slenderly to broadly sigmoidal with wide anterior and tail-like posterior end (Fig. 196b, c; 409a–d; Table 175). Usually conspicuously indented at oral opening, ventral margin thus more distinctly sigmoidal than dorsal; indentation varies from almost semicircular to angular. Preoral keel straight to slightly receding, distinctly serrate. Shape and size well-preserved in protargol preparations, oral indentation and tail, however, often less conspicuous. Location of nuclear apparatus highly variable, on average slightly underneath mid-body left of midline, that is, in postoral left quadrant of cell. Macronucleus globular to slightly ellipsoidal, in 16 out of 18 specimens analyzed with a conspicuous, central nucleolus, rarely with several small nucleoli. Micronucleus about 3.5 × 2 µm in vivo, attached to macronucleus (Fig. 196b, e, h;

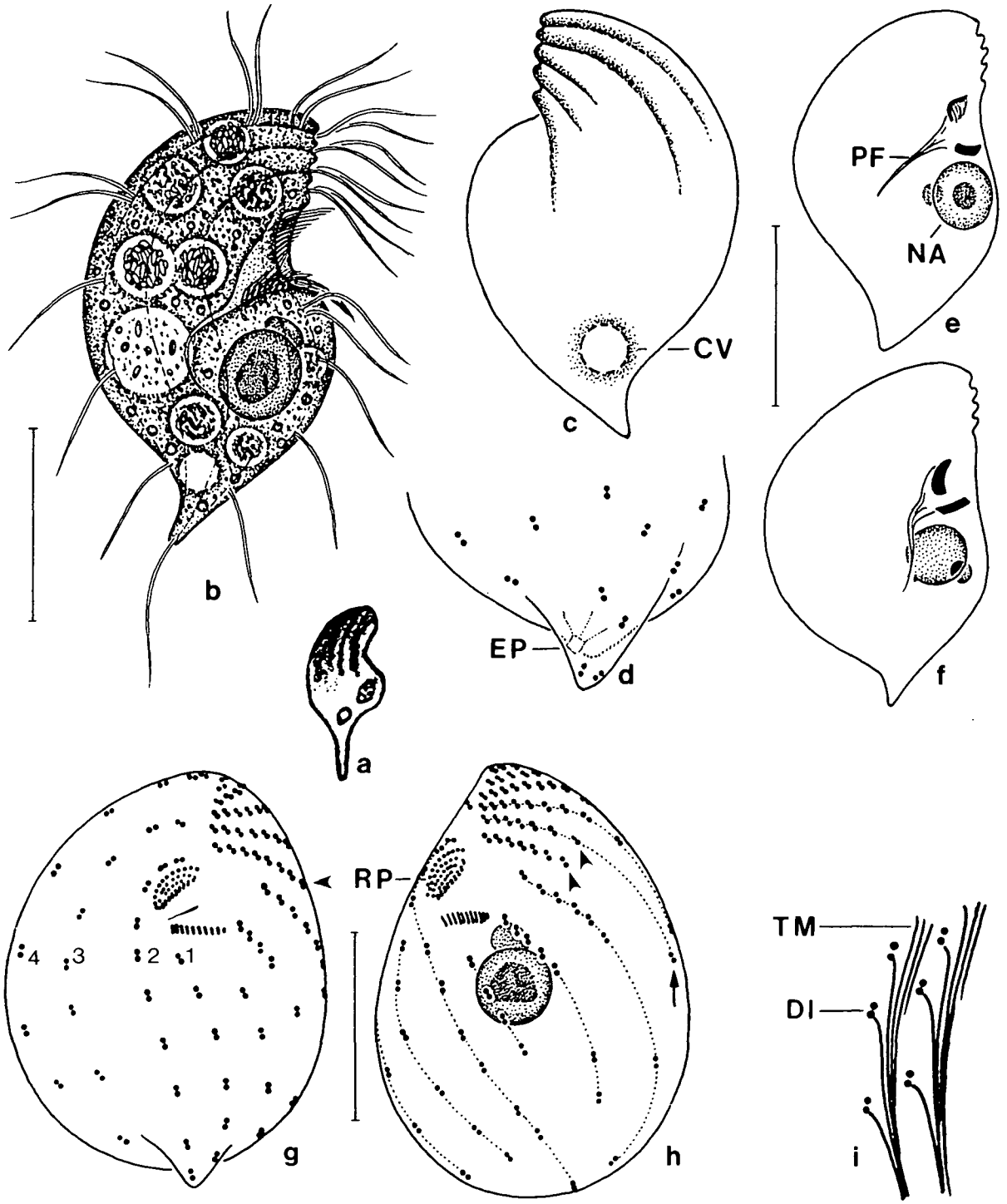


Fig. 196a–i. *Colpoda formisanoi* from life (a–c) and after protargol impregnation (d–i). **a:** *Colpoda steinii* of FORMISANO (1957), length 40 µm, is obviously the same species as described by us. **b:** Right lateral view of a representative specimen. **c:** Shape variant. **d:** Ciliary pattern in right posterior body region. The excretory pore is on the left surface. **e, f:** Slender and broad shape variant. **g, h:** Ventral and left lateral view of ciliary pattern. Arrowheads mark ends of two strongly shortened kineties; note, however, that the upper row sometimes possesses an isolated kinetid near mid-body (arrow). Numbers denote ciliary rows. **i:** Somatic fibrillar system. CV – contractile vacuole, DI – dikinetid, EP – excretory pore, NA – nuclear apparatus, PF – pharyngeal fibres, RP – right oral polykinetid, TM – transverse microtubule ribbons. Scale bars 15 µm.

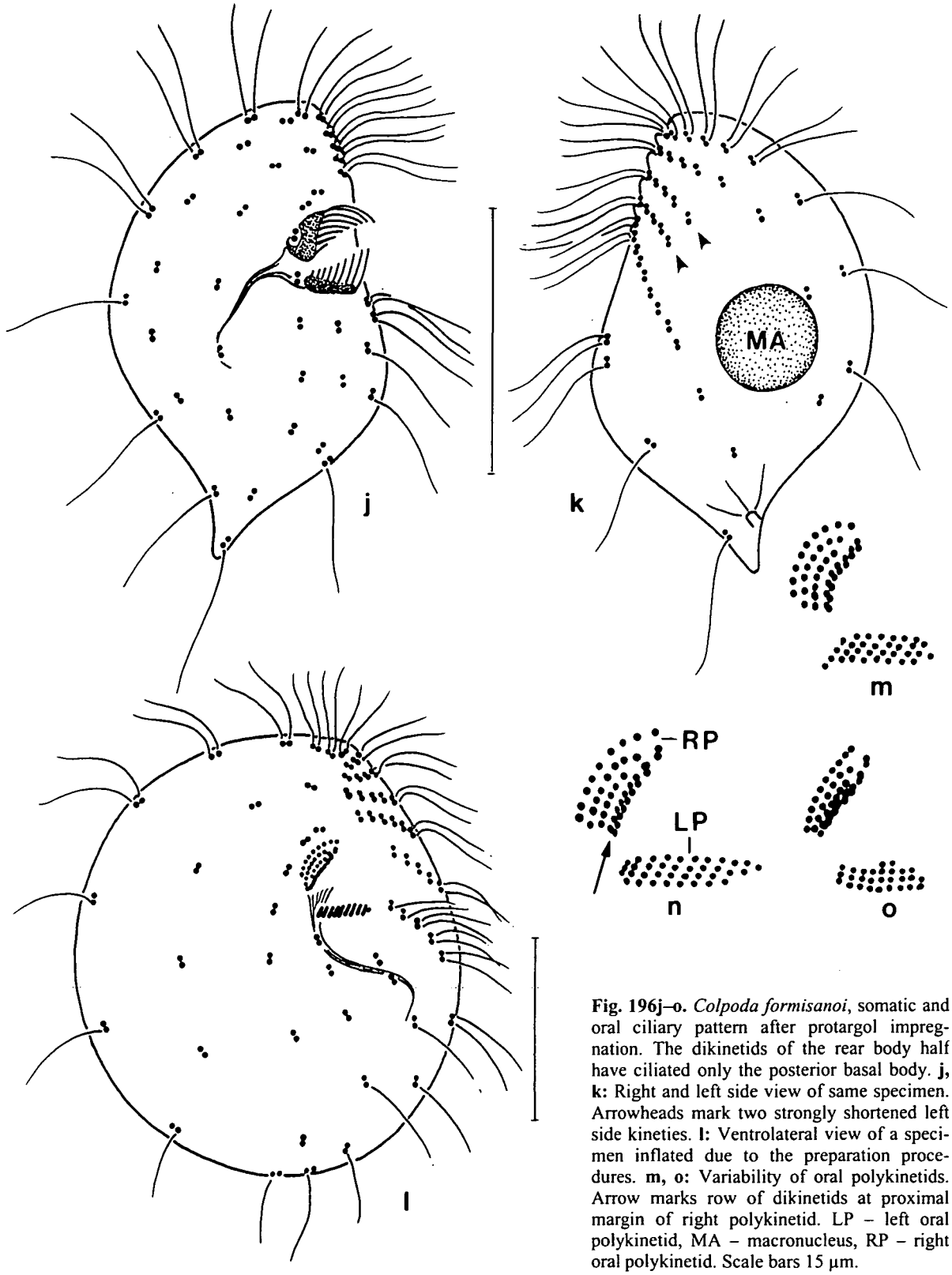


Fig. 196j–o. *Colpoda formisanoi*, somatic and oral ciliary pattern after protargol impregnation. The dikinetids of the rear body half have ciliated only the posterior basal body. **j, k:** Right and left side view of same specimen. Arrowheads mark two strongly shortened left side kineties. **l:** Ventrolateral view of a specimen inflated due to the preparation procedures. **m, o:** Variability of oral polykinetids. Arrow marks row of dikinetids at proximal margin of right polykinetid. LP – left oral polykinetid, MA – macronucleus, RP – right oral polykinetid. Scale bars 15 μm.

409a, b, d). Contractile vacuole subterminal at base of tail, with single, tubular excretory pore on left body side. Cortex inconspicuous, flexible, no extrusomes recognizable in vivo or protargol preparations. Cytoplasm colourless, contains some minute (< 0.5 µm) crystals sparkling under interference contrast illumination and numerous protargol-affine granules 0.5–1 µm across mainly in posterior half of cell. Feeds on up to 2 µm long bacteria digested in vacuoles 3–7 µm across. Glides rather rapidly on microscope slide and soil particles.

Somatic cilia 10 µm long in vivo, those on tail elongated to 12 µm, without, however, forming distinct caudal cilia. We checked this very carefully because of the general similarity with *C. steinii*, which has two 15 µm long caudal cilia (FOISSNER 1993c). On average 12 ciliary rows following body curvature, composed of dikinetids having both basal bodies ciliated in oral portion of body, while postorally only the posterior basal body bears a cilium. Loosely ciliated, except at left side of keel, where kinetids are closely spaced and two supernumerary, short ciliary rows occur. Left side kineties at margin of rather deep furrows anteriorly, producing serrate keel described above. Last kinetid on right side of tail very likely associated with kinety 2. Long transverse microtubule ribbons originate at left side of kinetids and extend rearwards, forming conspicuous bundles becoming thinner posteriorly, where kinetids are sparser (Fig. 196b, g–l; 409a, b, e–g; Table 175).

Table 175. Morphometric data on *Colpoda formisanoi*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	30.1	30.0	2.9	0.6	9.5	26.0	36.0	21
Body, width	21.4	22.0	3.9	0.9	18.2	15.0	27.0	21
Anterior body end to right oral polykinetid, distance	6.9	7.0	0.9	0.2	13.3	5.0	9.0	21
Anterior body end to posterior margin of left oral polykinetid, distance	12.7	13.0	1.2	0.3	9.1	11.0	15.0	21
Vestibular opening, length	5.7	6.0	0.6	0.2	11.3	5.0	7.0	21
Anterior body end to macronucleus, distance	13.3	13.0	2.4	0.5	17.7	9.0	17.0	21
Ventral body margin to macronucleus, distance	5.2	6.0	3.8	0.8	74.0	1.0	12.0	21
Macronucleus, length	6.3	6.0	0.9	0.2	13.5	5.0	8.0	21
Macronucleus, width	5.7	6.0	0.6	0.2	11.3	5.0	7.0	21
Micronucleus, length	2.7	3.0	–	–	–	2.0	4.0	18
Micronucleus, width	2.2	2.0	–	–	–	2.0	3.0	18
Somatic kineties, total number	11.8	12.0	0.6	0.1	5.1	11.0	13.0	21
Left side shortened kineties, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Kinetids in kinety 3, number [b]	7.9	8.0	1.0	0.2	12.9	6.0	10.0	21
Left oral polykinetid, length	4.5	4.0	0.8	0.2	17.2	4.0	7.0	21
Left oral polykinetid, width	1.6	2.0	–	–	–	1.0	2.0	21
Left oral polykinetid, number of kineties	9.5	9.0	1.3	0.3	13.2	7.0	13.0	21

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] For numbering of kineties, see figure 196g.

Oral apparatus occupies second quarter of ventral side, inconspicuous, funnel opening about 6 µm wide in vivo. Vestibulum broadly conical, with curved pharyngeal fibres extending posteriorly. Left oral polykinetid on vestibular bottom, elongate square, consists of an average of nine minute kineties each composed of usually four cilia 2 µm long at proximal end of organelle and 5 µm distally, do not form a distinct beard as in *C. steinii*; at distal end of organelle one, rarely two cilia, followed by a row with three cilia. Right oral polykinetid on right vestibular wall, consists of four to five, usually four curved ciliary rows forming an elliptical field; proximal row composed of about nine dikinetids. Cilia about 3 µm long in anterior portion of field, form curved, membranoid structure (Fig. 196b, e–h, j, l–o; 409a, c, e–g; Table 175).

Occurrence and ecology: To date found only at type location, but very likely also occurring in agricultural soil of Italy, from which FORMISANO (1957) illustrated this or a similar species (Fig. 196a). Furthermore, we found *C. formisanoi* in soil from Tunisia and the Republic of South Africa. However, conspecificity must still be confirmed by detailed investigations, which are difficult because the slides contain only a few specimens. Certainly, *C. formisanoi* is a rare species only occasionally reaching sufficient numbers to be recognized.

Comparison with related species: *Colpoda formisanoi* is easily identified by the small size, the sigmoidal shape, and the tail-like posterior end. This is a combination of features not found in any other colpodid (FOISSNER 1993c). At first glance, *C. formisanoi* resembles *C. steinii*, which has also strongly shortened left side kineties and a macronucleus with a central nucleolus. However, the shape of the left oral polykinetid is entirely different and resembles those of *C. aspera* and *C. elliotti*. The two strongly shortened left side ciliary rows highly resemble *C. steinii* and → *Dragescozoon terricola*, indicating that these three species build a special group within the Colpodidae. When food remnants have been released, *C. steinii* also may have an acute body end for some time.

Colpoda cavicola KAHL, 1935

We split this species into two subspecies according to the presence/absence of micronuclei; see detailed discussion under *C. cavicola amicronucleata*. The following diagnosis is based on the revision of FOISSNER (1993c).

Improved diagnosis: Size 40–150 × 25–100 µm, usually around 100–120 × 60–80 µm in vivo. Very small and large, macrostome specimens occur in flourishing cultures. Reniform and distinctly spiralized. Proportion of oral to postoral section 1:2.6 to 1:3 on average (1:1.2 or less in most congeners). Macronucleus globular. Two or more micronuclei or amicronucleate. Excretory pore of contractile vacuole in posterior pole centre. Usually 40–50 somatic ciliary rows distinctly condensed postorally and in deep diagonal groove. Left oral polykinetid hook-shaped or crescentic, composed of about 30 kineties. Prefers tree-hole and bark habitats.

Colpoda cavicola cavicola KAHL, 1935 **nov. stat.** (Fig. 410a–h; Table 177)

Diagnosis: With two or more micronuclei.

Locus classicus: Wohldorf near Hamburg (Germany), where KAHL (1935) discovered *C. cavicola cavicola* in a rainwater filled tree-hole.

Remarks: *Colpoda cavicola cavicola*, comprehensively reviewed by FOISSNER (1993c), occurs also in Namibia (Fig. 410a–h; Table 177). It could be cultivated with baker's yeast. Silver nitrate-impregnated voucher specimens have been deposited (Table 1).

Colpoda cavicola amicronucleata **nov. sspec.** (Fig. 411a–o; Tables 176, 177)

Diagnosis: Without micronuclei.

Type location: Bark from *Moringa* trees (*Moringa ovalifolia*) in the Etosha National Park, Namibia, 19°S 15°40'E (site 55 in figures 2, 3 and chapter 2.1.2).

Etymology: The Latin adjective *amicronucleata* (without micronucleus) refers to the main subspecies character.

Description and remarks: *Colpoda cavicola cavicola* has an as yet unexplained preference for tree-holes and is one of the few species in the genus having two or more micronuclei. This feature is very constant in populations world-wide and also found in the population from Namibian site (51). Accordingly, we classify another Namibian population, which lacks micronuclei both in raw and pure cultures, as a new subspecies; in all other features, *C. cavicola amicronucleata* is indistinguishable from *C. cavicola cavicola* (Table 177). Thus we refer the reader to the detailed description of this species in FOISSNER (1993c) and to the figures and figure explanations (Fig. 411a–o). A slight difference is found in the left oral polykinetid, which is hook-shaped in *Colpoda cavicola cavicola* and crescentic in *C. cavicola amicronucleata*. Certainly, this is a rather sophisticated feature, which is difficult to quantify and whose variability is largely unknown. We could cultivate *C. cavicola amicronucleata* in Eau de Volvic with ordinary baker's yeast as food supply. In flourishing cultures developed specimens of extraordinary size (length 200–250 µm) and a very large oral apparatus (about 60 kineties in left oral polykinetid; Fig. 411m, n). They co-existed with very small (length 70 µm) and ordinary-sized specimens.

Usually, we do not consider the presence/absence of a micronucleus as sufficient to split taxa into species or subspecies, although amicronucleate populations are excluded from the gene pool of the species. However, special circumstances suggest such a separation in *C. cavicola*: (i) the species is multimicronucleate in populations world-wide (FOISSNER 1993c); (ii) several seemingly identical species of the *Colpoda magna* flock can be distinguished by concrete morphological traits and the number of micronuclei (FOISSNER 1993c), for instance, *Colpoda magna* (with vestibular kineties and several micronuclei) and *C. orientalis* (without vestibular kineties and 1 micronucleus); (iii) *Colpoda* species are highly diverse according to recent sequence data, suggesting that many of them consist of species flocks (NANNEY et al. 1998).

Table 176. Morphometric data on *Colpoda cavicola amicronucleata*.

Characteristics [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	CHL	101.5	100.0	15.8	3.5	15.6	64.0	125.0	21
Body, width	CHL	73.3	70.0	12.9	2.8	17.6	47.0	95.0	21
Anterior body end to proximal end of left polykinetid (buccal vertex), distance	CHL	34.0	34.0	4.4	1.0	12.9	28.0	45.0	21
Macronucleus, length	FE	19.6	20.0	1.6	0.4	8.2	16.0	23.0	21
Macronucleus, length	PA	21.0	21.0	2.1	0.5	9.8	18.0	25.0	21
Macronucleus, width	FE	18.8	19.0	1.6	0.4	8.6	16.0	21.0	21
Macronucleus, width	PA	19.9	20.0	1.8	0.4	9.2	17.0	23.0	21
Left oral polykinetid, length [b]	PA	11.7	12.0	0.9	0.2	7.8	10.0	14.0	21
Left oral polykinetid, width	PA	3.6	4.0	0.6	0.1	16.3	3.0	5.0	21
Left oral polykinetid, number of kineties	PA	30.8	30.0	2.5	0.6	8.2	27.0	37.0	21
Somatic kineties, number [c]	CHL	49.4	50.0	6.2	1.4	12.6	39.0	63.0	21

[a] Data based on prepared specimens from a pure culture. Randomly selected, except for macrostomes larger than 200 µm, which were discarded. Measurements in µm. CHL – CHATTON-Lwoff silver nitrate impregnation, CV – coefficient of variation in %, FE – Feulgen stain, M – median, Max – maximum, Min – minimum, n – number of specimens investigated, PA – protargol impregnation (FOISSNER's method), SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Measured as chord from anterior to posterior end.

[c] Difficult to assess because strongly spiralized. Values thus approximate.

Table 177. Morphometric comparison of *Colpoda cavicola* and *Colpoda cavicola amicronucleata*.

Characteristics [a]	*C. cavicola* I [b]	*C. cavicola* II [c]	*C. cavicola amicronucleata* [d]
Body, length	64–110 (82)	62–170 (121)	64–125 (102)
Body, width	43–79 (58)	55–130 (96)	47–95 (73)
Anterior end to proximal buccal vertex, distance	26–37 (31)	35–54 (47)	28–45 (34)
Macronucleus, length	?	20–36 (27)	18–25 (21)
Macronucleus, width	?	20–36 (26)	17–23 (20)
Left oral polykinetid, length	10–18 (15)	13–16 (14)	10–14 (12)
Left oral polykinetid, number of kineties	?–? (28)	30–39 (32)	27–37 (31)
Somatic ciliary rows, number	39–55 (46)	38–47 (42)	39–63 (49)

[a] Data based on cultivated, mounted, and CHATTON-LWOFF silver nitrate-impregnated specimens. Measurements in µm. Extremes and arithmetic means (in brackets) are given.

[b] Canadian population studied by NOVOTNY et al. (1977), n = 30.

[c] South American population studied by FOISSNER (1993c), n = 13.

[d] See table 176.

Dragescozoon nov. gen.

Diagnosis: Moderately small Colpodida with hemispherical vestibulum in ventral anterior body half. Somatic ciliature conspicuously condensed preorally due to the special arrangement of the ciliary rows. Right oral ciliary field composed of single row of dikinetids.

Type species: *Dragescozoon terricola* nov. spec.

Dedication: The name is a composite of *Dragesco* and the Greek *zoon*, meaning an animal dedicated to Prof. Dr. Jean DRAGESCO (France), who provided the sample containing the organism and spent a lifetime on African freshwater ciliate research. The genus has neuter gender.

Classification and comparison with related genera: *Dragescozoon terricola* has a clear identity due to its specific somatic and oral ciliary pattern and the curious location of the macronucleus. The familial classification, in contrast, is difficult because each of the three main families of the Colpodida contains a genus with a single-rowed right oral ciliary field (FOISSNER 1993c): *Kuehneltiella* in the family Colpodidae, *Ilsiella* in the family Marynidae, and *Avestina* in the family Hausmanniellidae. Certainly, the single-rowed right oral ciliary field evolved independently in several lines, as shown by the Colpodidae and Marynidae, and thus cannot be used to unite such taxa in a distinct family.

Within the Colpodidae, *D. terricola* resembles small species of the genus *Colpoda* (for instance, *C. steinii* and → *C. formisanoi*) and *Apocolpoda africana*, which also has a conspicuous preoral ridge (Fig. 197i). *Kuehneltiella*, in contrast, comprises large, predatory organisms with a huge vestibulum (→ *K. namibiensis* and FOISSNER 1993c). Within the Hausmanniellidae, *D. terricola* resembles *Avestina*, which is similar in size, ciliature, and nuclear apparatus. Thus, *Dragescozoon* might belong to this group. On the other hand, *Avestina* is a "left-sided" colpodid, that is, has the oral apparatus and the condensed preoral ciliature on the left body side. Thus, the general appearance of *Avestina* and *Dragescozoon* is rather different.

Dragescozoon terricola nov. spec. (Fig. 197a–h; 412a–e; Table 178)

Diagnosis: Size about 40 × 27 µm in vivo; reniform. Nuclear apparatus in anterior body end, macronucleus ellipsoidal and with central nucleolus. 10 somatic ciliary rows and about 5 rows in minute left oral polykinetid.

Type location: Soil in the surroundings of Cotonou, Benin, Africa, 06°N 02°30'E.

Etymology: The Latin adjective *terricola* (living in soil) refers to the habitat the species was discovered.

Description: This species was difficult to investigate because its fragility and dense packing with food vacuoles disturbed live observation and silver carbonate impregnation; protargol preparations failed, too, for unknown reasons. Thus, most data are from silver nitrate-impregnated specimens.

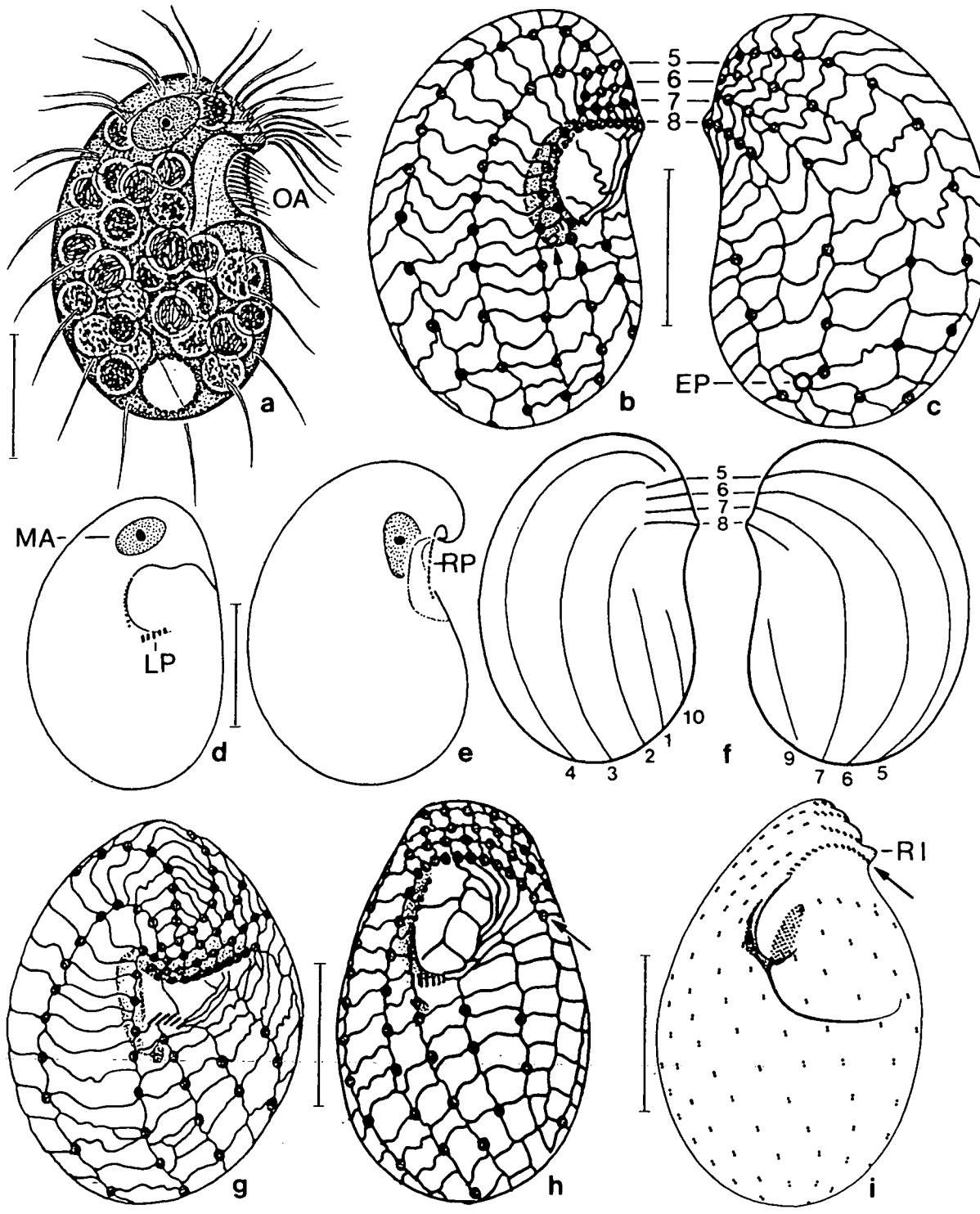


Fig. 197a–i. *Dragescozoon terricola* (a–h) and *Apocolpoda africana* (i) from life (a) and after CHATTON-LWOFF silver nitrate (b, c, f–h) and protargol impregnation (d, e, i). **a:** Right lateral view of a representative specimen. **b, c:** Ciliary pattern and silverline system of right and left side. Arrow marks tubular pharynx. **d, h, i:** Ventral views. Note the conspicuous "preoral" ciliary row (arrows), indicating that *Apocolpoda africana* (i) is probably the nearest relative of *D. terricola* (d, h). **e:** Right lateral view of a *Colpoda maupasi*-shaped specimen. **f:** Numbering of ciliary rows. **g:** Slightly oblique ventral view showing overhanging preoral portion. EP – excretory pore, MA – macronucleus, LP – left oral polykinetid, OA – oral apparatus, RI – ridge, RP – right oral polykinetid. Numbers denote ciliary rows. Scale bars 15 µm.

Size about 35–45 x 25–30 µm in vivo, usually near 40 x 27 µm. Shape fairly constant and often similar to that of *Colpoda maupasi* and *Apocolpoda africana*, that is, broadly reniform due to rather distinct, obliquely truncate preoral projection (Fig. 197a, b, e); indistinctly flattened laterally. Nuclear apparatus invariably near anterior body end, an unusual location making the species easily recognizable (Fig. 197a, d, e). Macronucleus broadly (about 1.5:1) to slenderly (3:1) ellipsoidal, on average near 2:1 (Table 178); very hyaline, contains central nucleolus impregnating intensely with protargol, similar as in *Colpoda steinii* (FOISSNER 1993c). Micronucleus not seen, does not impregnate with protargol. Contractile vacuole in posterior body end with single excretory pore in midline of left side. Cortex bright and fragile, often does not withstand formalin fixation as used for silver carbonate impregnation. Extrusomes recognizable neither in vivo nor in protargol preparations, where the cortex is yellowish or does not impregnate at all. All specimens packed with 3–6 µm-sized food vacuoles containing bacteria. Swims rather rapidly.

Somatic cilia about 8 µm long in vivo, paired in oral body portion, arranged in ten curved (hardly spiralized as in most *Colpoda* species), comparatively widely spaced rows anteriorly more densely ciliated than posteriorly, especially on left side where a conspicuous preoral ciliary tuft is produced by the densely ciliated anterior end of rows 5 to 8 (Fig. 197a–c, g, h; 412a–e). Ciliary rows very particularly arranged, abut preorally without, however, forming a distinct suture (for numbering of rows, see Fig. 197f and FOISSNER 1993c): row 2 extends parallel to right margin of vestibular opening and abuts on row 8 anteriorly; rows 3 and 4 abut on anterior portion of row 5; rows 5 to 7 commence between rows 2 and 3, extend across preoral ventral surface, and then curve posteriorly becoming loosely ciliated; row 8 begins on the preoral ridge and extends from right to left margin of vestibular opening, producing a densely ciliated "preoral row"; rows 9, 10 and 1 are postoral, each comprising only a few kinetids (Fig. 197b, c, g, h; 412a–e).

Oral apparatus subapical, rather large compared to that of small *Colpoda* species. Vestibulum roughly hemispherical, with minute, tubular pharynx in posterior dorsal corner, right vestibular margin sharply defined, left gradually flattens and merges into body proper. Left oral polykinetid on vestibular bottom, composed of about five minute ciliary rows. Right oral field extends along right vestibular margin, inconspicuous in vivo and after protargol impregnation, where it stains clearly and is composed of about 15 closely spaced kinetids in a single row (Fig. 197a, d, e). After silver nitrate impregnation, the right oral margin is much more distinct, very likely due to somatic ciliary row 2, whose anterior portion is close to the vestibular margin (Fig. 197b, g, h; 412a–e).

Silverline system in *Colpoda* pattern, conspicuous because of widely spaced ciliary rows; a median silverline is formed postorally between ciliary rows 7 and 8 and 8 and 9, indicating that preoral row 8 is a shortened left side row. A widely meshed silverline pattern extends in vestibular wall (Fig. 197b, c, g, h; 412b–e).

Occurrence and ecology: To date found only at type location. The material was a composite of dark soil and plant litter from the Abomey University Campus and the Godomey sports field. The sample was rich in colpodids (four *Maryna* species, see *M. lichenicola* and *M. minima*, several *Colpoda* species), including two further new species [a new *Avestina* and a new genus (?)], which could not be processed because they were rare and several other species (*Dragescozoon*, *Maryna* spp.) had to be studied. *Dragescozoon terricola* was abundant already 8 h after wetting the sample, indicating that it is a highly r-selected

organism. After 24h it had disappeared, probably due to the changed milieu because fresh water was added to compensate for the soil percolate used for preparations.

Comparison with related species: This inconspicuous species is easily confused with other small colpodids, for instance, *Colpoda maupasi* (length usually ≥ 50 µm, nuclear apparatus in mid-body) and *Apocolpoda africana* (nuclear apparatus in mid-body, left oral polykinetid more conspicuous; Fig. 197i). Basically, however, *D. terricola* is easily identified by the almost unique location of the macronucleus in the anterior body end (Fig. 197a, d, e). Within colpodids, only *Kreyella minuta* and *Orthokreyella schiffmanni* are similar in this respect. These species are smaller (≤ 30 µm) and have a much more conspicuous left oral polykinetid than *D. terricola*. See FOISSNER (1993c) for a detailed description of all species mentioned.

We are not entirely satisfied with our data, especially of the oral structures, which should be re-studied in silver carbonate preparations.

Table 178. Morphometric data on *Dragescozoon terricola*.

Characteristics [a]	Me [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	CHL	35.9	35.0	2.9	0.8	8.1	30.0	40.0	15
Body, length	PA	33.5	33.0	2.8	0.7	8.3	28.0	38.0	15
Body, width	CHL	26.0	26.0	2.2	0.6	8.5	23.0	30.0	15
Body, width	PA	23.1	23.0	1.8	0.5	7.6	20.0	26.0	15
Anterior body end to 1st ciliary row above oral aperture, distance	CHL	7.4	7.0	1.1	0.3	14.3	5.0	9.0	15
Anterior body end to left oral polykinetid, distance	CHL	17.0	17.0	2.0	0.5	11.6	13.0	20.0	15
Anterior body end to macronucleus, distance	PA	3.3	3.0	1.8	0.5	53.6	1.0	7.0	15
Macronucleus, length	PA	6.5	7.0	1.0	0.3	15.3	5.0	8.0	15
Macronucleus, width	PA	4.2	4.0	1.0	0.3	24.2	3.0	7.0	15
Left oral polykinetid, length	CHL	3.5	4.0	–	–	–	3.0	4.0	15
Right oral ciliary row, length	CHL	9.1	9.0	1.2	0.3	12.8	7.0	11.0	15
Ciliary rows, total number (Fig. 197f) [b]	CHL	10.0	10.0	0.0	0.0	0.0	10.0	10.0	15
Postoral ciliary rows, number	CHL	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
Kinetids in 2nd ciliary row, number (Fig. 197f)	CHL	10.0	10.0	0.9	0.2	8.5	9.0	12.0	15
Kinetids in 6th ciliary row, number (Fig. 197f)	CHL	10.4	10.0	1.5	0.4	14.5	8.0	13.0	15
Kinetids in 2nd plus 8th ciliary row, number (Fig. 197f)	CHL	20.2	20.0	1.7	0.4	8.4	18.0	24.0	15

[a] Data based on silver-impregnated and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Me – methods, Min – minimum, n – number of specimens investigated, PA – protargol impregnation (FOISSNER's method), SD – standard deviation, SE – standard error of mean, $\bar{x}$ – arithmetic mean.

[b] Number depends on counting site and interpretation of row course (Fig. 197f). If counted postorally, there are only nine rows because the preoral row (row 8, Fig. 197f) is strongly shortened. Nine rows are also obtained, if row 8 is considered as part of row 2.

Kuehneltiella namibiensis nov. spec. (Fig. 198a–p; 413a–z; Table 179)

Diagnosis: Size about 180 × 120 µm in vivo. Ellipsoidal with straight or slightly notched left vestibular wall not covered by right wall. Several micronuclei. On average 90 somatic ciliary rows and 28 kineties in left oral polykinetid, which forms a conspicuous ciliary plate in main body axis. Resting cyst ellipsoidal, covered with smooth, about 20 µm thick ectocyst.

Type location: Bark from *Sterculia africana* near the Ameib Guest Farm, Namibia, 21°50'S 15°35'E (site 45 in figure 2 and chapter 2.1.2).

Etymology: Named after the country discovered.

Description: In the raw culture and pure culture trials (see below) ovate, usually rather slender and small (length about 120 µm) specimens occurred, whose oral structures were more or less completely reduced (Fig. 413n, o, r). In spite of this, they frequently contained some or many food vacuoles and occasionally were even of ordinary size (Fig. 198k). Such probably precystic or injured specimens were also observed in the other species of the genus (FOISSNER 1993c) and excluded from the description and morphometric analysis.

Size 130–300 × 80–200 µm in vivo, usually about 180 × 120 µm; the largest specimen seen measured 300 × 200 × 150 µm. In vivo measurements shown in table 179 are slightly selected for large specimens and thus match the prepared cells, if 5–10% shrinkage are taken into account due to the preparation procedures. Shape broadly ellipsoidal on average (1.6–1.7:1; Table 179), usually slightly more slender and reniform than other large colpodids providing the species with a rather distinct appearance (Fig. 198a); highly variable in details: broadly ellipsoidal with more or less distinctly projecting vestibular bottom and straight left vestibular wall, very reminiscent of *Krassniggia*, *Bresslauides*, and *Corticocolpoda* (Fig. 179a, b, h, j, m, n; 413a, b, f, k); broadly ellipsoidal with more or less distinctly projecting vestibular bottom and distinctly notched left vestibular wall, similar as in *Kuehneltiella terricola* (Fig. 198i; 413e, l); reniform with vestibular bottom neither projecting nor notched (Fig. 198d, e). Laterally slightly flattened, even if well-fed, right side flat, left convex and lacking diagonal groove (Fig. 198c; 413d, e, l); starved specimens leaf-like. Shape rather fragile, that is, often changes more or less distinctly when specimens are transferred with a micropipette. Macronucleus usually in posterior body half, ellipsoidal to broadly ellipsoidal, never globular, with reticular nucleolus. Several slightly ellipsoidal micronuclei, each surrounded by a distinct membrane, attached to macronucleus (Fig. 198a, c; 413g, m). Contractile vacuole in posterior body end with single, subterminal excretory pore on left side, projects from body proper when completely filled (Fig. 198c); no collecting canals. Cortex colourless, very flexible, contains numerous, 3–4 µm long, rod-shaped extrusomes (Fig. 198f; 413h). Cytoplasm without special inclusions, usually so crammed with large food vacuoles that specimens appear black at low magnification (≤ ×40). Feeds on various medium-sized ciliates (*Colpoda inflata*, *C. maupasi*, *Gonostomum affine*) and even on large rotifers heavily deforming the ciliate (Fig. 413g). Glides rapidly on flat right surface or swims by rotation about main body axis. Never rests, except when ingesting large prey items; occasionally attaches to bacterial masses or soil particles (Fig. 198c).

Cilia about 10 µm long in vivo, elongated to 15 µm on bottom and inner surface of vestibular roof, paired except in posterior pole area. Ciliary pattern and silverline system as in other large colpodids (Fig. 198m–p; 413a–f, i–l, q). Basically, the about 90 ciliary rows originate

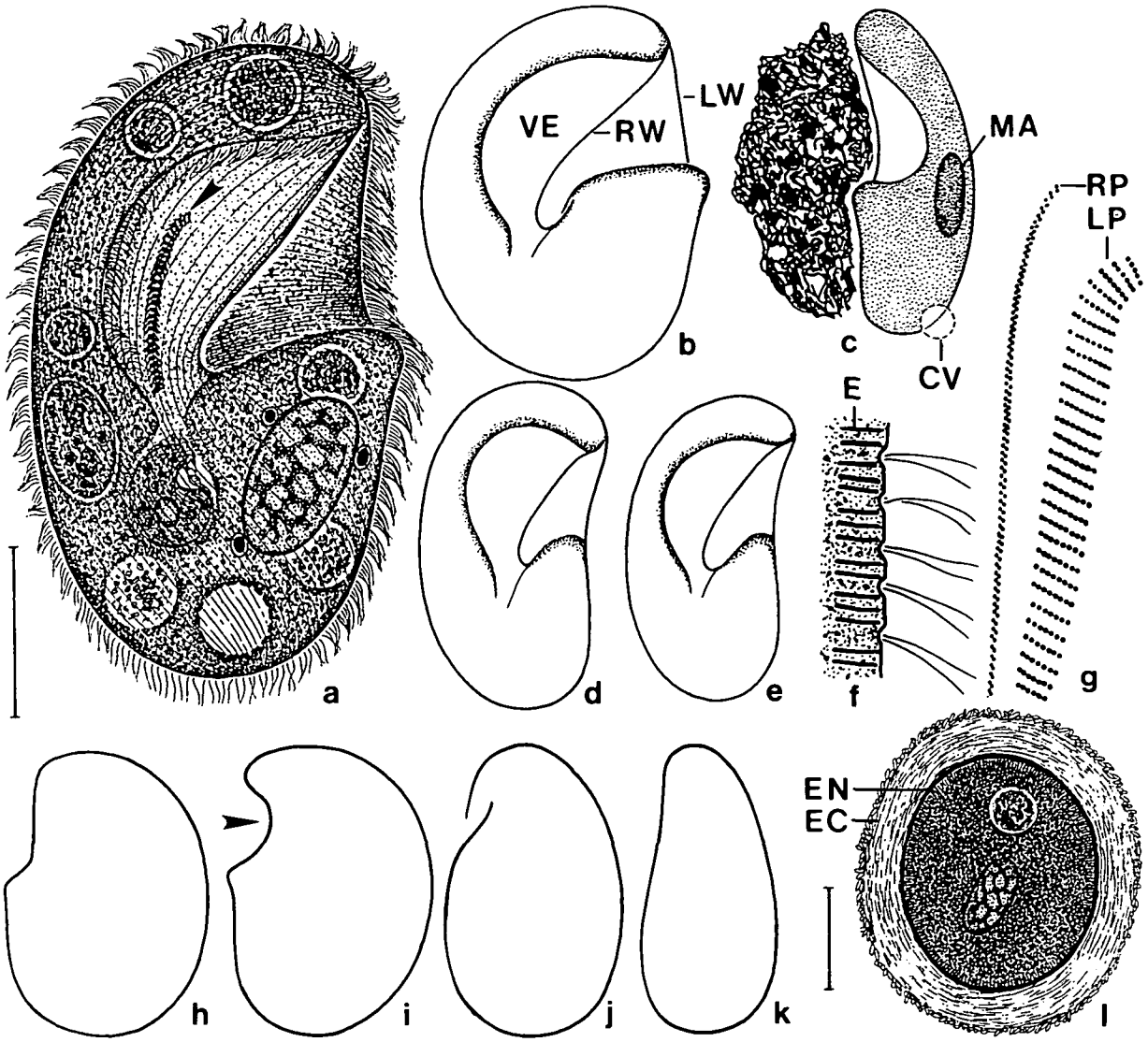
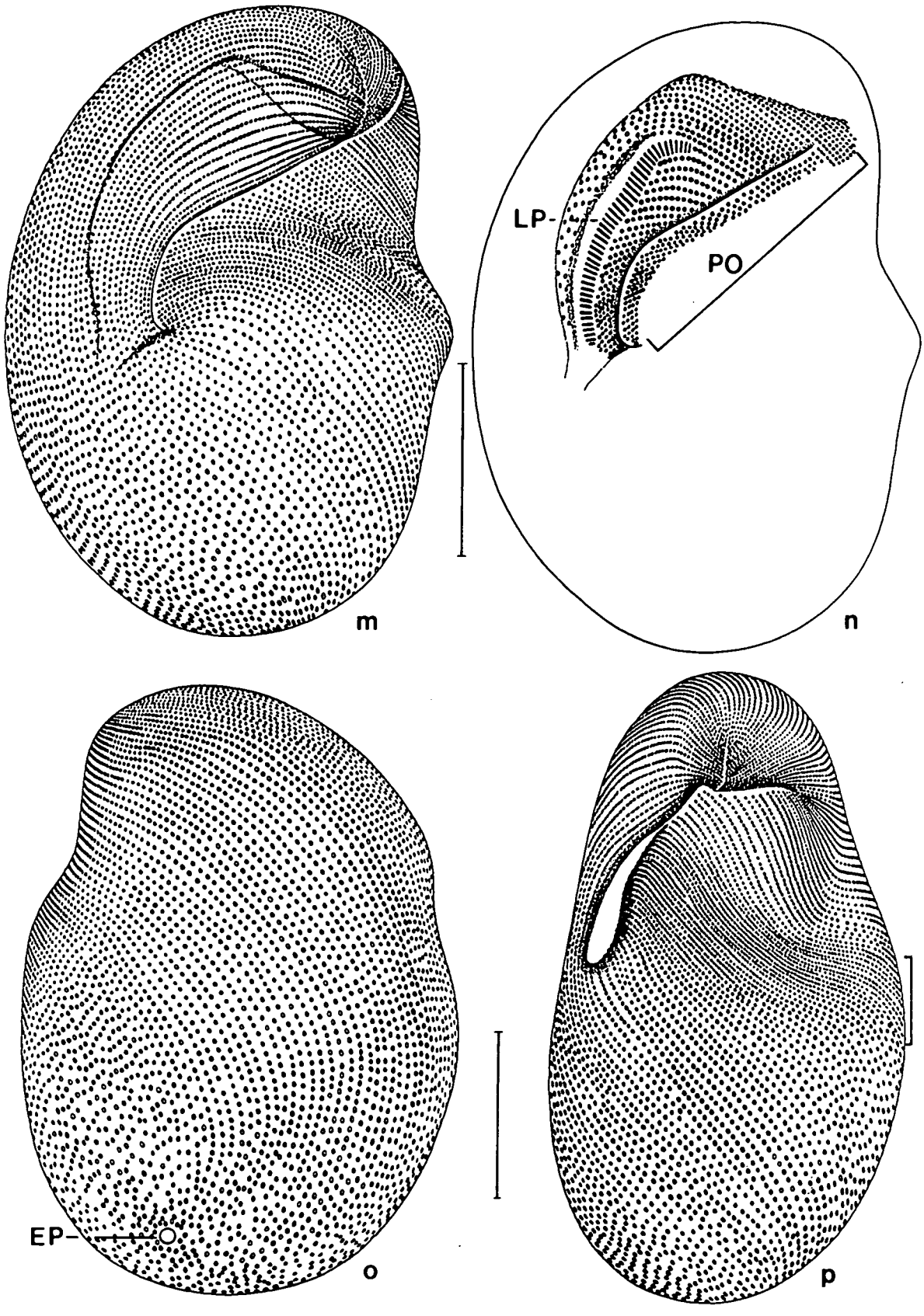


Fig. 198a–l. *Kuehneltiella namibiensis* from life (a–f, h–l) and after silver carbonate impregnation (g). **g:** Right side view of a representative specimen packed with large food vacuoles containing ciliates. Note the three micronuclei attached to the macronucleus. The left oral polykinetid (arrowhead) appears as dense stripe of cilia on the left vestibular wall. **b:** The largest specimen observed, about 300 × 200 × 150 µm. **c:** Ventral view of a specimen attached to a soil particle. Note the projecting contractile vacuole. **d, e:** Reniform specimens are frequent. **f:** Optical section of cortex showing fringe formed by the about 3 µm long extrusomes. **g:** Oral structures. The left polykinetid consists of equidistant short kineties, showing that the Namibian species belongs to *Kuehneltiella* because *Corticocolpoda* has paired kineties (FOISSNER 1993a). The right "polykinetid" consists of a single row of dikinetids, as in the other species of the genus and in *Corticocolpoda*. **h–j:** Shape variants, including a specimen with notched left vestibular wall (arrowhead), as is typical for *Kuehneltiella*. **k:** An ovate, probably precystic specimen. **l:** The resting cysts of *K. namibiensis* are large (~ 160 × 140 µm) and massive. The exemplar shown is from the raw culture and thus has an unknown age. Both the ectocyst and endocyst are smooth. The 2–3 µm thick endocyst is brownish, while the 20 µm thick ectocyst is colourless and very hyaline; its surface is colonized by bacteria. CV – contractile vacuole, E – extrusomes, EC – ectocyst, EN – endocyst, LP – left oral polykinetid, LW – left vestibular wall, MA – macronucleus, RP – right oral polykinetid, RW – right vestibular wall, VE – vestibulum. Scale bars (a, l) 50 µm.

Fig. 198m–p. *Kuehneltiella namibiensis*, somatic and oral ciliary pattern after CHATTON-LWOFF silver nitrate impregnation. **m, n:** Right side view of same specimen at two focal planes to show vestibular ciliary pattern. **o:** Left side view. Note that the diagonal (postoral) groove does not extend onto the left side (see next figure). **p:** Ventral view. Bracket marks kineties with very closely spaced kinetids in the postoral groove. EP – excretory pore, LP – left oral polykinetid, PO – postoral ciliary rows. Scale bars 50 µm.


m
LP
PO
n
EP
o
p

along the preoral suture and left oral polykinetid coursing spirally backwards, where they become more loosely ciliated, ending in the surroundings of the excretory pore of the contractile vacuole. About ten ciliary rows at the posterior vestibular vertex extend onto the inner side of the right vestibular wall to become widely spaced vestibular kineties seen only in live and silver carbonate-impregnated specimens. Ciliary rows equidistantly spaced except for vestibular bottom, where a stripe of condensed ciliature indicates a postoral (diagonal) groove on ventral side.

Vestibulum very large, occupies almost entire anterior body half, funnel-shaped with cytostome right of cell's midline. Right vestibular wall does not overhang left, extends obliquely from ventral anterior end to centre of right body surface; left wall straight to rather distinctly notched (Fig. 198a, b, d, e, h–j, m–p; 413a, b, d–f, i, k, l). Oral polykinetids in dorsal third of cell, do not protrude from vestibulum, small compared to size of cell. Left polykinetid extends in main body axis, as proved in CHATTON-LWOFF silver-impregnated specimens (Fig. 413b, c); slightly curved, on average 45 × 5 µm and composed of 28 equidistant kineties bearing 5 µm long cilia. Right "polykinetid" composed of closely spaced dikinetids in a single row, to which the vestibular kineties obliquely abut (Fig. 198a, g, m, n; 413b, c, p–t).

Division in reproductive cysts, not studied. Resting cysts globular to ellipsoidal, on average broadly ellipsoidal, that is, 155 × 138 µm, appear brown and massive at a magnification of ×100 (Fig. 198j; 413u–z; Table 179). Endocyst 2–3 µm thick, smooth, light brown (determined in squashed exemplars). Ectocyst 20 µm thick on average, very hyaline, colourless, smooth, elastic (does not break into pieces or dissolve when cyst is heavily squashed), possibly composed of many fine membranes; interspersed by many kinds of bacteria in cysts from "pure" cultures (see below), while only the surface is colonized in cysts from the raw culture (Fig. 198 l; 413y, z). Cyst content colourless, mainly composed of fat globules 1–3 µm across (rarely up to 10 µm) and an about 25 µm-sized vacuole bearing unidentified remnants; extrusomes retained, form indistinct, 3 µm thick fringe.

Occurrence and ecology: To date found only at type location, a very special habitat described in chapter 2.1.2. Trials to cultivate *K. namibiensis* in pure Eau de Volvic, diluted garden soil extract, and diluted (with Eau de Volvic) bark water from the original sample failed, although adequate food (*Colpoda maupasi* and *Gonostomum*) was added. Only once, the species grew for a couple of days in a trial with diluted bark water from the original sample. This indicates that *K. namibiensis* was not accidentally found in the bark but needs this special milieu.

Comparison with related species: *Kuehneltiella namibiensis* is easily distinguished from the two congeners reviewed in FOISSNER (1993c). Both are on average distinctly smaller (≤ 140 vs. 180 µm) and have only a single micronucleus and much fewer somatic ciliary rows (< 70 vs. 90) and kineties in the left oral polykinetid (< 20 vs. 28). Furthermore, the left vestibular wall is much more distinctly notched in *K. terricola* and *K. muscicola* than in *K. namibiensis*, weakening the diagnosis of the genus. The resting cysts are also different, indicating that the three species are rather distantly related. Likewise, all species are very rare and live in different geographic regions and habitats: *K. terricola* in arid grassland soil of Australia; *K. muscicola* in mosses from Germany; and *K. namibiensis* in *Sterculia* bark from Namibia.

In vivo, *K. namibiensis* is easily confused with other large colpodids, especially *Krassniggia*

auxiliaris and *Bresslauides* spp. (right oral polykinetid composed of a field of scattered kinetids) as well as *Corticocolpoda kaneshiroae* FOISSNER, 1993a (left oral polykinetid composed of **pairs** of kineties). There is no simple in vivo feature separating these species although, for instance, the paired oral kineties of *C. kaneshiroae* can be rather easily seen with interference contrast optics. Thus, silver impregnation of the oral structures is indispensable for a reliable identification.

Table 179. Morphometric data on *Kuehneltiella namibiensis*.

Characteristics [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	IV	201.8	200.0	50.0	15.1	24.8	130.0	300.0	11
Body, length	CHL	158.4	160.0	17.0	5.1	10.7	125.0	180.0	11
Body, width	IV	120.9	120.0	36.8	11.1	30.4	75.0	200.0	11
Body, width	CHL	102.9	103.0	17.2	5.2	16.7	76.0	125.0	11
Anterior end to anterior vestibular vertex, distance	CHL	22.7	23.0	3.7	1.1	16.1	17.0	30.0	11
Anterior end to posterior vestibular vertex, distance	CHL	82.1	80.0	10.2	3.1	12.4	66.0	97.0	11
Anterior body end to left polykinetid, distance	CHL	37.1	37.0	7.0	2.1	18.7	30.0	48.0	11
Anterior body end to proximal end of left oral polykinetid, distance	CHL	82.6	80.0	12.0	3.6	14.5	65.0	100.0	11
Left body margin to dorsal vestibular wall, distance	CHL	79.0	78.0	14.2	4.3	17.9	55.0	100.0	11
Macronucleus, length	CHL	41.9	40.0	5.0	1.5	12.1	33.0	53.0	11
Macronucleus, width	CHL	24.2	23.0	4.6	1.4	19.2	20.0	35.0	11
Micronucleus, length	CHL	4.8	5.0	–	–	–	4.0	5.0	11
Micronucleus, width	CHL	3.8	4.0	–	–	–	3.0	5.0	11
Micronuclei, number	SC	3.2	3.0	1.0	0.3	32.3	2.0	5.0	10
Left oral polykinetid, length	CHL	45.3	45.0	6.6	2.0	14.6	34.0	55.0	11
Left oral polykinetid, maximum width	CHL	5.2	5.0	–	–	–	5.0	6.0	11
Left oral polykinetid, number of kineties	SC+CHL	28.4	28.0	6.4	1.2	22.4	17.0	44.0	30
Somatic kineties, total number [b]	CHL	90.3	90.0	–	–	–	76.0	100.0	11
Postoral kineties, number [b]	CHL	47.0	48.0	–	–	–	38.0	58.0	11
Kinetids in 10th kinety right of vestibular opening, number [b]	CHL	111.8	110.0	–	–	–	90.0	130.0	11
Resting cysts, length without ectocyst	IV	120.7	118.0	22.2	5.9	18.4	100.0	170.0	14
Resting cysts, length with ectocyst	IV	155.4	158.0	24.1	6.4	15.5	120.0	210.0	14
Resting cysts, width without ectocyst	IV	101.4	98.0	16.0	4.3	15.8	75.0	135.0	14
Resting cysts, width with ectocyst	IV	137.9	130.0	19.4	5.2	14.1	110.0	180.0	14

[a] Data based on randomly selected specimens from a non-flooded Petri dish culture, except for the resting cysts, which are from a pure culture, as described in the ecology section. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, IV – in vivo, M – median, Max – maximum, Min – minimum, n – number of specimens investigated, SC – silver carbonate impregnation, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Approximate values because difficult to count.

Family Exocolpodidae nov. fam.

Diagnosis: Colpodida PUYTORAC et al., 1974, as defined by FOISSNER (1993c), dividing in freely motile (non-encysted) condition. Vestibular opening in anterior body half.

Type genus: *Exocolpoda* nov. gen.

Classification: It is textbook knowledge that members of the order Colpodida, especially species of the family Colpodidae reproduce in division cysts, usually generating four offspring (for a review, see FOISSNER 1993c). When division commences, the trophont rounds up, despiralizes the somatic ciliary rows, and resorbs the oral structures, which later are re-built by anlagen fields. We were thus highly surprised to find a "typical" *Colpoda* species, viz., *Colpoda augustini* FOISSNER, 1987c, that divides in non-encysted condition. Although the reproduction process is the same as in *Colpoda* (despiralization of ciliary rows etc.), we consider this difference as a family character. Furthermore, reproduction has been studied in rather few species/genera of the order, and thus division in freely motile condition might be more common than hitherto recognized. Indeed, we know a freely dividing "*Colpoda*", which produces division chains with four tomites, from the tanks of South American bromeliads (FOISSNER & CORDEIRO 2000). This still unnamed new genus will be described later and included in the family Exocolpodidae established here.

Certainly, it is debatable whether the different life cycle is sufficient for familial separation. In our opinion it is, especially because the family Colpodidae already contains seven genera making a cladistic classification difficult. Further, the family is not monotypic, as shown by the new genus from the tanks of bromeliads.

Exocolpoda nov. gen.

Diagnosis: Medium-sized, microphagous Exocolpodidae with small, conical vestibulum. Left wall of vestibulum overhangs right. Right oral polykinetid composed of few to many short, more or less distinctly disordered kineties.

Type species: *Colpoda augustini* FOISSNER, 1987c.

Etymology: Composite of the Greek prefix *exo* (beyond, devoid of) and the Greek generic name *cólpos* (Colpoda, bosom), referring to the freely motile division (devoid of division cysts so common in other members of the order) and the relationship with *Colpoda*. Feminine gender.

Remarks: The diagnosis is adapted to the revision of the group by FOISSNER (1993c). Basically, *E. augustini* differs from *Colpoda* and related genera by the life cycle (family character). Furthermore, it is the sole species having a boomerang-shaped left oral ciliary field, a distinct feature used by FOISSNER (1987c) to define the species. It is also unique in having a very thick resting cyst wall (see below).

Exocolpoda augustini (FOISSNER, 1987) **nov. comb.** (Fig. 198a–c; 414a–q, 415a–t, 416a–v, 417a–w; Table 179)

The following paragraphs summarize observations made on various populations over the years. Most data are from a Namibian site (39) population, which could be cultivated for some weeks in diluted soil percolate (Eau de Volvic plus run off from the Petri dish and some wheat grains for stimulating bacterial growth). Generally, however, *E. augustini* is difficult to cultivate; many trials with populations from other sites failed.

All observations match or supplement the original description. Thus, a full redescription is not necessary, and our contribution will focus on details not mentioned by FOISSNER (1987c, 1993c). Furthermore, we refer to the table with morphometric data and the copious illustration.

(1) Usually, *Exocolpoda augustini* is well-recognizable by its shape, which is between that of *C. inflata* and *C. maupasi* with the anterior end more distinctly pointed (Fig. 198a; 414a–c, 415a, g–i, 416a–c).

(2) The nucleolar pattern is rather variable and thus cannot be used as a species characteristic (Fig. 414q). Portuguese specimens even have a large, central nucleolus, like *Colpoda steinii*.

(3) *Exocolpoda augustini* is difficult to impregnate with various protargol techniques because the cortical extrusomes, likely some sort of mucocysts, usually impregnate heavily, hidding the infraciliature. The extrusome pattern is sometimes highly conspicuous because it matches the silverline pattern (Fig. 414d, e, g). Other populations, however, have rather scattered mucocysts (Fig. 414f, h, 416h).

(4) *Exocolpoda augustini* has a conspicuous preoral keel because it is comparatively long and the anterior portion of the left keel kineties is very densely ciliated (Fig. 198a; 414a, c, i–l, 415a–e, 416a, c, d).

(5) The vestibulum and the right oral polykinetid are comparatively small, while the left polykinetid is conspicuous, not only because of its boomerang-like shape but also due to the distal portion which has elongated cilia, producing a rather distinct "beard", as in *Colpoda steinii* (Fig. 414a, i–p, 415a–d, 416e–g, l, n, p).

(6) The resting cysts are globular with an average diameter of 31 µm, which accounts for a volume of about 17000 µm^3 (Fig. 198c; 415 l–t; Table 179). They are unique by the very thick and stable endo- and mesocyst wall having a larger volume (about 5000 µm^3) than the encysted cell proper (about 3500 µm^3). If the thick ectocyst is added, which has a volume of about 9000 µm^3, the difference becomes dramatic. In similarly sized *Colpoda* species, the endo-and mesocyst wall volume is lower than that of the encysted cells, for instance, in *C. maupasi* (about 3600 µm^3 vs. 5600 µm^3) and *C. inflata* (about 2300 µm^3 vs. 2600 µm^3), as calculated from the values provided by FOISSNER (1993c). The endo-and mesocyst, which hardly can be distinguished light microscopically and stain blue with methyl green-pyronin, have a light to deep honey-yellow colour and appear to be composed of many tightly spaced membranes. They are very stable and can be disrupted only if cysts are heavily squashed between slide and cover glass. The ectocyst is distinct from

the mesocyst because it is colourless, rather hyaline, structureless, and rather thick (Table 179). Usually, there are few to many bright, 2–3 × 1–2 µm-sized granules in the ectocyst (Fig. 198c; 415 l, n, q, s). These inclusions, which are insoluble in water and do not stain with methyl green-pyronin, might be bacterial spores released from the food vacuoles of the encysting cell. The rather hyaline cyst content is colourless and contains some fat globules 0.5–2 µm across. The nuclear apparatus is in the centre and surrounded by highly refractive, minute granules. As in *Colpoda* spp., resting cysts with two specimens in a common wall occur (Fig. 415q).

(7) *Exocolpoda augustini* has a distinct preference for hot and dry habitats, that is, deserts and semi-deserts, which might explain the extraordinary cyst wall. Thus, it is rare and infrequent in samples from Central Europe (FOISSNER 2000a). In Namibia, it was abundant, inter alia, in the slightly saline samples from sites 38 and 39, that is, in soil covered with the shrub-like lichen *Teloschistes capensis*. The samples were crowded with *E. augustini* two days after rewetting, showing that many cysts were present.

(8) Many dividing cells were found in the pure cultures and silver nitrate slides. The entire process could also be followed in the scanning electron microscope because division occurs in freely motile condition without forming a membrane. Thus, only two offspring are produced, contrary to many other species of the order, which generate four to sixteen daughters in a single division cyst (FOISSNER 1993c). However, basically division of *Exocolpoda augustini* proceeds as in *Colpoda* spp.; thus, we document the process not by line drawings but by a multitude of micrographs, with details mentioned in the figure explanations.

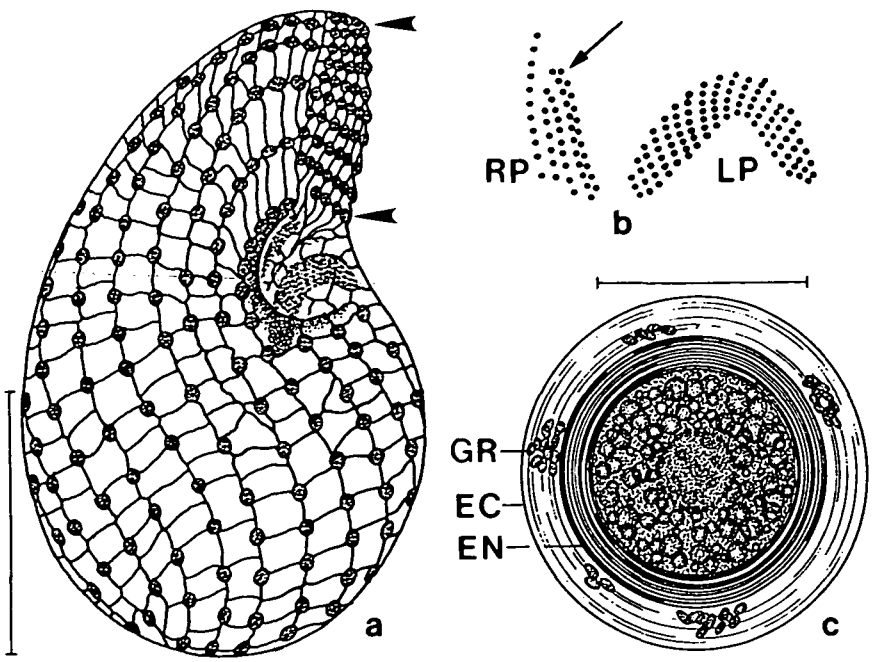


Fig. 198a–c. *Exocolpoda augustini* from Namibian site (39). **a:** Ventrolateral view of ciliary and silverline pattern after CHATTON-LWOFF silver nitrate impregnation. Arrowheads delimit the closely spaced and ciliated left side keel kineties, which abut to the widely spaced right side ciliary rows. **b:** Oral structures after silver carbonate impregnation. Arrow marks proximal row of dikinetids. **c:** Resting cyst in vivo. Note the centrally located macronucleus covered by a layer of refractive granules. EC – ectocyst, EN – meso- and endocyst, GR – granules, LP – left oral polykinetid, RP – right oral polykinetid. Scale bars 20 µm.

Table 179. Morphometric data on *Exocolpoda augustini* from Namibian site (39).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	47.0	48.0	5.4	1.2	11.5	38.0	57.0	21
Body, width in lateral view	29.2	30.0	2.4	0.5	8.2	25.0	33.0	21
Anterior body end to first kinety right of oral apparatus (~ oral opening), distance	13.4	13.0	1.3	0.3	9.9	11.0	15.0	21
Anterior body end to proximal end of left oral polykinetid (~end of oral opening), distance	24.0	24.0	2.1	0.5	8.6	20.0	27.0	21
Anterior body end to macronucleus, distance	21.1	20.0	5.7	1.2	26.8	11.0	30.0	21
Macronucleus, length	9.0	9.0	1.2	0.3	13.4	7.0	11.0	21
Macronucleus, width	8.5	8.0	1.1	0.2	12.7	7.0	11.0	21
Micronucleus, largest diameter	2.1	2.0	–	–	–	2.0	3.0	21
Left oral polykinetid, length of chord	7.7	8.0	0.7	0.1	8.6	7.0	9.0	21
Left oral polykinetid, maximum width	2.7	2.8	–	–	–	2.0	3.0	21
Ciliary rows, right side number	6.1	6.0	0.4	0.1	7.2	5.0	7.0	21
Ciliary rows, left side number	9.2	9.0	1.1	0.3	12.3	7.0	11.0	21
Ciliary rows, postoral number	5.1	5.0	0.9	0.2	18.5	4.0	7.0	21
Ciliary rows, total number	20.4	20.5	1.6	0.3	7.6	17.0	24.0	28
Left oral polykinetid, number of ciliary rows	17.0	17.0	1.5	0.3	8.5	15.0	20.0	21
Resting cysts, total length (in vivo)	32.1	33.0	6.4	1.6	19.9	20.0	43.0	17
Resting cysts, total width (in vivo)	31.1	30.0	5.4	1.3	17.3	20.0	40.0	17
Resting cysts, length without ectocyst (in vivo)	25.4	26.0	3.4	0.8	13.2	18.0	30.0	17
Resting cysts, width without ectocyst (in vivo)	25.4	26.0	3.4	0.8	13.2	18.0	30.0	17
Mesocyst + endocyst, width (in vivo)	3.3	3.0	0.9	0.2	28.9	2.0	5.0	30

[a] Data, if not otherwise stated, from mounted, CHATTON-LWOFF silver nitrate-impregnated, and randomly selected specimens from a mixed culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Division commences by rounding up of the cell and resorption of the cilia around the oral apparatus, especially in the area where the oral anlagen will develop (Fig. 416i–p). This particularity, which has not been described in other colpodids, is important in distinguishing early dividers from post-dividers, which look very similar, except for these cilia (lacking vs. present). Concomitantly, the ciliary rows become radially arranged, the vestibulum flattens, and the cilia of the oral fields are resorbed from the distal to the proximal end of the organelles. It is at this stage, that the shape of the polykinetids and the arrangement of the basal bodies within the organelles can be seen very clearly. As in most *Colpoda* species, the proximal margin of the right polykinetid is made by a row of dikinetids (Fig. 416i–v). When cell furrowing commences, the oral ciliary fields and the remaining somatic cilia are resorbed with new ones concomitantly sprouting within the rows (Fig. 417a–j). Then, basal bodies are generated at the anterior end of each 4–5 kineties in proter and opisthe, but with the division axis of the opisthe shifted by 90° relative to that of the proter, as in → platyophryids and → woodruffiids (Fig. 417i–n). Five to six anlagen but only four to five stomatogenic kineties are recognizable because the rightmost anlage splits transversely: the upper half becomes the right oral polykinetid, while the posterior half contributes to the anlagen for the left oral

polykinetid (Fig. 417k–n). The newly formed basal bodies at the anterior end of the kineties arrange to oral polykinetids in the very late dividers (Fig. 417h, p, q). However, only half or less of the basal bodies produced in the anlagen are used, while the others are resorbed. When the daughter cells separate, they are still globular. Body and vestibulum shaping as well as the final shaping of the oral polykinetids occur only in post-dividers. The elongated cilia at the distal end of the left oral polykinetid are very distinct at this stage (Fig. 417r–u).

Family Hausmanniellidae FOISSNER, 1987

FOISSNER (1993c) thoroughly reviewed the knowledge available about the Hausmanniellidae. However, some updating is necessary because FOISSNER (1993c), although mentioning macrostome formation in *Hausmanniella patella*, did not recognize that *Corallocolpoda pacifica* ALEKPEROV, 1991 is the fully developed macrostome of *H. patella*. Thus, this genus and species must be abandoned. Likewise, FOISSNER (1993c) described the macrostome of *H. patella* as a distinct species within the genus *Anictostoma*, *A. terricola*. This species must also be synonymized with *H. patella*, while the genus *Anictostoma* FOISSNER, 1993c, too hastily synonymized with *Corallocolpoda* by FOISSNER (1993c), is resurrected with the curious *Anictostoma grelli* FOISSNER, 1993a as the type species.

Interestingly, we were unable to produce experimentally macrostomes in *H. discoidea*, the second species of the genus. Likewise, we never observed distinct macrostomes in raw cultures of this species, with the exception mentioned in FOISSNER (1993c), although we observed it in at least 200 samples from terrestrial biotopes world-wide.

Hausmanniella patella (KAHL, 1931) FOISSNER, 1984 (Fig. 199a–d; 418a–l; Table 180)

1931 *Colpoda patella* KAHL, Tierwelt Dtl., 21: 276.
1950 *Colpoda patella* KAHL — GELEI & SZABÁDOS, Annls biol. Univ. szeged, 1: 260, 281.
1984 *Hausmanniella patella* (KAHL, 1931) — FOISSNER, Stapfia, 12: 102.
1987 *Hausmanniella patella* (KAHL, 1931) FOISSNER, 1984 — FOISSNER, Zool. Beitr., 31: 265 (authoritative redescription).
1991 *Corallocolpoda pacifica* ALEKPEROV, Zool. Zh., 70: 125 (new synonym).
1993 *Hausmanniella patella* (KAHL, 1931) FOISSNER, 1984 — Colpodea: 280 (ordinary specimens: Fig. 121 a–e, g–i, p; intermediates: Fig. 121f, j, k, n, o; macrostomes: 129a–l, 133a, b).
1993 *Anictostoma terricola* FOISSNER, Colpodea: 313.

Hausmanniella patella has been reviewed in detail by FOISSNER (1993c). Thus, we comment only on macrostome formation and morphology.

Induction of macrostomy: Fully developed macrostomes of *H. patella* occur, albeit rarely, in raw (non-flooded Petri dish) cultures and were described as distinct genera and

species, as explained above. In the laboratory, the process is rather difficult to verify because the species is not easily cultivated and, in successful cultures, most specimens are macrostomes. However, now we have two lines of evidences that true macrostomy occurs in specimens from Namibian site (15), where the species is abundant: (i) We isolated three *Corallocolpoda pacifica*-like looking specimens, that is, cells with large, flat oral field from the non-flooded Petri dish culture and stored the slide in a wet chamber. After a week, when the cells were encysted for about five days, they were reactivated by addition of baker's yeast. The excysted specimens looked like ordinary *H. patella*, that is, had an ordinary-sized oral field. As the specimens did not grow on yeast, the experiment was broken off. (ii) We isolated ten small-mouthed specimens from the raw culture mentioned above and added them to a flourishing culture of small *Colpoda* species (*C. steinii*, *C. maupasi*, *C. inflata*, *C. cucullus*) cultivated in Eau de Volvic with baker's yeast as main food source. This provided a flourishing culture after a few days, composed, at the time of fixation, of about 95% macrostomes and 5% cells showing all transitions from small-mouthed ordinary specimens to large-mouthed *Corallocolpoda pacifica*-like looking cells. Four slides each of CHATTON-LWOFF silver nitrate and protargol-impregnated specimens from this culture have been deposited (Table 1). A series of transitions is marked on the cover glass of each silver nitrate slide.

Table 180. Morphometric data on ordinary (upper line: mainly stage 0 cells as shown in Fig. 199a) and macrostomous (lower line: mainly stage 2 cells as shown in Fig. 199c) individuals of *Hausmanniella patella* from Namibian site (15).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	82.5	81.0	10.9	2.1	13.2	64.0	104.0	25
	81.1	81.0	13.4	2.6	16.5	54.0	100.0	25
Body, width	62.6	61.0	9.0	1.9	14.4	46.0	81.0	25
	62.0	63.0	10.3	2.0	16.5	41.0	79.0	25
Oral opening, length	21.9	20.0	5.5	1.1	25.1	13.0	31.0	25
	27.4	26.0	4.1	0.9	15.0	21.0	35.0	25
Oral opening, width	22.4	24.0	4.8	1.0	21.2	13.0	31.0	25
	28.6	29.0	4.6	0.9	16.1	19.0	36.0	25
Postoral kineties, number	10.1	10.0	1.3	0.3	13.2	7.0	13.0	25
	11.4	11.0	1.2	0.2	10.4	9.0	13.0	25
Body length:width, ratio	1.3	1.3	0.1	0.1	8.1	1.1	1.5	25
	1.3	1.3	0.1	0.1	11.2	1.1	1.6	25
Body length:oral opening length, ratio	3.8	3.6	0.7	0.1	18.6	2.9	6.0	25
	3.0	2.9	0.4	0.1	13.9	2.3	4.1	25
Body length:oral opening width, ratio	3.8	3.5	0.6	0.1	16.2	2.9	5.1	25
	2.9	2.9	0.3	0.1	11.4	2.1	3.5	25
Body width:oral opening width, ratio	2.9	2.7	0.5	0.1	16.8	2.3	4.1	25
	2.2	2.1	0.3	0.1	14.4	1.6	3.0	25

[a] Data based on cultivated, mounted, CHATTON-LWOFF silver nitrate-impregnated, and selected (as described in table head) specimens. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

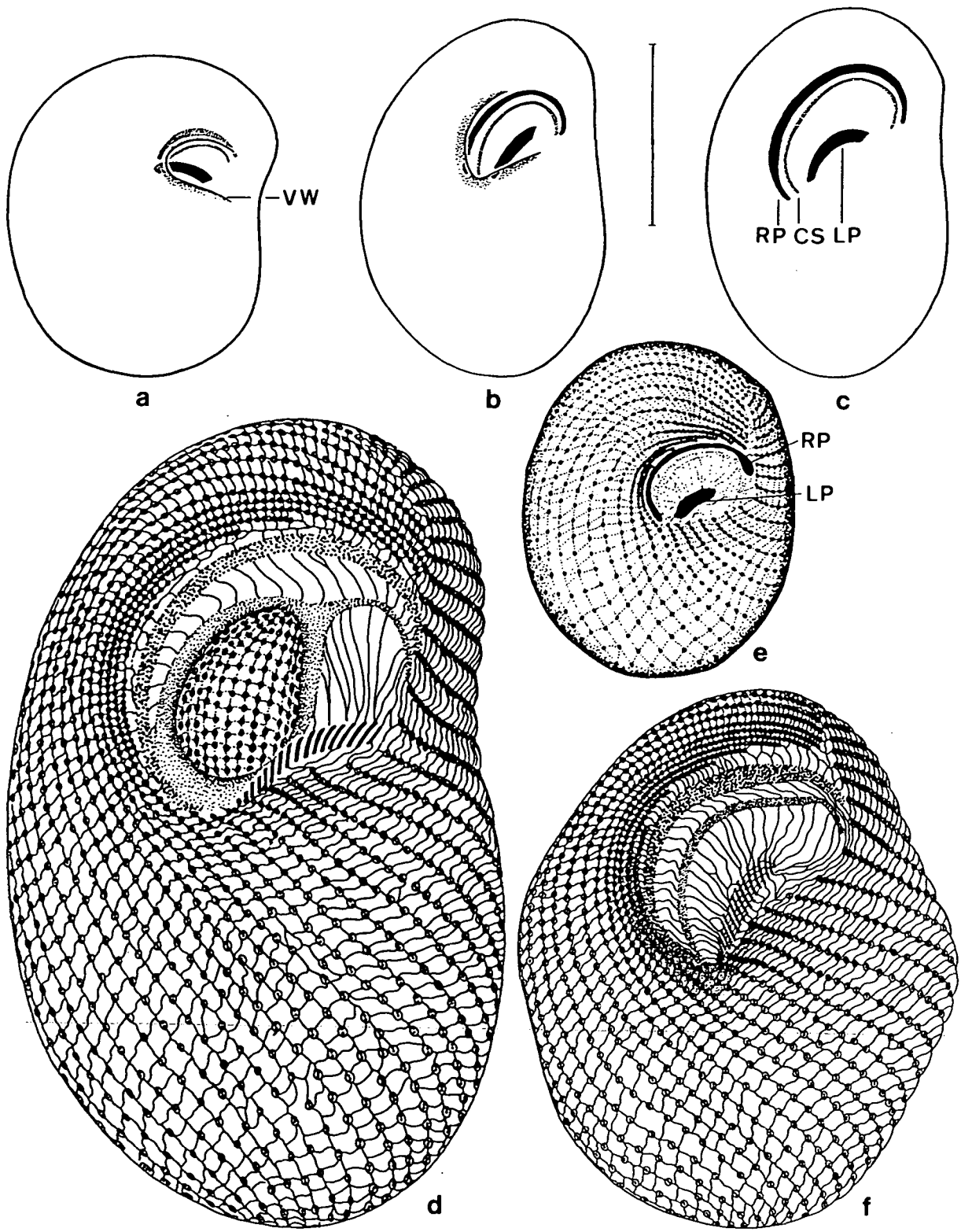


Fig. 199a–d. *Hausmanniella patella*, cultivated, CHATTON-LWOFF silver nitrate-impregnated specimens from Namibian site (15). **a–c:** Three similarly sized specimens showing macrostome formation by flattening and spreading of the vestibulum. Drawn to scale = 50 µm. **d:** Ventral view of a macrostome just ingesting a *Colpoda*, length 98 µm. **Fig. 199e, f:** *Corallocolpoda pacifica* (160 µm) and *Anictostoma terricola* (84 µm), macrostomous synonyms of *H. patella*. CS – cytostomial slit, LP – left oral polykinetid, RP – right oral polykinetid, VW – right vestibular wall

Macrostome morphology: Fully developed macrostomes are readily distinguished from ordinary specimens, as also evident from the descriptions as two distinct taxa (see above). Usually, however, fully developed macrostomes are rare and mixed with many transition stages and ordinary specimens, possibly because *H. patella* is omnivorous and becomes macrostomous only when it is forced to feed mainly on motile prey. Thus, morphometry, as performed in table 180, can document macrostomy only partially. Fully developed macrostomes differ by three features from ordinary specimens: (i) The oral field, which is broadly funnel-shaped in ordinary specimens, flattens greatly exposing the oral structures to the cell surface and the prey (Fig. 199a–c). We depict, for the first time, a macrostomous *H. patella* just ingesting a *Colpoda* through the cytostomial slit traversing the "open mouth" (Fig. 199d). This shows that macrostomy facilitates ingestion of large, motile prey. Unfortunately, vestibular flattening is difficult to assess morphometrically because specimens rarely assume the appropriate orientation in the silver preparations. Fortunately, vestibular flattening can be documented by scanning electron microscopy (Fig. 418i–l) and even with micrographs from CHATTON-LWOFF silver nitrate-impregnated specimens, where the whole, large mouth area can be shown in a single focal plane because it is almost flat (Fig. 418e–g). (ii) The oral field enlarges by about 30% relative to body size, which, like the number of postoral kineties, is very similar in ordinary and macrostomous cells, indicating that macrostomy is archived by two simple processes, viz., flattening via spreading of the vestibulum and some growth of the oral structures (Table 180; Fig. 199a–c; 418a–l). (iii) The left oral polykinetid, which is orientated in an angle of about 90° to the main body axis in ordinary specimens, assumes an oblique orientation (about 45°). However, this change is pronounced only in fully developed macrostomes (cp. figures 418a–h). Likewise, it is indistinct in SEM micrographs, possibly due to some deterioration of the specimens during the preparation procedure.

Maryna lichenicola (GELEI, 1950) FOISSNER, 1993 (Fig. 200a–g; 419a–k; Table 181)

1950 *Mycterothrix lichenicola* GELEI, Hidrol. Közl., 30: 117.
1975 *Mycterothrix tuamotensis* BALBIANI, 1887 – BUITKAMP, Protistologica, 11: 323.
1993 *Maryna lichenicola* (GELEI, 1950) nov. comb. – FOISSNER, Colpodea: 353.

Material: Protargol-impregnated specimens from Namibian site (42) and the surroundings of Cotonou, Benin. The Benin population is from the same sample as → *Dragescozoon terricola*. Voucher slides from both populations have been deposited (Table 1). The material cannot serve as neotype because of problems in identification (see below).

Description of Namibian population: Size 30–45 × 25–35 µm in vivo, usually near 40 × 30 µm. Calix inverted U-shaped and unflattened, rather distinctly set off from small, obconical uvula; prepared specimens more globular and with uvula less distinctly set off (Fig. 200a, e, f). Nuclear apparatus slightly underneath mid-body on average. Macronucleus globular, with reticular nucleolus. Micronucleus attached to macronucleus, globular, with distinct membrane. Contractile vacuole in uvula, with excretory pore in centre of terminal uvula surface. Cortex thin, flexible, extrusomes recognizable neither in vivo nor in

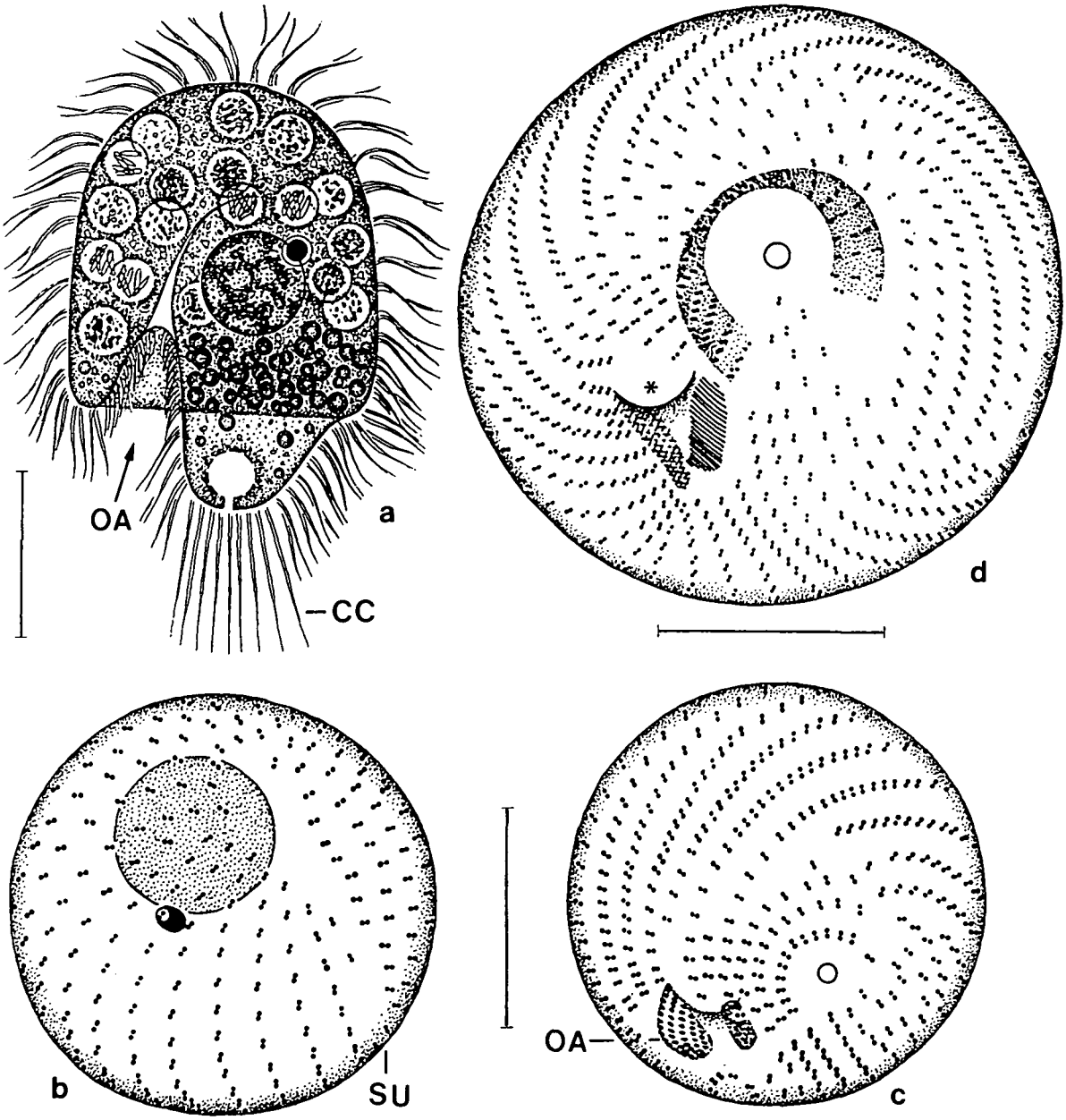


Fig. 200a–d. *Maryna lichenicola* (a–c) and *M. ovata* (d) from life (a) and after protargol impregnation (b–d). Figures 200b–d drawn to scale and only very slightly schematized because the preparations are of excellent quality. **a:** Left lateral optical section at level of oral apparatus of a representative specimen packed with food vacuoles. A dark zone composed of small lipid (?) droplets is dorsal of the oral apparatus. The caudal cilia are rather stiff and about twice as long as the ordinary somatic cilia (cp. figure 419a). Mucocysts and a case are very likely lacking. **b, c:** Same specimen, oblique anterior and posterior polar view of ciliary pattern. The ciliary rows have a strongly spiral course and are composed of dikinetids. The kinetids of the elongated caudal cilia form a conspicuous, semicircular array on the ventrolateral uvula margin, that is, originate from the last kinetid of about 12 postoral and left lateral ciliary rows. The uvula is indistinctly set off from the calix and contains the contractile vacuole, whose excretory pore is in the centre of the terminal surface. **d:** Posterior polar view of the somatic and oral ciliary pattern of a *M. ovata* specimen from the sample containing → *Dragescozoon terricola*. The ciliary pattern is obviously very similar to that of *M. lichenicola* (b, c). However, *M. ovata* is considerably larger (b–d are at same scale!) and thus has more ciliary rows. Furthermore, the uvula is a conspicuous plug distinctly set off from the calix (indicated by stippled lateral uvula surface). Thus, the Namibian *Maryna* is very likely not *M. ovata*. Asterisk marks vestibular entrance. CC – caudal cilia, OA – oral apparatus, SU – preoral suture. Scale bars 15 μm.

silver carbonate and protargol preparations. Cytoplasm colourless, without brown flakes, but with many minute (≤ 0.5 µm) crystals sparkling under interference contrast illumination. Dorsal of oral apparatus a dark zone (at low magnification and bright field illumination) composed of many refractive lipid (?) droplets about 2 µm across. Cell usually packed with food vacuoles, each containing only few bacteria or bacterial remnants. Swims rather rapidly in narrow spiral.

Somatic cilia about 8 µm long in vivo, paired, arranged in strongly spiral rows and thus difficult to count. Flattened specimens show about 28 rows (Fig. 419h–k), which is rather close to the 25 rows counted in protargol preparations (Table 181). Row pattern as in *M. ovata* (Fig. 200d; FOISSNER 1993c) and shown in figures 200b, c, e, f and figures 419d–k. Preoral suture straight and spoon-like widened apically. Terminal uvula surface without cilia, contains excretory pore of contractile vacuole. Caudal cilia about twice as long (15 µm) as ordinary somatic cilia and rather stiff and distinct in vivo, originate from last kinetid of about 12 ciliary rows left of oral apparatus; form conspicuous, semicircular array on ventrolateral margin of uvula (Fig. 200a, c; 419a, e, f, h, j); very likely, only one basal body of the dikinetids is ciliated because merely about 10 caudal cilia are recognizable in vivo. Silverline system as in other members of genus, that is, in *Colpoda* pattern, seen only in Benin population.

Oral apparatus rather large compared to size of cell, of ordinary structure (Fig. 200a, c, e, g; 419a, b, d, g, j; Table 181). Vestibulum extends to mid-body, entrance in rear body third. Left oral polykinetid roughly elliptical because narrowed at both ends. Right polykinetid composed of rather regularly arranged, curved ciliary rows, of which the innermost is dikinetidal.

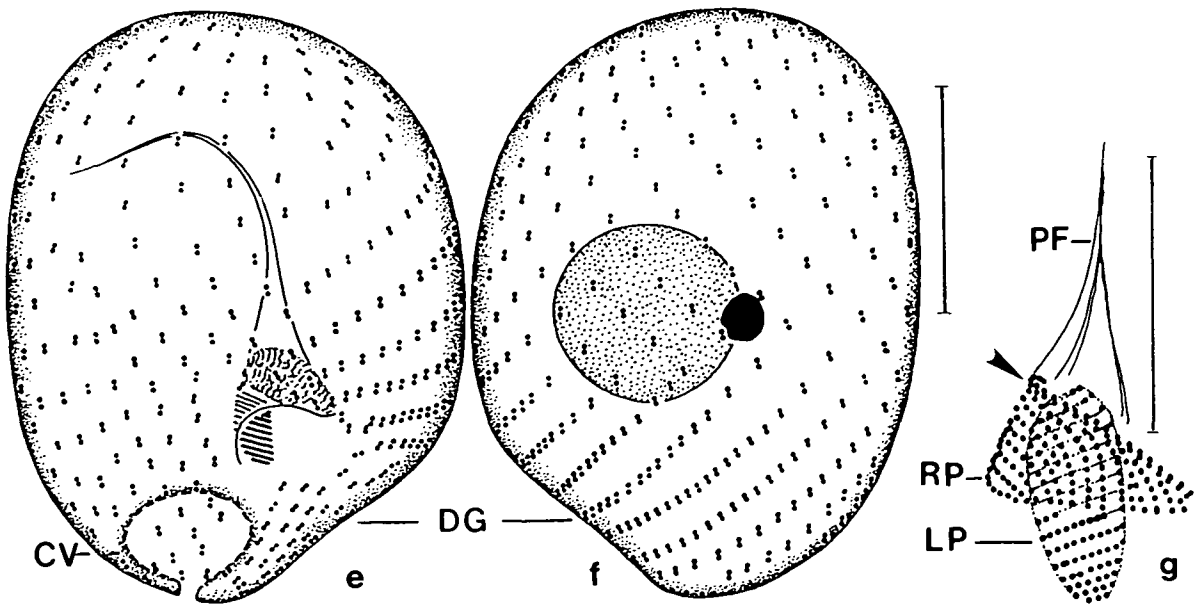


Fig. 200e–g. *Maryna lichenicola* from Namibian site (42), somatic and oral ciliary pattern after protargol impregnation. **e, f:** Same specimen, ventral and dorsal view. The kinetids of the left lateral kineties are condensed in the diagonal (postoral) groove. **g:** Oral apparatus in a left laterally orientated specimen. Arrowhead marks row of dikinetids at proximal margin of right polykinetid. CV – contractile vacuole, DG – diagonal groove, LP – left oral polykinetid, PF – pharyngeal fibres, RP – right oral polykinetid. Scale bars 15 µm (e, f) and 10 µm (g).

Table 181. Morphometric data on *Maryna lichenicola* from Namibian site (42; upper line) and a soil from Cotonou, Benin (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length (height)	37.1	38.0	3.8	0.9	10.2	29.0	42.0	17
	38.0	39.0	2.7	0.8	7.1	34.0	42.0	12
Body, calix width	29.7	30.0	3.1	0.8	10.4	23.0	34.0	17
	31.6	32.0	2.4	0.7	7.5	28.0	35.0	12
Body, uvula length [b]	9.2	9.0	1.6	0.4	17.8	7.0	13.0	17
	9.2	10.0	1.8	0.5	19.6	5.0	11.0	12
Anterior body end to macronucleus, distance	13.3	15.0	4.1	1.0	31.1	6.0	19.0	17
	14.6	14.0	2.7	0.8	18.4	10.0	20.0	12
Anterior body end to proximal end of left oral polykinetid, distance	18.9	20.0	2.8	0.7	14.6	12.0	23.0	17
	22.1	22.0	3.1	0.9	14.1	17.0	28.0	12
Macronucleus, length	11.8	12.0	1.4	0.3	11.8	10.0	14.0	17
	12.0	13.0	1.4	0.4	11.2	10.0	14.0	12
Macronucleus, width	11.1	11.0	1.3	0.3	12.2	9.0	14.0	17
	13.3	11.0	1.0	0.3	8.6	10.0	13.0	12
Micronucleus, largest diameter	3.0	3.0	–	–	–	3.0	4.0	17
	2.9	3.0	–	–	–	2.0	3.0	4
Somatic and postoral kineties, number (approximate)	25.2	25.0	–	–	–	22.0	29.0	17
	24.4	25.0	–	–	–	22.0	26.0	12
Postoral kineties, number (approximate)	3.3	3.0	–	–	–	3.0	4.0	17
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	12
Oral opening, width (distance between distal ends of polykinetids)	7.5	8.0	0.6	0.2	8.3	6.0	8.0	17
	6.7	7.0	0.7	0.2	9.8	6.0	8.0	12
Left oral polykinetid, length	7.9	8.0	0.8	0.2	9.9	6.0	9.0	17
	6.4	7.0	0.9	0.3	14.1	5.0	8.0	12
Left oral polykinetid, width	3.4	3.0	–	–	–	3.0	4.0	16
	2.8	3.0	–	–	–	2.0	3.0	9
Left oral polykinetid, number of kineties	15.9	16.0	1.4	0.3	8.5	14.0	19.0	23
	13.1	13.0	1.4	0.4	10.5	12.0	16.0	12
Right oral polykinetid, length	8.1	8.0	0.8	0.2	9.6	7.0	10.0	17
	6.8	7.0	0.7	0.2	10.6	6.0	8.0	12
Right oral polykinetid, width	3.6	4.0	–	–	–	3.0	4.0	16
	2.8	3.0	–	–	–	2.0	3.0	9

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Distance from distal end of left oral polykinetid to posterior body end.

Occurrence and ecology: In Namibia, *M. lichenicola* occurred only at site (42), that is, in rock-pools containing a thin soil layer mixed with lichen and grass litter. This is similar to the type location, viz., lichens and tree mosses in Hungary (GELEI 1950b). BUITKAMP (1975) isolated *M. lichenicola*, as we did in Cotonou, from a grassland soil near an ecological station in Lamto (Ivory Coast, Africa). However, the identification is uncertain (FOISSNER 1993c).

Comparison with previous descriptions: Small marynids are difficult to identify. The Namibian population does not fit well to any of the described species reviewed in FOISSNER (1993c), mainly due to the lack of a case. As the Namibian specimens apparently lack mucocysts, they very likely cannot build a lorica. If this is true, they would belong to a new species. Unfortunately, the lack of a case is difficult to prove without permanent cultures. Thus, we prefer to identify our population with *M. lichenicola*, a rather superficially described species from Hungary, which is similar to the Namibian specimens in size, shape of body and macronucleus, and the rather short caudal cilia. Alternatively, the Namibian population may be considered as a small "variety" of *M. ovata*, which, however, is distinctly larger (length > 40 µm) and has a more sharply defined uvula (Fig. 200d and FOISSNER 1993c).

The second population from Cotonou is morphologically and morphometrically very similar to the Namibian specimens (Table 181). Furthermore, it also lacks a case. Thus, this species has a firm identity. However, European populations must be studied to confirm/reject our identification.

Maryna minima (GELEI, 1950b) FOISSNER, 1993c (Fig. 201a–d; 420a–k)

Material: If not otherwise stated, all observations are from a Tunisian population. Some data are from Cotonou, Benin, where *M. minima* occurred in the same sample as → *Dragescozoon terricola* (Fig. 420j, k). Unfortunately, material was too sparse for permanent preparations at both sites. Thus, detailed morphometrics and illustrations cannot be provided.

Description of Tunisian population: Size about 25 × 20 µm in vivo, that is, almost globular with minute uvula wart-like projecting from midline of rear end; diagonal (postoral) groove lacking both in vivo and silver preparations (Fig. 201a; 420a, b, h–j). Impaired specimens more slender and ovoidal (Fig. 201b). Nuclear apparatus sub-equatorial and thus often hides oral apparatus in silver carbonate preparations (Fig. 201a; 420c, f, h). Macronucleus about 7 µm across in vivo, with globular, central nucleolus or several small, scattered nucleoli. Micronucleus attached to macronucleus, lenticular, about 3 µm long, compact and thus highly refractive. Contractile vacuole and excretory pore at dorsal margin of uvula. Cortex flexible and without extrusomes; minute (< 0.5 µm) granules stain in the Namibian specimens after addition of methyl green-pyronin. Cytoplasm rather hyaline, cells thus greyish or brownish at low magnification, contains many minute (≤ 0.5 µm) crystals conspicuously sparkling under interference contrast illumination. Often packed with compact food vacuoles 2–4 µm across during the acidic phase and up to 10 µm in the alkaline state, where the content is loose. Feeds mainly on minute, curved bacteria. Swims extremely rapidly.

Calix cilia 10 µm long in vivo, arranged in about 15 slightly spiral, subterminally not condensed rows, obviously due to the lacking diagonal groove. About 15 kinetids in longest kineties. Preoral suture indistinct. On distal end of uvula a semicircular array of slightly elongated, 12 µm long cilia originating from a conspicuous, fan-like array of about six minute ciliary rows (Fig. 201a, c; 420a, d–f, h–k).

Oral apparatus near posterior end of cell. Vestibulum conical and rather flat, cilia of oral polykinetids thus project from oral opening, those of left polykinetid form a distinct beard (Fig. 201a, b). Left oral polykinetid about 7 × 3 µm in vivo, consists of 10–12 ($\bar{x}$ = 11, n = 4; silver carbonate impregnation) rows with about 6 µm long cilia. Right polykinetid of similar size as left, consists of about 4–6 slightly irregular rows having 3–4 µm long cilia (Fig. 201c; 420a, d, f–h, j, k).

Occurrence and ecology: GELEI (1950b) discovered *M. minima* in soda puddles near Szeged, Hungary. DRAGESCO & DRAGESCO-KERNÉIS (1986) probably found it in soil from Benin (see FOISSNER 1993c for nomenclature and taxonomy), as we did (same sample as → *Dragescozoon terricola*). In Namibia, *M. minima* occurred at several saline and non-saline sites (Table 4). Abundances, however, were low. In Tunisia, we found *M. minima* about 200 m inshore of Cape Bon (37°N 13°E) in a sample composed of brownish sand, grass litter, and litter and roots from *Erica multiflora* and *Andromeda* sp. The sample, kindly collected by Mag. Aline BERTHOLD, was slightly saline and had pH 7.7. Obviously, *M. minima* is euryhaline and has a wide geographic distribution.

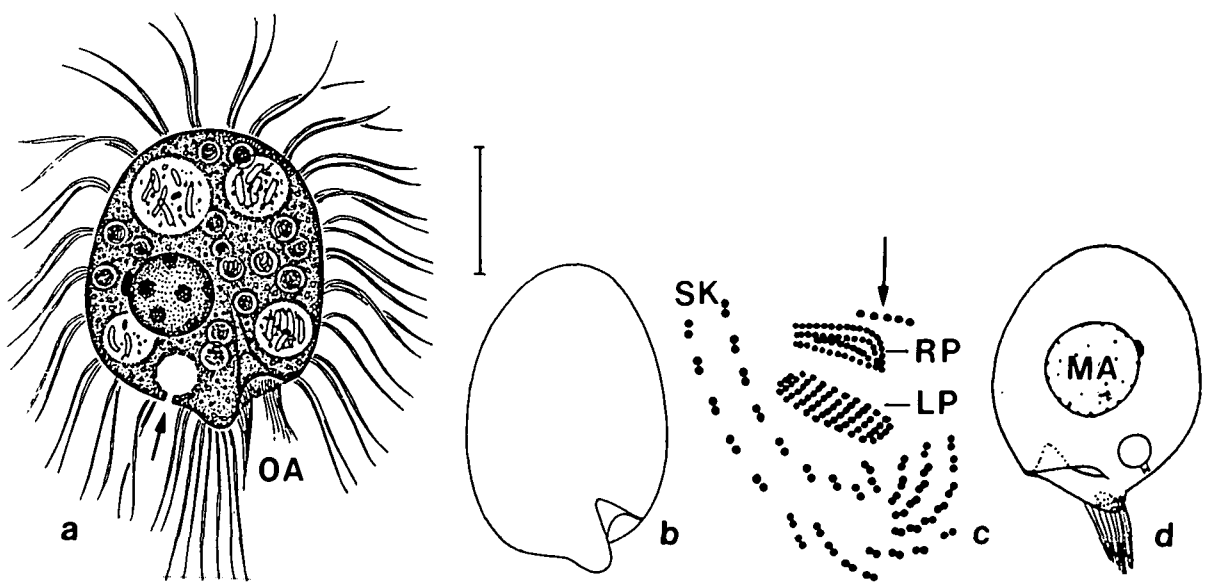


Fig. 201a–d. *Maryna minima*, Tunisian specimens (a–c) and Hungarian type specimen (d, from GELEI 1950b) from life (a, b), after silver carbonate impregnation (c), and mercuric chloride preservation (d). **a:** Right side view of a representative specimen with slightly elongated (12 µm) uvula cilia. Arrow marks excretory pore of contractile vacuole, whose location at the dorsal uvula margin is an important feature of this species. The oral cilia project distinctly from the flat vestibulum. **b:** Slightly impaired specimens are ovoidal. **c:** Oral and uvula ciliature. The right oral polykinetid consists of several distinct ciliary rows. Thus, the species belongs to *Maryna* and not to *Ilsiella*, whose right ciliary field consists of a single row of dikinetids (FOISSNER 1993c). The arrow marks a minute, densely ciliated row in the upper left oral region. This row is more conspicuous in the Benin specimens (Fig. 201j, k). The minute, fan-like arranged uvula kineties make the species easily recognizable in silver slides. **d:** Hungarian type specimen, length about 25 µm. The uvula cilia appear like elongated caudal cilia because GELEI (1950b) did not illustrate the other cilia, which are also very long (10 µm) compared to the size of the cell (Fig. 201a). Thus, *M. minima* lacks distinctly elongated caudal cilia. LP – left oral polykinetid, MA – macronucleus, OA – oral apparatus, RP – right oral polykinetid, SK – somatic ciliary rows right of oral opening. Scale bar 10 µm.

Comparison with original description (GELEI 1950b): This minute species has not been reported since the original description (FOISSNER 1993c), with which our observations largely agree, especially as concerns the unusual location of the contractile vacuole, that is, not within the uvula but at its dorsal margin. Furthermore, GELEI describes and illustrates, albeit vaguely, another important feature of *M. minima*, viz., the minute uvula kineties, whose fan-like arrangement makes this species so easily recognizable in silver preparations (Fig. 420a, d, e, f, k). However, GELEI describes a "tuft of distinctly elongated caudal cilia", which are lacking in our specimens, although the uvula cilia are slightly longer (12 µm) than the calix cilia (10 µm). On the other hand, GELEI does not provide any measurements of cilia length and mentions that "the somatic cilia are long", which is indeed the case if compared with the small size of the organism. If the somatic cilia were removed from our figure 201a, the organism would look very similar to GELEI's illustration, here reproduced as figure 201d. GELEI also mentions that *M. minima* often rests for a long time and thus probably lives in a case. Our specimens neither rested nor built a lorica. Taken together all data, our identification is likely correct. If the interpretation of the caudal cilia is not accepted or disproved by investigations on European material, than our population must be classified as a new species, similar to *M. minima* but without caudal cilia.

At the present state of knowledge, *M. minima* can be characterized as follows: Minute, that is, 20–30 µm; almost globular. Macronucleus globular. Contractile vacuole at dorsal margin of uvula. About 13–16 somatic ciliary rows and circa 11 rows in left oral polykinetid. Uvula very small and thus with only few, short kineties showing a remarkable fan-like arrangement. Accordingly, *M. minima* is distinctly different from *M. antarctica* FOISSNER, 1993c, the sole congener with such a small size. In vivo, *M. minima* can easily be confused with marynids of the genus *Ilsiella*, which have a similar size, shape, and location of the oral apparatus.

Maryna namibiensis nov. spec.

Diagnosis: Size 80–160 × 65–130 µm in vivo. Broadly pyriform with large uvula distinctly set off from body proper by deep postoral groove. Macronucleus globular or ellipsoidal; two or more micronuclei. On average 60–80 somatic ciliary rows and 30–43 kineties in left oral polykinetid.

Generic classification: *Maryna namibiensis* looks rather similar to certain medium-sized species of the genus *Colpoda*, especially *C. henneguyi* and *C. variabilis*, as reviewed in FOISSNER (1993c). However, it is a true *Maryna* species because (i) the oral funnel and the pharyngeal fibres are directed anteriorly (invariably posteriorly in *Colpoda*) and (ii) the colpodid, left lateral postoral sac is modified to a posterior plug (uvula) distinctly set off from body proper. The latter difference is not distinct, but evident on comparison of figures.

Comparison with related species: We split *Maryna namibiensis* into two subspecies distinctly differing in some features (Table 183), especially by the shape of the macronucleus, which is considered as relevant at species level (DINGFELDER 1962, FOISSNER 1993c). Thus, subspecies level is probably too conservative. On the other hand, the overall appearance of the Namibian and the Costa Rican population is so similar that species rank appears unjustified.

There is only one species which resembles *M. namibiensis*, namely *M. galeata* GELEI, 1950b (see FOISSNER 1993c for a detailed review of all *Maryna* species). However, both differ in several features (Fig. 201a, n; 421a–v, 424p–s by *M. namibiensis costaricensis*): body shape (broadly pyriform with long uvula vs. helmet-shaped with short uvula), size (length usually ≤ 150 µm vs. ≥ 150 µm), location of the oral apparatus (oral opening underneath mid-body vs. near posterior body end), case (absent vs. present, in both species checked in cultures), and number of micronuclei (two or more vs. one). The last feature is of special interest and a main species character because all other *Maryna* species have only one micronucleus. The same situation occurs in the closely related genus *Colpoda*, where only few species are multimicronucleate (FOISSNER 1993c). Very likely, there are further differences because *M. galeata* has not yet been investigated with modern methods. For instance, behaviour is unique in *M. namibiensis* because most other *Maryna* species are restless, fast swimmers, at least when out of case.

Maryna namibiensis namibiensis nov. sspec. (Fig. 201a–q; 294–297, 421a–z, 422a–k, o–z, 423a–g; Tables 182, 183)

Diagnosis: Size 80–130 × 65–105 µm in vivo. Macronucleus globular. On average 62 somatic ciliary rows and 30 kineties in left oral polykinetid.

Type location: Rock-pool of a brook in the Daan Viljoen Game Park near Windhoek, Namibia, 22°35'S 17°05'E (site 73 in figure 2 and chapter 2.1.2).

Etymology: Named after the country discovered.

Description: Although the species could be cultivated for some time (see ecology section), all observations, if not otherwise stated, are from specimens obtained from a non-flooded Petri dish culture. Furthermore, some observations from the population of site (29) are included because conspecificity is beyond doubt (Table 182).

Size in vivo and preparations 80–130 × 65–105 µm, usually about 105 × 90 µm, uvula about half as wide as calix; length:width ratio little variable, that is, 1.1–1.4:1, usually between 1.2–1.3:1 (Table 182). Shape likewise fairly constant, that is, broadly pyriform or dumb-bell-like; cells basically composed of a large anterior globule (calix) and a small posterior globule (uvula) both more or less distinctly flattened and even slightly concave ventrally and separated from each other by a conspicuous postoral (diagonal) groove gradually deepening from ventral to dorsal side. This produces two main aspects of *M. namibiensis namibiensis* (Fig. 201k–m; 421a–u, 422f, v): (i) it is dumb-bell-shaped when viewed ventrally and dorsally because the full depth of the postoral groove is recognizable, and (ii) it is roughly pyriform when viewed laterally because of the flattened ventral and vaulted dorsal side. Calix usually globular, rarely indistinctly pyramidal (Fig. 421 l), never helmet-like. Uvula conspicuous, more or less distinctly spheroidal. Rarely occur specimens flattened dorsally (Fig. 421z). In declining pure cultures, fast-swimming, cylindroidal specimens occur.

Macronucleus in middle body third, usually near body centre, more pre-equatorial in population from site (29) than from site 73 (Table 182), spherical to slightly ellipsoidal (1.1:1), with distinct membrane and reticular nucleolus. Usually two micronuclei attached to

macronucleus at variable positions, in vivo about 5 µm across and with distinct membrane, compact and thus easy to recognize (Fig. 201a, h, o; 421v, w, 422r). Contractile vacuole in posterior body end with single excretory pore in centre of uvula surface, associated with many narrow collecting canals extending to mid-body (Fig. 201a, g, h, p; 421a, c). Cortex flexible and comparatively inconspicuous because without extrusomes (checked in many specimens and with various stains because uncommon in such a large species!), contains numerous type I crystals (see below) and minute granules (< 0.5 µm, mucocysts?) around ciliary bases (Fig. 201d; 421y). Cytoplasm colourless, specimens however dark at low magnification in posterior portion due to the refractive crystals contained, shows strong cyclosis preorally; contains three main inclusions: (i) innumerable, minute (0.5–1.5 µm), yellowish type I crystals conspicuously sparkling under interference contrast illumination (Fig. 201b, d; 421y); (ii) many medium-sized (3–4 µm), ellipsoidal to cylindroidal type II crystals, partially in small vacuoles (Fig. 201c; 423a, f); and (iii) many food vacuoles, which contain exclusively bacteria and are conspicuously small (4–6 µm across) compared to size of cell (Fig. 201a; 421w). Type I crystals scattered in cortex and cytoplasm, type II crystals con-

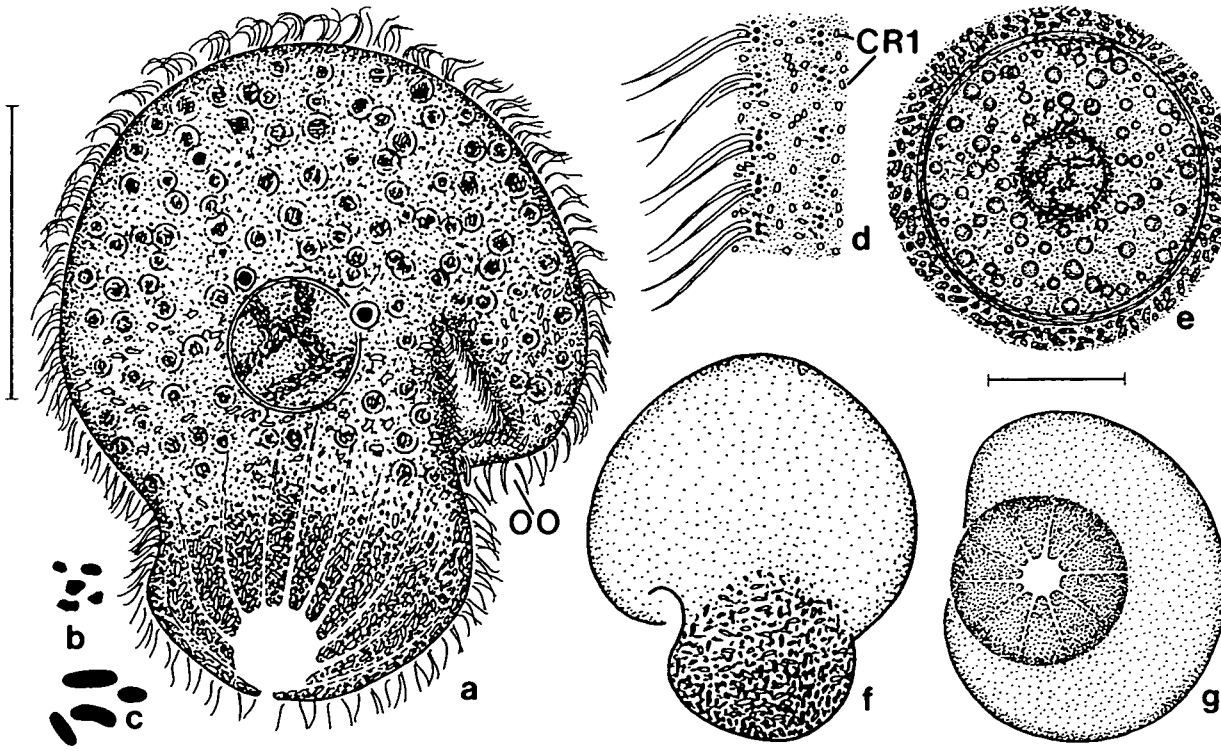


Fig. 201a–g. *Maryna namibiensis namibiensis* from life. **a:** Dorsolateral view of a representative specimen packed with food vacuoles, which are small compared to the size of the cell. Note the two conspicuous micronuclei. **b:** Cytoplasmic type I crystals, 1–1.5 µm. **c:** Cytoplasmic type II crystals, 3–4 µm. **d:** Surface view of cortex, which contains type I crystals and minute granules (mucocysts?) around the dikinetids. **e:** Resting cysts have a rather conspicuous ectocyst composed of type II crystals and food residues embedded in a viscous matrix. The macronucleus is covered by type I crystals and thus stands out as dark globule from the lighter cytoplasm. **f:** Type I and II crystals are concentrated in the uvula, which thus appears dark under bright field illumination. **g:** Posterior polar view of a specimen resting on the anterior pole area. The contractile vacuole is in the centre of the uvula and has many fine canals extending to mid-body (a). CR1 – cytoplasmic type I crystals, OO – oral opening. Scale bars 50 µm (a), 30 µm (e).

centrated in uvula, food vacuoles mainly in calix; some (parasitic?) bacterial rods lie freely in the cytoplasm. Swims rather rapidly by rotation about main body axis, does not build a case as obvious in pure cultures, where specimens slowly circle on the bottom of the dish or swim in the medium; likewise, although abundant, no cases were observed in the non-flooded Petri dish culture. *Maryna namibiensis namibiensis* shows a distinct tendency to adhere with the anterior pole region on debris and the microscope slide, remaining almost immobile for some time; thus, it is easily photographed, even upside-down, that is, when standing on the calix (Fig. 421a–o); if debris is lacking two or more specimens adhere anteriorly (Fig. 421x).

Cilia about 12 µm long in vivo, sprout from deep, broadly elliptical pits; usually paired, except above uvula and on posterior uvula surface, where kinetids with barren anterior basal body occur (Fig. 422a, b). Elongated caudal cilia lacking, terminal uvula surface, however, studded with scattered cilia from posterior end of ordinary somatic ciliary rows (Fig. 201a, h, p; 294, 421s, 422u). All ciliary rows, except those on right half of ventral side, subterminally condensed producing the heavily ciliated diagonal (postoral) groove. Most ciliary rows abut on a ventral suture, except for 6–8 (usually 7, n = 10) postoral rows (Fig. 201i, n, q; 422d–g, o–q, w). Preoral suture conspicuous, especially in silver nitrate preparations, commences at upper mouth margin and extends straight to anterior pole centre. Postoral suture also distinct because in a "stripe contrast" zone, that is, the region where the loosely ciliated rows right of the suture obliquely abut on the densely ciliated postoral rows.

The cilia and the silverlines connecting their basal bodies form a highly ordered pattern, whose spiral course causes many aspects, depending on the angle viewed (Fig. 201h, n–q; 421p–s, 422f–h, o–v). However, the pattern is obviously as in other members of the genus and homologous with the *Colpoda* pattern, which is well recognizable in this large species. Basically, the ciliary rows perform a spiral course more pronounced left than right of the preoral suture. The rows commencing left of the preoral suture extend obliquely (~ 45°) above the ventral and dorsal surface, those of the upper third course sigmoidally onto the posterior right lateral and ventral surface. Right of the preoral suture are about seven shortened, only slightly curved rows, most of which abut on the right margin of the oral apparatus. They are followed by about 15 slightly sigmoidal rows, some of which abut on the postoral kineties, while the others extend onto the uvula filling the ventrolateral space left by the left side ciliary rows. Postoral ciliary rows rather conspicuous, indistinctly separated from left side rows; first row, on which some right side kineties abut, often more loosely ciliated than the other rows.

Oral opening farther subterminal than in other members of genus due to the long uvula (Table 182). Vestibulum about 25 µm deep in vivo, conical with flattened bottom, extends slightly obliquely anteriad; upper and right margin of oral overture distinct, left merges into diagonal (postoral) groove (Fig. 201a, n; 295, 421a, f, k, p, z, 422y, z). Left oral polykinetid on flattened vestibular bottom, plug-shaped because composed of an average of 30 monokinetidal ciliary rows decreasing gradually in length distally and especially proximally; cilia about 5 µm long, form distinct plates (Fig. 422z). Two thick fibre bundles, not described in any other member of the order, originate from base of left polykinetid and obliquely extend into the cell (Fig. 201i). Right oral polykinetid on vestibular roof, crescentic, composed of a proximal row of dikinetids and irregular, curved rows of monokinetids, extends to distal mouth margin, which thus appears densely ciliated (Fig. 295, 422y, z); no vestibular kineties. Pharyngeal fibres inconspicuous, extend anteriorly (Fig. 201a, i, j; 422f, g, o, s, t, w–z).

Silverline system in *Colpoda* pattern. Meshes narrow and longitudinally orientated in preoral suture and posterior pole area (Fig. 201h, n, p; 422c–e, i–k).

Resting cysts observed in cultures as described below; globular with an average diameter of

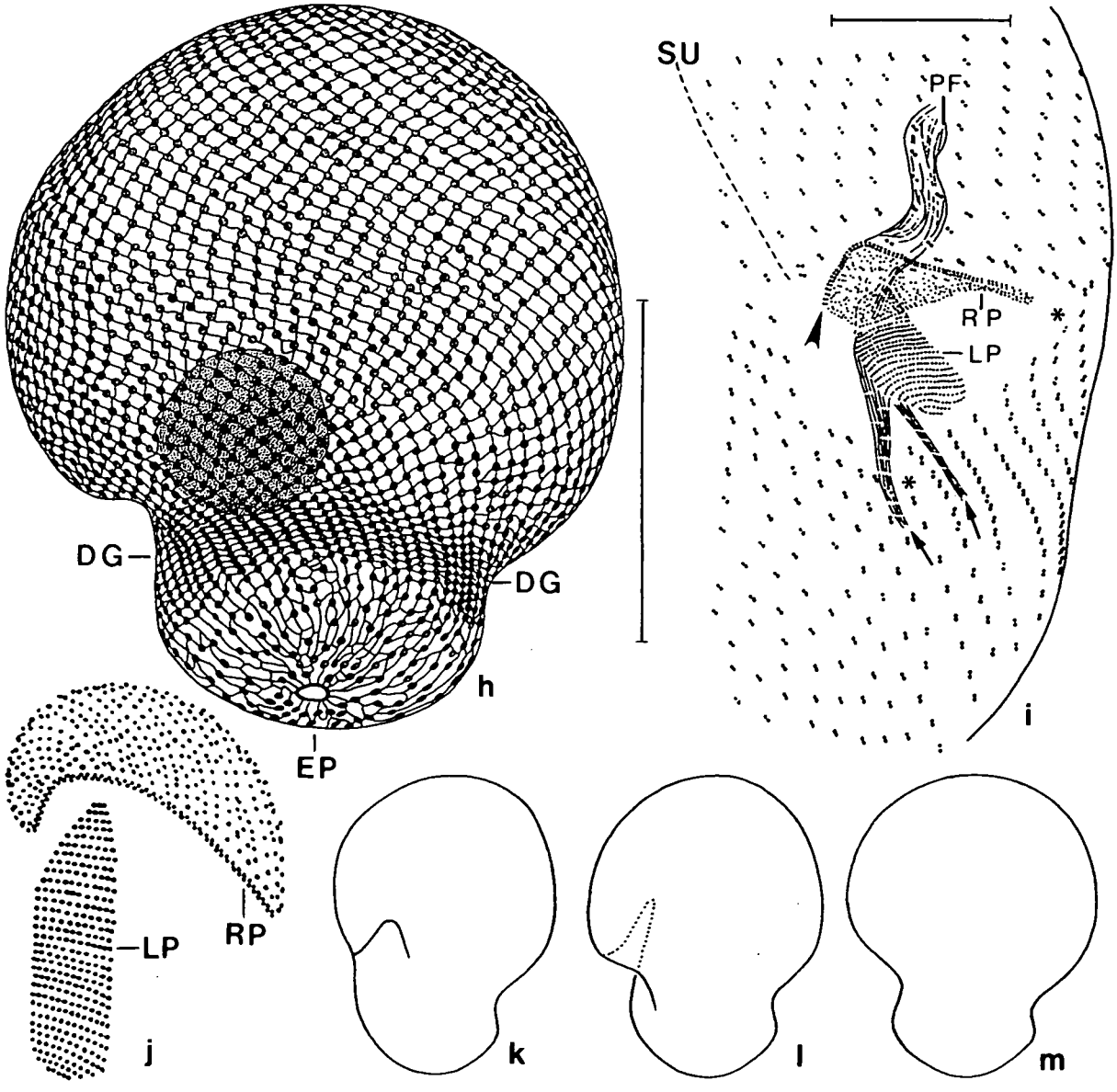


Fig. 201h–m. *Maryna namibiensis namibiensis* from life (k–m), after CHATTON-LWOFF silver nitrate impregnation (h), and protargol impregnation (i, j). **h:** Dorsolateral view showing ciliary pattern and silverline system of a *Colpoda henneguyi*-shaped specimen. The silverline system becomes very irregularly meshed on the posterior uvula surface, the centre of which contains the excretory pore of the contractile vacuole. **i, j:** Oral and circumoral infraciliature. Arrows mark fibre bundles originating from left oral polykinetid. Arrowhead marks row of dikinetids at proximal margin of right oral polykinetid. The left oral polykinetid is plug-shaped due to the distinctly shortened proximal ciliary rows. Asterisks in figure (i) mark first and last postoral kinety. **k–m:** Ventrolateral, dorsolateral, and dorsal view of same specimen (redrawn from micrographs). DG – diagonal (postoral) groove, EP – excretory pore of contractile vacuole, LP – left oral polykinetid, PF – pharyngeal fibres, RP – right oral polykinetid, SU – preoral suture. Scale bars 50 μm (h), 25 μm (i).

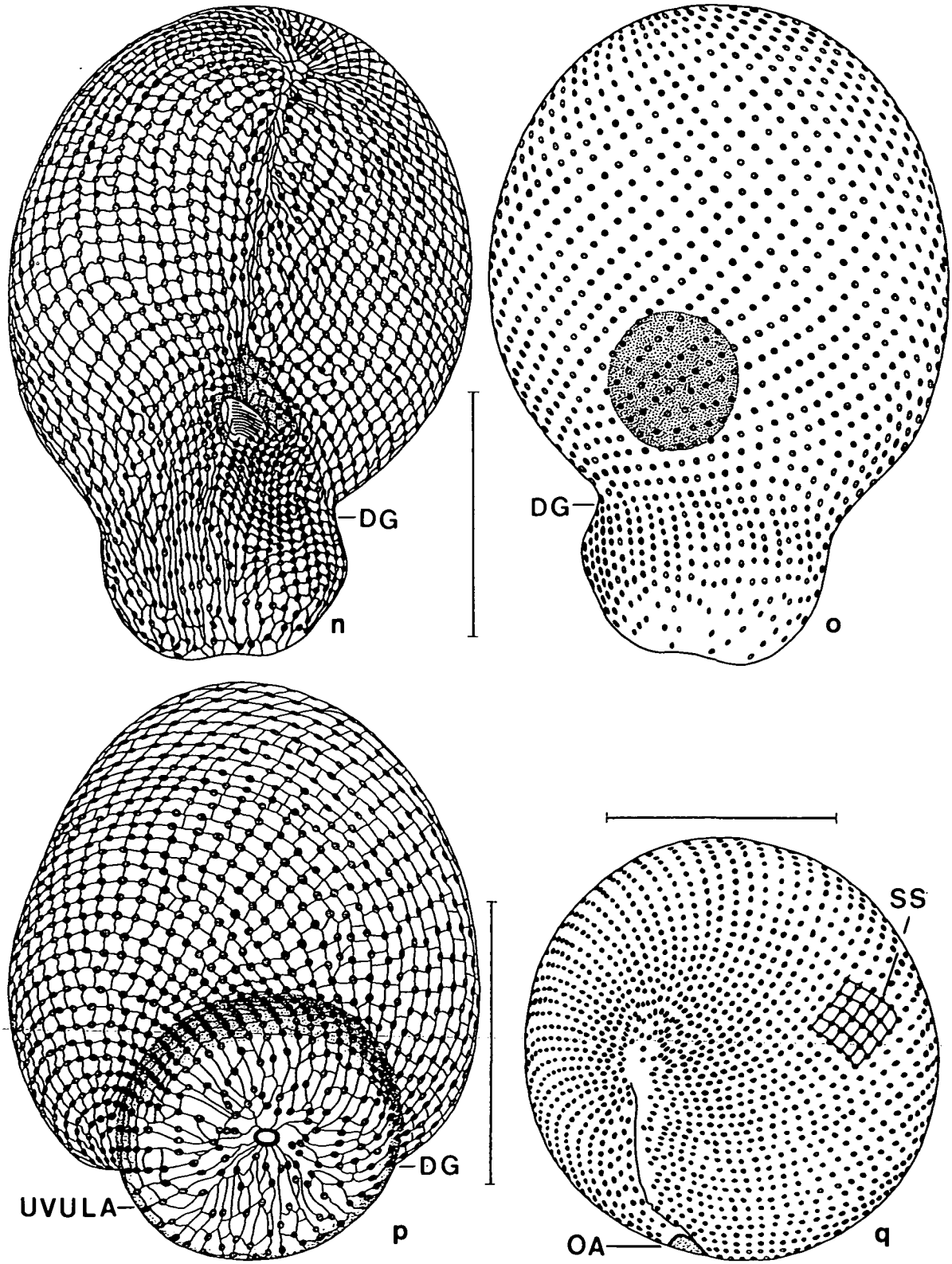


Fig. 201n–q. *Maryna namibiensis namibiensis*, ciliary pattern and silverline system after silver nitrate impregnation. **n, o:** Ventral and dorsal view of same specimen. **p, q:** Oblique posterior and anterior polar view. DG – postoral (diagonal) groove, OA – oral apparatus, SS – silverline system. Scale bars 40 μm.

Table 182. Morphometric data on *Maryna namibiensis namibiensis* from Namibian sites (73; type location) and (29).

Characteristics [a]	Site	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	73	IV	103.5	105.0	11.7	2.8	11.3	80.0	120.0	17
Body, length	29	IV	114.4	120.0	13.3	4.4	11.7	90.0	130.0	9
Body, length	73	CHL	104.0	105.0	7.3	1.6	7.0	88.0	120.0	21
Body, length	29	CHL	97.9	97.0	12.1	3.1	12.3	78.0	115.0	15
Body, calix width	73	IV	87.4	90.0	11.6	2.8	13.3	65.0	110.0	17
Body, calix width	29	IV	90.0	90.0	12.0	4.0	13.3	70.0	105.0	9
Body, calix width	73	CHL	75.2	77.0	8.7	1.9	11.5	62.0	92.0	21
Body, calix width	29	CHL	77.7	76.0	8.9	2.3	11.4	66.0	92.0	15
Body, maximum uvula width	73	CHL	44.3	43.0	4.7	1.0	10.6	37.0	52.0	21
	29	CHL	46.3	45.0	6.7	1.7	14.5	33.0	60.0	15
Anterior body end to anterior margin of buccal overture, distance	73	CHL	59.8	60.0	6.8	1.5	11.3	45.0	77.0	21
	29	CHL	59.0	60.0	7.6	2.0	12.9	40.0	72.0	15
Anterior body end to macronucleus, distance	73	CHL	44.4	45.0	9.2	2.0	20.8	24.0	58.0	21
	29	CHL	37.3	38.0	9.2	2.4	24.6	22.0	50.0	15
Macronucleus, length	73	CHL	22.9	22.0	2.2	0.5	9.5	20.0	26.0	21
	29	CHL	23.1	23.0	1.9	0.5	8.4	20.0	26.0	15
Macronucleus, width	73	CHL	22.3	22.0	2.0	0.4	9.1	20.0	26.0	21
	29	CHL	22.2	22.0	2.2	0.6	10.1	19.0	26.0	15
Micronuclei, number	73	SC	2.5	2.0	1.1	0.3	44.4	2.0	6.0	15
Somatic kineties, number [b]	73	CHL	60.3	60.0	5.7	1.2	9.4	50.0	70.0	21
	29	CHL	64.0	65.0	5.2	1.6	8.2	55.0	70.0	11
Left oral polykinetid, number of kineties	73	SC	29.8	30.0	2.2	0.6	7.4	25.0	33.0	13
	73	PA	30.4	31.0	2.2	0.5	7.3	27.0	35.0	19
	29	CHL	about 28–30 (n = 3)							
Left oral polykinetid, length	73	SC	18.1	19.0	2.2	0.6	12.1	14.0	20.0	13
	73	PA	19.4	20.0	3.5	0.8	17.8	14.0	27.0	19
	29	CHL	15.0	15.0	0.8	0.4	5.4	14.0	16.0	4
Left oral polykinetid, width	73	SC	6.5	7.0	–	–	–	6.0	7.0	13
	73	PA	8.4	9.0	2.4	0.6	28.9	5.0	13.0	19
	29	CHL	5.8	6.0	–	–	–	5.0	6.0	4
Right oral polykinetid, length	73	SC	24.6	25.0	3.3	1.0	13.4	17.0	28.0	11
	73	PA	23.7	23.0	4.2	1.0	17.9	17.0	32.0	19
	29	CHL	21.2	20.0	1.6	0.7	7.8	20.0	23.0	5
Right oral polykinetid, width	73	SC	8.3	8.0	1.0	0.3	12.2	7.0	10.0	11
	73	PA	9.7	9.0	2.8	0.7	29.2	5.0	15.0	19
Resting cysts, length	73	IV	76.7	76.0	10.8	3.1	14.1	60.0	100.0	12
Resting cysts, width	73	IV	76.7	76.0	10.8	3.1	14.1	60.0	100.0	12

[a] Data based on randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, IV – in vivo, M – Median, Max – maximum, Min – minimum, n – number of individuals investigated, PA – protargol impregnation (FOISSNER's method) of inflated specimens stored for two weeks in distilled water, SC – silver carbonate impregnation, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Approximate values because difficult to count due to the strong body spiralization.

76 µm (Table 182), dark-brown at low magnification (≤ ×100), colourless at higher magnification. About one third of cysts contained two specimens, possibly cells which transformed into resting cysts during division. Endocyst smooth and colourless, 2–3 µm thick and very flexible, covered by an about 5 µm thick, rough ectocyst obviously composed of excreted material, viz., cytoplasmic type II crystals and food residues glued together by a very viscous material becoming membrane-like wrinkled in squashed cysts. Cytoplasm packed with minute granules, type I crystals, and small fat globules; the macronucleus stands out as dark globule because covered by an about 1 µm thick layer of cytoplasmic type I crystals, as in *M. umbrellata* (Fig. 201e; 423a–g).

The resting cysts of *M. namibiensis namibiensis* lack the yellowish globules composing the ectocyst of → *M. umbrellata*. Thus, they are more similar to those of *M. atra*, which, however, have a thicker (7 µm) endocyst (FOISSNER 1993c).

Occurrence and ecology: To date found only in Namibia, viz., in mud from rock-pools at sites (29) and (73). Such ephemeric habitats are generally preferred by marynids (FOISSNER 1993c). However, *M. namibiensis* is possibly restricted, or least prefers, river rock-pools because both subspecies were found as yet only in such habitats. We could cultivate *M. namibiensis namibiensis* in Eau de Volvic enriched with some salad medium, two unsquashed wheat grains, and backer's yeast as food source. All cultures, however, encysted after a few divisions.

Comparison with related species (see also comparison of species above): *Maryna namibiensis namibiensis* differs from *M. namibiensis costaricensis* mainly by the features compiled in table 183, especially in the shape and size of the macronucleus. Furthermore, the numbers of somatic ciliary rows and kineties in the left oral polykinetid do not overlap.

Table 183. Comparison of main morphometrics in *Maryna namibiensis namibiensis* (MN) and *Maryna namibiensis costaricensis* (MC).

Characteristics [a]	Species	Method [a]	$\bar{x}$	Min	Max	n
Body, length	MN	CHL	104.0	88.0	120.0	21
	MC	CHL	129.8	100.0	150.0	17
Body, calix width	MN	CHL	75.2	62.0	92.0	21
	MC	CHL	100.9	65.0	120.0	17
Macronucleus, length	MN	CHL	22.9	20.0	26.0	21
	MC	PA	48.5	38.0	61.0	17
Macronucleus, width	MN	CHL	22.3	20.0	26.0	21
	MC	PA	35.0	30.0	40.0	17
Left oral polykinetid, number of kineties	MN	SC	29.8	25.0	33.0	13
	MC	SC	42.6	38.0	51.0	17
Somatic kineties, number	MN	CHL	60.3	50.0	70.0	21
	MC	CHL	80.2	70.0	92.0	17

[a] Data based on specimens from non-flooded Petri dish cultures. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, Max – maximum, Min – minimum, n – number of individuals investigated, PA – protargol impregnation (FOISSNER's method), SC – silver carbonate impregnation, $\bar{x}$ – arithmetic mean.

Maryna namibiensis costaricensis nov. sspec. (Fig. 202a –h; 424a–y, 425a–m; Tables 183, 184)

Diagnosis: Size 110–160 × 70–130 µm, usually 140 × 105 µm in vivo. Macronucleus broadly ellipsoidal. On average 80 somatic ciliary rows and 43 kineties in left oral polykinetid.

Type location: Rock-pools at bank of Rio Corobici in the surroundings of the hacienda "La Pacifica" (Centro Ecológico "La Pacifica") near the town of Cañas in Costa Rica, Central America, 10°28'N 85°10'W.

Etymology: Named after the country discovered.

Description and comparison with related species: This subspecies is very similar to *M. namibiensis namibiensis* in general morphology and behaviour. Thus, we do not provide a separate description, but emphasize the differences given in the diagnosis. Furthermore, we refer to the detailed morphometrics (Tables 183, 184), figures, and figure explanations. Resting cysts were not observed.

Generally, *M. namibiensis costaricensis* is distinctly larger than *M. namibiensis namibiensis* and thus appears more massive. Accordingly, most morphometrics do not or only slightly overlap (Table 183). *Maryna namibiensis costaricensis* feeds not only on bacteria, which are digested in 6–10 µm-sized vacuoles, but also on large, heterotrophic euglenids.

Table 184. Morphometric data on *Maryna namibiensis costaricensis*.

Characteristics [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	CHL	129.8	130.0	12.0	2.9	9.2	100.0	150.0	17
Body, length	PA	133.5	135.0	12.5	3.0	9.4	110.0	155.0	17
Body, calix width	CHL	100.9	100.0	13.6	3.3	13.4	65.0	120.0	17
Body, calix width	PA	105.2	105.0	10.3	2.5	9.8	88.0	127.0	17
Body, maximum uvula width	CHL	68.8	68.0	10.3	2.5	14.9	47.0	85.0	17
Anterior body end to buccal opening, distance	CHL	75.5	75.0	9.6	2.3	12.7	55.0	95.0	17
	PA	76.4	75.0	8.5	2.1	11.2	65.0	95.0	17
Anterior body end to macronucleus, distance	PA	46.6	45.0	16.5	4.0	35.4	25.0	80.0	17
Macronucleus, length	PA	48.5	47.0	5.9	1.4	12.2	38.0	61.0	17
Macronucleus, width	PA	35.0	35.0	3.6	0.9	10.3	30.0	40.0	17
Somatic kineties, number [b]	CHL	80.2	80.0	5.5	1.3	6.9	70.0	92.0	17
Left oral polykinetid, number of kineties	PB	42.6	42.0	3.6	0.9	8.4	38.0	51.0	17
Left oral polykinetid, length	PA	27.7	26.0	5.4	1.3	19.4	21.0	38.0	17
Left oral polykinetid, length	PB	37.5	37.0	6.1	1.5	16.2	30.0	53.0	17
Left oral polykinetid, width	PB	11.6	12.0	1.5	0.4	12.6	10.0	15.0	17
Right oral polykinetid, length	PB	46.1	45.0	6.5	1.6	14.1	38.0	62.0	17
Right oral polykinetid, width	PB	14.5	15.0	2.2	0.5	15.0	11.0	20.0	17

[a] Data based on silver-impregnated and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, PA – protargol impregnation (FOISSNER's method), PB – protargol impregnation (WILBERT's method) and squashed, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Approximations because difficult to count due to the strong body spiralization.

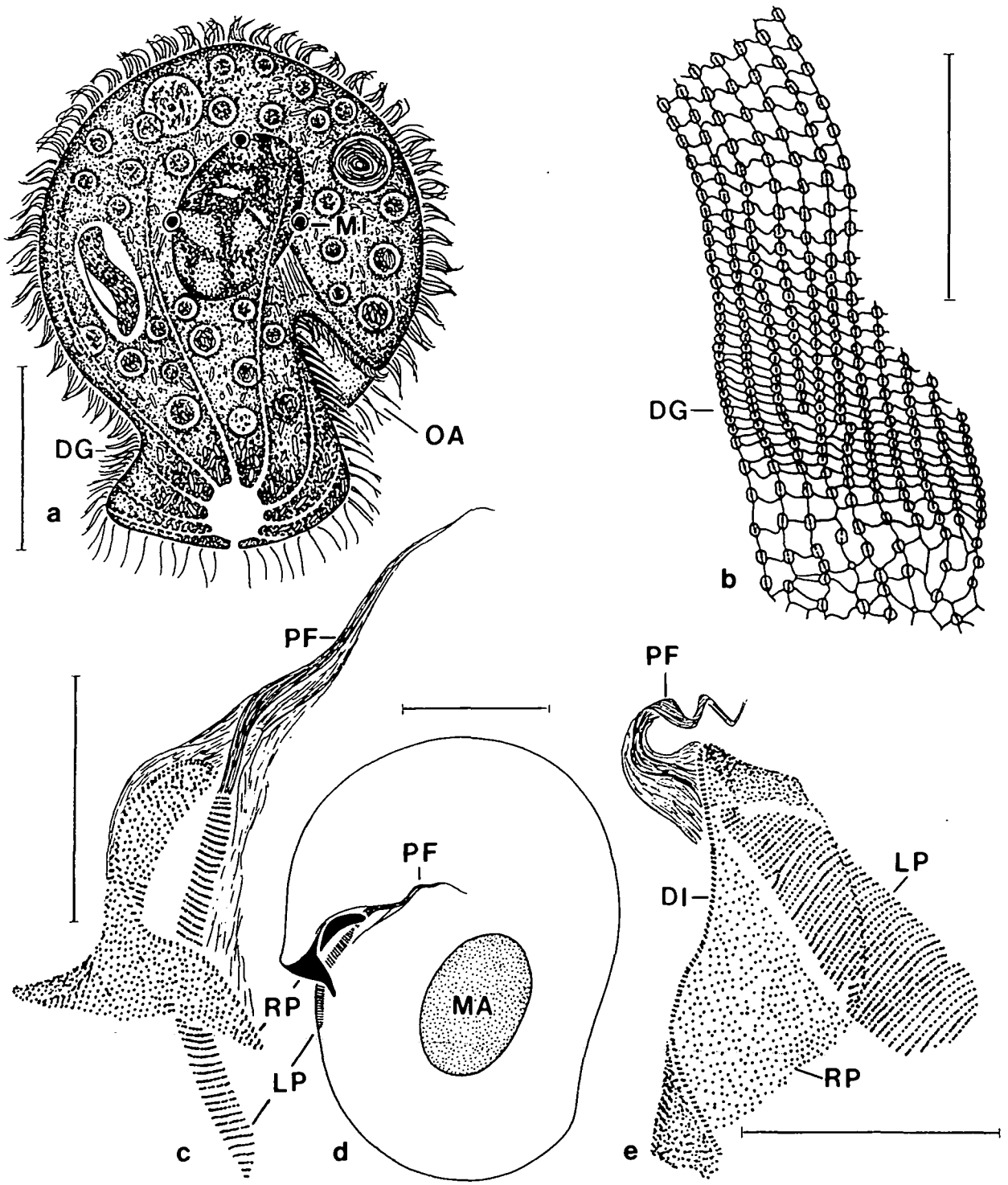


Fig. 202a–e. *Maryna namibiensis costaricensis* from life (a) and after CHATTON-LWOFF silver nitrate (b) and protargol (c–e) impregnation. **a:** Right side view of a representative specimen with three micronuclei and some large food vacuoles containing heterotrophic euglenids. **b:** Ciliary pattern and silverline system in dorsal portion of postoral (diagonal) groove. **c, d:** Overview and detail of oral apparatus. The pharyngeal fibres extend anteriorly, an important *Maryna* feature. **e:** Oral structures. The left polykinetid is rounded distally and distinctly narrowed proximally. DG – diagonal (postoral) groove, DI – row of dikinetids, LP – left oral polykinetid, MA – macronucleus, MI – micronucleus, OA – oral apparatus, PF – pharyngeal fibres, RP – right oral polykinetid. Scale bars 50 μm (a, d) and 25 μm (b, c, e).

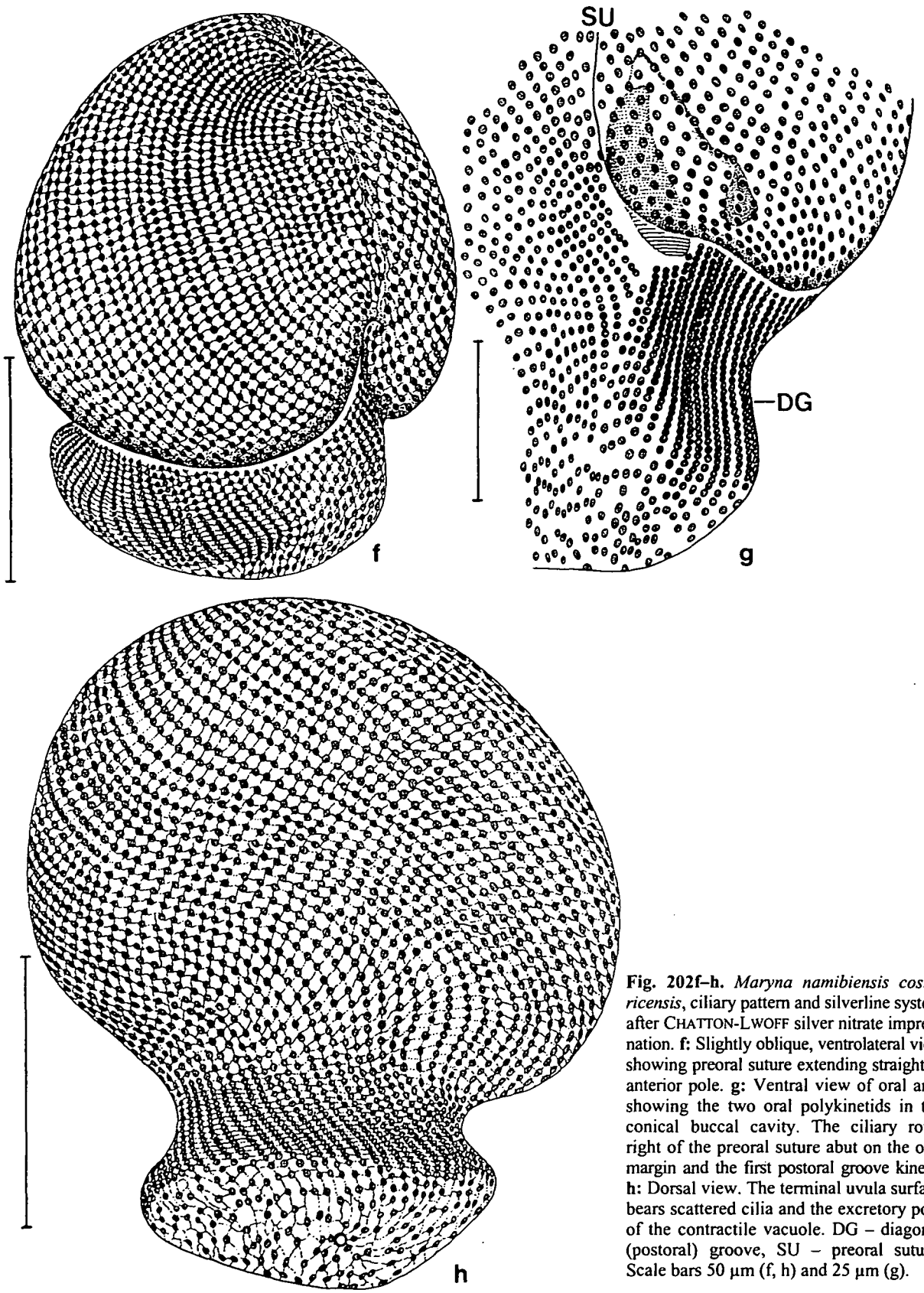


Fig. 202f–h. *Maryna namibiensis costaricensis*, ciliary pattern and silverline system after CHATTON-LWOFF silver nitrate impregnation. **f:** Slightly oblique, ventrolateral view showing preoral suture extending straight to anterior pole. **g:** Ventral view of oral area showing the two oral polykinetids in the conical buccal cavity. The ciliary rows right of the preoral suture abut on the oral margin and the first postoral groove kinety. **h:** Dorsal view. The terminal uvula surface bears scattered cilia and the excretory pore of the contractile vacuole. DG – diagonal (postoral) groove, SU – preoral suture. Scale bars 50 µm (f, h) and 25 µm (g).

Maryna umbrellata (GELEI, 1950) FOISSNER, 1993 (Fig. 203a–n; 426a–z, 427a–z; Table 185)

1950 *Mycterothrix umbrellata* GELEI, Hidrol. Közl., 30: 112.
1962 *Maryna umbrellata* (GELEI 1950) GELEI 1954 – DINGFELDER, Arch. Protistenk., 105: 581 (redescription from life).
1993 *Maryna umbrellata* (GELEI, 1950) nov. comb. – FOISSNER, Colpodea: 339 (see this review for further literature and nomenclature).

Neotype material: Neotypified from Costa Rican population, according to reasons 1, 4, 6 given in chapter 2.4.2.

Improved diagnosis: Size around 100 µm in vivo, slightly broader than long. Distinctly mushroom-shaped, that is, with umbrella-like calix and button-shaped, minute uvula. Macronucleus globular. Extrusomes rod-shaped, form rather conspicuous fringe. About 50 somatic ciliary rows and 20 kineties in left oral polykinetid.

Description of Costa Rican neotype population: Overall size 80–110 µm in vivo (70–120 µm in Australian specimens and 70–90 µm in Namibian site 66 specimens). General appearance like a mushroom with a very short trunk (Fig. 203a); disc-shaped specimens occurred in Australia (Fig. 203b). Calix (cap) conical to broadly conical, that is, usually slightly broader than long (high) and inconspicuously flattened ventrally; transverse view thus broadly elliptical with a more or less distinct ventral groove marking preoral suture. Uvula (trunk) set off from body proper by comparatively flat diagonal (postoral) groove, broad but very short and thus inconspicuous, discoidal except for flattened portion right of oral opening (Fig. 203a, h, i; 426a, c–f, r, s, x, y; Table 185). Nuclear apparatus dorsal of body centre. Macronucleus globular, with reticular nucleolus and 1 µm thick membrane becoming very distinct in stained specimens, when the nuclear material shrinks (nuclear membrane also conspicuous in a South African population, but less so in Australian specimens). Micronucleus attached to macronucleus, about 3 µm across and surrounded by distinct membrane (Fig. 203a, i; 426g–i, k). Contractile vacuole in uvula, with inconspicuous collecting canals and single excretory pore in centre of uvula surface (Fig. 203a, k; 426e, f, t, y, z). Cortex very flexible, punctated by deep ciliary pits and, in optical section, rather distinctly striated by the extrusomes. Ciliary pits occasionally stand out as white circles from yellowish impregnated cortex in protargol slides, filled with silver precipitation and surrounded by a circular to slightly irregular silverline in silver nitrate preparations (Fig. 203 l, m; 426b, 427b–d). Extrusomes of very similar arrangement (in narrow stripes within ciliary rows), shape (rod-like), and size (about 4 × 0.2 µm) in Namibian, Costa Rican, Australian, and Venezuelan specimens; produce rather distinct fringe, individual extrusomes, however, difficult to recognize due to their slenderness; become extruded and stain pink, but elongate only slightly when methyl green-pyronin is added (Fig. 203a, c, d; 426a, m). Subcortical mitochondria conspicuously large, ellipsoidal (Fig. 203c). Cytoplasm viscid and packed with various inclusions, viz., innumerable minute crystals, some large crystals, few to rather many dark-brown flakes, and usually many food vacuoles containing bacterial residues. Cells thus opaque and brownish at low magnification (≤ ×100). Minute crystals (< 1 µm) conspicuously

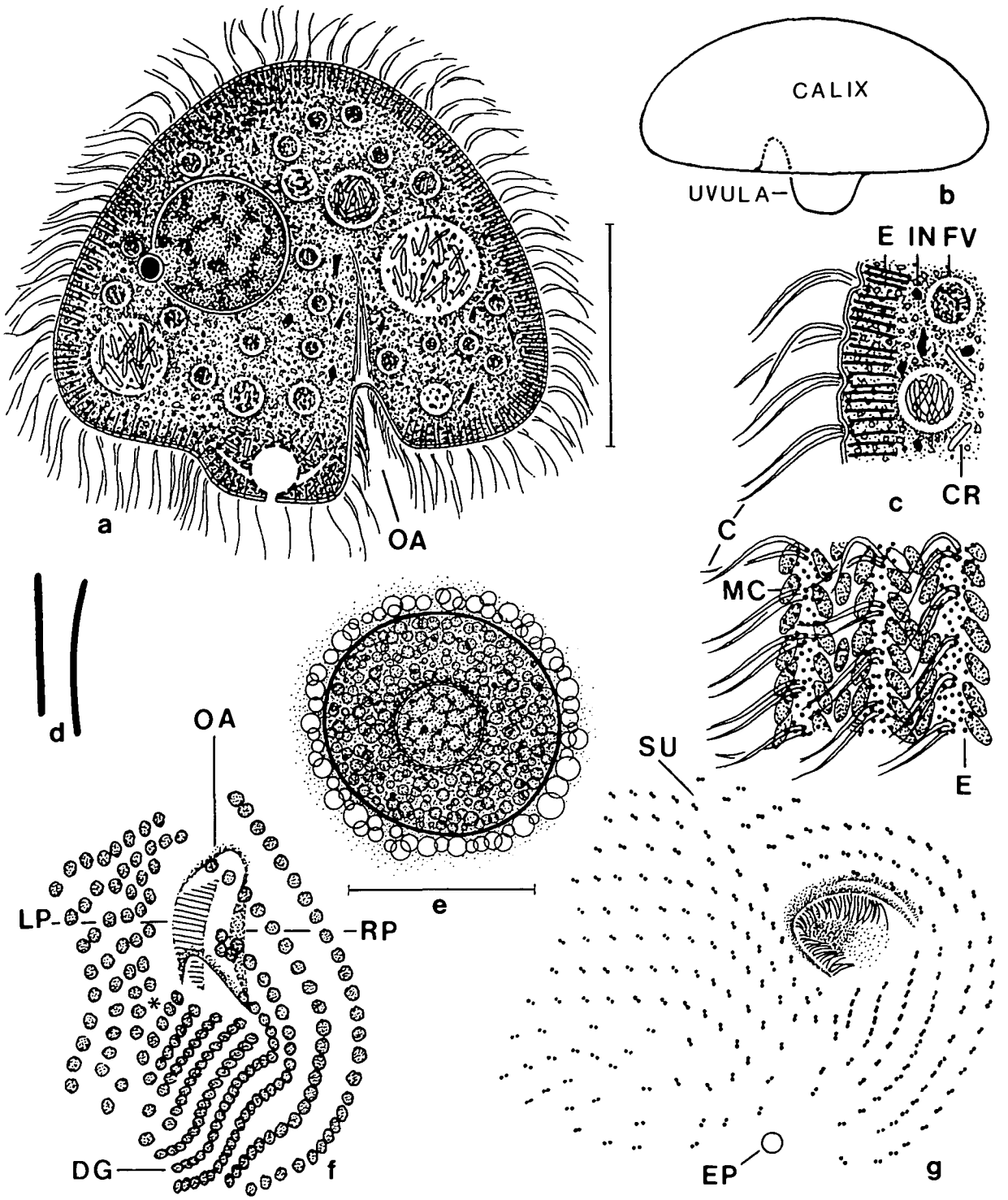


Fig. 203a–g. *Maryna umbrellata* from life (a–e), after silver nitrate impregnation (f), and a deciliated specimen in the SEM (g). **a:** Right lateral view of a representative specimen. Note extrusome fringe ("thick cortex"). **b:** Discoidal Australian specimen. **c, d:** Optical section and surface view of cell periphery. **e:** Resting cysts have a conspicuous envelope of globules. **f, g:** Ventral and oblique posterior polar view showing arrangement of ciliary rows in oral area. Asterisk marks postoral suture. C – paired cilia, CR – crystals, DG – diagonal groove, E – extrusomes EP – excretory pore, FV – food vacuole, IN – dark brown inclusion, LP – left oral polykinetid, MC – mitochondria, OA – oral apparatus, RP – right oral polykinetid, SU – preoral suture. Scale bars 40 μm.

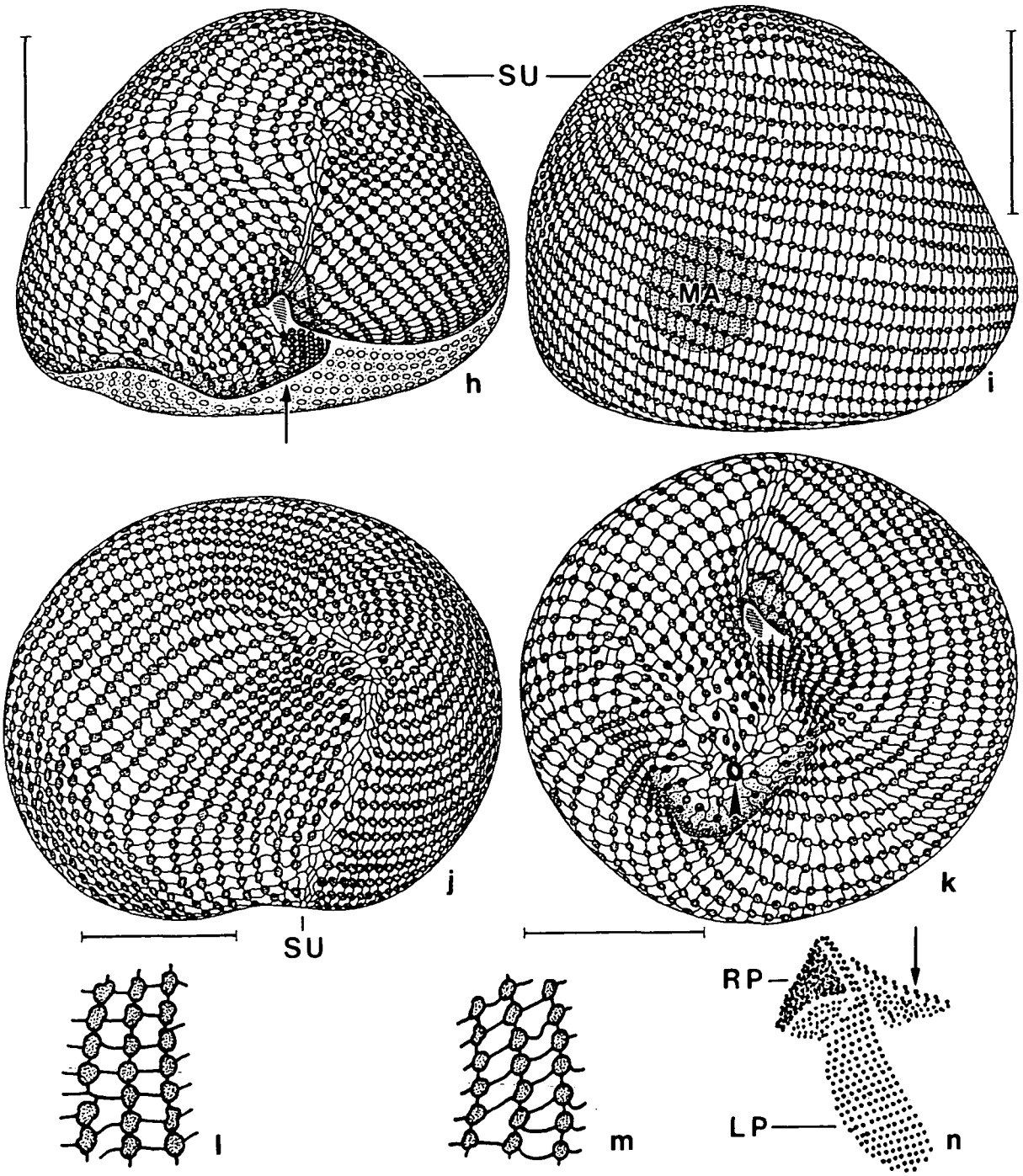


Fig. 203h–n. *Maryna umbrellata* after silver nitrate (h–m) and silver carbonate (n) impregnation. The ciliary rows and the silverlines form a complicated, highly ordered pattern and abut on a distinct suture extending from the oral apparatus to the anterior pole. The postoral suture (arrow in Fig. 203h) is minute but distinct because it is at a "stripe contrast" zone, where the densely ciliated diagonal groove abuts on the loosely ciliated ventral kineties. **h, i:** Ventral and dorsal view. Arrow marks postoral suture. **j, k:** Anterior and posterior polar view. The uvula is inconspicuous and bears the excretory pore of the contractile vacuole (arrowhead), while the densely ciliated lateral surface bears the so-called diagonal groove. **l, m:** Silverline pattern right and left of ventral suture. **n:** The oral ciliature consists of a right and left ciliary field. The right field, which is on the roof of the vestibulum, consists of disordered monokinetids and a row of dikinetids proximally (arrow). Note that the figure is from a squashed specimen, where the orientation of the right polykinetid is slightly changed. LP – left oral polykinetid, MA – macronucleus, RP – right oral polykinetid, SU – preoral suture. Scale bars 30 µm.

sparkling under interference contrast illumination and dark in transmitted light, often concentrated in uvula, in a subapical spot in calix, and underneath cortex (Fig. 203a; 426a, j, l); even more numerous in Australian specimens often making black anterior body third. Up to 5 µm long, ellipsoidal, colourless crystals and dark-brown flakes of unknown nature scattered throughout cells, crystals concentrated around contractile vacuole. Food vacuoles 4–7 µm across, rarely up to 30 µm, Namibian site (66) and Australian specimens packed with 3–5 µm-sized food vacuoles and some almost empty vacuoles up to 20 µm across (Fig. 203a, c). Swims fast to very fast performing a characteristic spiral, rocking course; never rests. No dwelling tubes were observed, even not in pure cultures from an Australian population.

Somatic and oral ciliary pattern as in congeners (FOISSNER 1993c). However, it will be described in some detail because of several specializations and new observations. Cilia sprout from deep, elliptical pits and are usually paired, except above uvula and on posterior uvula surface, where the anterior basal body is barren (Fig. 426d, q). Elongated caudal cilia lacking, posterior uvula surface, however, contains scattered cilia originating from posterior end of kineties (Fig. 203a, g, k; 426e, f, p, t, w, y, z). All ciliary rows, except about ten rows right of oral apparatus, have a condensed subterminal portion producing the heavily ciliated diagonal (postoral) groove. Most ciliary rows abut on a ventral suture (Fig. 203h, j, k; 427a–h). Preoral suture conspicuous, especially in silver nitrate preparations, extends slightly obliquely from right buccal vertex to anterior pole, where it performs a sharp right-turn and widens. Postoral suture, although being minute due to the flat uvula, also distinct because in a "stripe contrast" zone, that is, the region where the loosely ciliated rows right of the suture abut on the densely ciliated postoral kineties, which extend into the postoral groove.

The cilia and the silverlines connecting their basal bodies form a highly ordered pattern, whose spiral course causes many aspects of the pattern, depending on the angle viewed (Fig. 203h–k; 426u–y, 427b–h). However, the pattern is obviously as in other members of the genus (FOISSNER 1985, 1993c). Briefly, the about 50 ciliary rows extend spirally backward, especially from the left side of the preoral suture, and spiral across the dorsal side to extend again onto the ventral side right of the oral apparatus, where they merge, on the flattened portion of the uvula, into the almost straight ventral kineties. The left suture kineties above the oral apparatus are about twice as widely spaced anteriorly than posteriorly and those in the anterior half of the cell.

Oral apparatus between calix and uvula, minute compared to size of cell (Table 185). Vestibulum conical, extends anteriorly; right margin of oral overture distinct, left merges into diagonal groove (Fig. 203a, f, g; 426c, e, f, 427j). Left oral polykinetid on bottom of vestibulum, composed of an average of 21 monokinetidal rows decreasing gradually in length proximally at right side and distally at both sides. Right oral polykinetid on vestibular roof, cuneate, composed of a proximal row of dikinetids and of slightly irregular, oblique rows of monokinetids (Fig. 203n; 426u, 427i–o).

Silverline system in *Colpoda* pattern. Meshes narrow and irregular in preoral suture and posterior pole area (Fig. 203h–m; 426z, 427b–d).

Division and resting cysts were observed in cultures from an Australian population. Reproduction generates up to four tomites and occurs in a cyst covered by a thin membrane. The infraciliature is reorganized (Fig. 427p–s). Resting cysts have an average diameter of 64 µm (Table 185) and are blackish at low magnification ($\leq \times 100$; Fig. 427t) and yellowish at higher magnification ($\geq \times 250$; Fig. 427w). Rarely, resting cysts with dividing cells were observed,

possibly specimens which transformed into resting cysts during division. Endocyst smooth, only about 1 µm thick and colourless, covered by an about 4 µm thick, conspicuous layer (ectocyst) of yellowish, fatty shining globules, which, like the cyst membrane, stain blue with methyl green-pyronin (Fig. 203e; 427u–y). Globules 1–6 µm across and structureless in the light and scanning electron microscope (Fig. 427u, v, z), remain on cyst wall when inhabitant excysted. Cyst surrounded by rather voluminous, very hyaline mucous envelope usually colonized by bacteria and lost when transferred from culture dish to microscope slide (Fig. 427t). Nuclear apparatus stands out from colourless cytoplasm as a conspicuous, brownish globule because covered by the minute, sparkling crystals described above (Fig. 203e; 427w, x). Cytoplasm granular, contains few to many 1–3 µm-sized fat globules, making cysts dark and opaque at low magnification .

Table 185. Morphometric data on various populations of *Maryna umbrellata*.

Characteristics [a]	Pop [a]	Me [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length (height)	CR	CHL	71.9	70.0	6.3	1.4	8.7	76.0	104.0	21
Body, calix width (lateral axis)	CR	CHL	84.3	85.0	5.6	1.2	6.7	74.0	96.0	21
Body, calix width (dorsoventral axis)	CR	CHL	79.0	80.0	4.3	0.9	5.5	70.0	86.0	21
Body, uvula width	CR	CHL	33.1	34.0	4.1	0.9	12.2	25.0	40.0	20
Anterior end to macronucleus, distance	CR	CHL	36.0	35.0	6.6	1.4	18.4	20.0	47.0	21
Anterior end to oral opening, distance	CR	CHL	54.3	55.0	9.6	2.1	17.7	35.0	75.0	21
Macronucleus, length	CR	PB	25.7	26.0	3.0	0.7	11.8	17.0	30.0	21
Macronucleus, width	CR	PB	24.4	25.0	2.3	0.5	9.5	20.0	29.0	21
Macronucleus, number	CR	PB	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Somatic and postoral kineties, number	CR	CHL	46.9	47.0	3.0	0.7	6.3	42.0	52.0	21
Postoral kineties, number	CR	CHL	4.4	4.0	–	–	–	4.0	5.0	21
Left oral polykinetid, length	CR	PS	15.3	15.0	2.1	0.6	14.0	11.0	18.0	12
Left oral polykinetid, width	CR	PS	5.5	5.0	0.7	0.2	12.3	5.0	7.0	12
Left oral polykinetid, length	CR	PB	10.6	11.0	1.4	0.4	13.6	8.0	13.0	12
Left oral polykinetid, number of kineties	CR	PS	21.4	21.0	0.9	0.2	4.1	20.0	23.0	13
Left oral polykinetid, number of kineties	AU	SC	20.0	21.0	2.7	0.7	13.4	16.0	25.0	15
Left oral polykinetid, number of kineties	VE	SC	16.1	16.0	0.6	0.2	4.0	15.0	17.0	8
Right oral polykinetid, length	CR	PS	19.9	19.0	3.5	1.0	17.6	16.0	26.0	12
Right oral polykinetid, width	CR	PS	8.0	8.0	1.1	0.3	14.1	6.0	10.0	12
Cysts, length with envelope	AU	IV	66.1	64.0	5.0	1.1	7.5	59.0	76.0	19
Cysts, width with envelope	AU	IV	62.3	64.0	3.7	0.8	5.9	56.0	72.0	19
Cysts, length without envelope	AU	IV	54.3	56.0	4.7	1.1	8.6	48.0	64.0	19
Cysts, width without envelope	AU	IV	52.1	52.0	3.8	0.9	7.3	44.0	60.0	19
Cysts, diameter of globules in envelope	AU	IV	2.8	3.0	1.6	0.3	56.0	1.0	6.0	29

[a] Data based on randomly selected specimens from non-flooded Petri dish or pure cultures (Australian population). Measurements in µm. AU – Australian population, CHL – CHATTON-LWOFF silver nitrate impregnation, CR – Costa Rican population, CV – coefficient of variation in %, IV – in vivo, M – median, Max – maximum, Me – methods, Min – minimum, n – number of individuals investigated, PB – protargol impregnation (WILBERT's method and mounted), Pop – population, PS – protargol impregnation (WILBERT's method; wet, squashed preparation), SC – silver carbonate impregnation, SD – standard deviation, SE – standard error of arithmetic mean, VE – Venezuelan population, $\bar{x}$ – arithmetic mean.

The resting cyst of *M. umbrellata* is distinctly different from those of *M. galeata*, *M. atra*, and *M. namibiensis*, but highly resembles that of *Mycterothrix tuamotensis* (for review, see FOISSNER 1993c). However, we did not observe an equatorial thickening.

Occurrence and ecology: Literature data (FOISSNER 1993c) and the present observations show that *M. umbrellata* is not a typical soil ciliate but prefers ephemeral puddles. However, in Namibia it was found in ordinary but highly saline soil samples (sites 66, 70), which agrees with the type location, that is, soda puddles (sziliszék) in Hungary; in Costa Rica (Central America), *M. umbrellata* occurred in the mud of deep, cylindroidal rock-pools at the bank of the Rio Corobici at the hacienda "La Pacifica" (Centro Ecológia "La Pacifica") near the town of Cañas, 10°28'N 85°10'W); in Australia, we isolated it from the dark mud (pH 7.0) of rock-pools at the bank of the Shoalhaven River near the town of Bungonia (35°S 149°E); in Venezuela, *M. umbrellata* occurred in rock-pools (Lajas) near the airport of Puerto Ayacucho. We could cultivate the Australian population for two weeks in Eau de Volvic enriched with some cracked wheat grains. Cultures then declined and encysted. Some air-dried cysts could be reactivated after two months, but the specimens did not reproduce. As yet, *M. umbrellata* was known only from Europe. Our data show that it is a cosmopolitan, euryhaline ciliate preferring ephemeral puddles.

Comparison with literature and related species: Our observations agree well with the original description and the redescription by DINGFELDER (1962). All populations are very similar and easily identified by the mushroom-like shape, the size (around 100 µm), the globular macronucleus, the extrusome fringe (described as "thick cortex" by GELEI), and the lack of elongated caudal cilia. Accordingly, identification is beyond reasonable doubt. However, neotypification is necessary because the original description does not unequivocally define *M. umbrellata*, which is easily confused or even identical to *M. cardioides* (macronucleus ellipsoidal) and *M. pinguis* (almost globular), two poorly described species reviewed in FOISSNER (1993c).

Ilsiella elegans nov. spec. (Fig. 204a–p; 428j, k; Table 186)

Diagnosis: Size about 35 × 20 µm in vivo. Fusiform with conspicuous subterminal indentation at oral opening. Macronucleus globular. 10 somatic ciliary rows, five of which distinctly condensed above and left of oral apparatus. Right oral ciliary field composed of an average of 10 dikinetids, left elongate rectangular consisting of 9 ciliary rows.

Type location: Bark of a *Colophospermum mopane* tree at the Bambatsi Guest Farm, Namibia, 20°10'S 15°25'E (site 51 in figure 2 and chapter 2.1.2).

Etymology: The Latin adjective *elegans* refers to the elegant shape of this species.

Description: Size 25–40 × 18–25 µm in vivo, usually about 35 × 20 µm. Shape highly characteristic and very similar in the three populations studied (Fig. 204a, d–g; 428k): fusiform (2:1) to elongate fusiform (3:1) with distinct subterminal indentation at oral opening; slenderest specimens slightly sigmoidal and looking very elegant (Fig. 204d). Unflattened and non-contractile. Location of nuclear apparatus highly variable, on average slightly below mid-

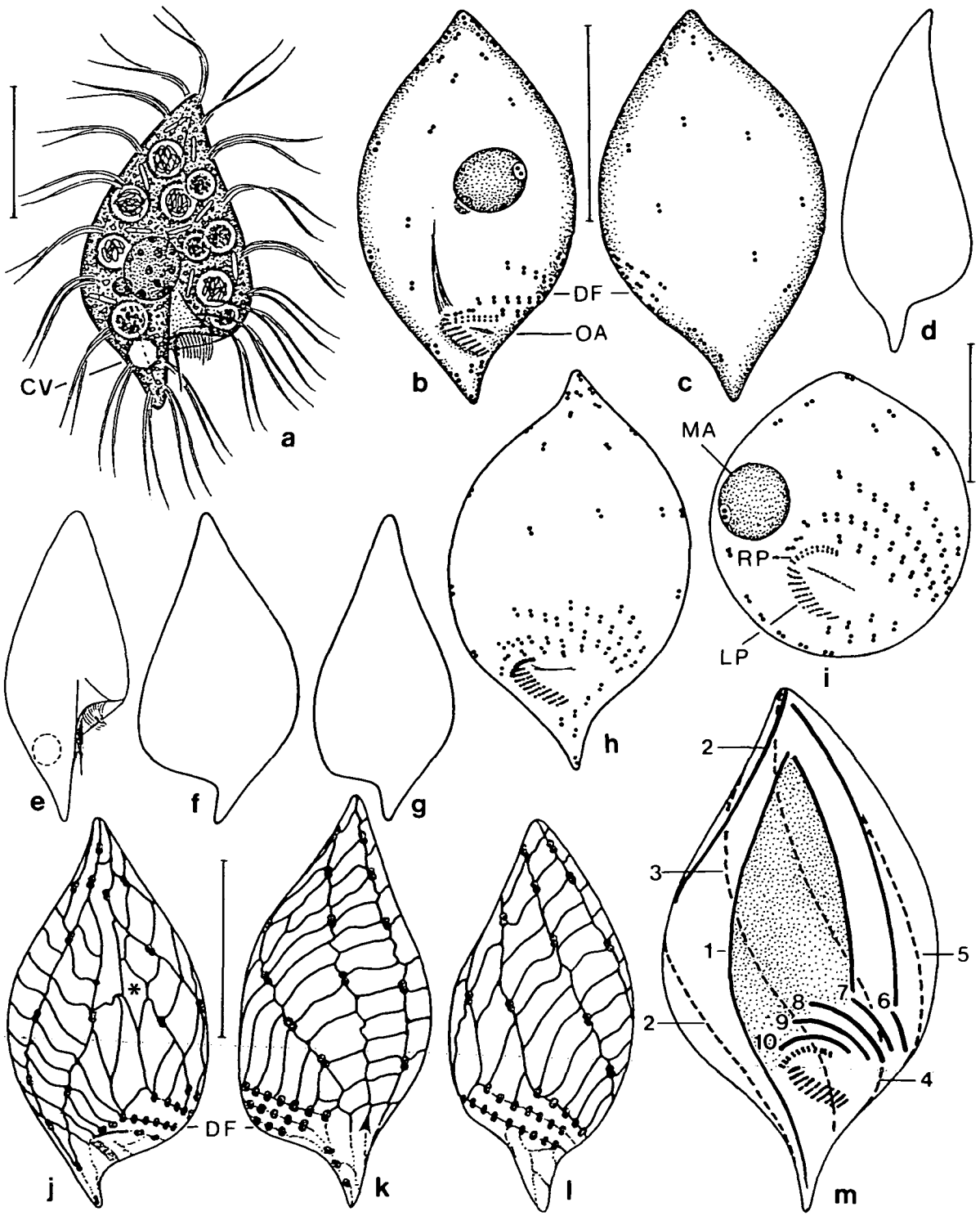


Fig. 204a–m. *Ilsiella elegans* from life (a, d–g), after protargol impregnation (b, c, h, i), and CHATTON-LWOFF silver nitrate impregnation (j–l). **a:** Right lateral view. **b, c:** Ciliary pattern of ventral and dorsal side. **d, f, g:** Shape variability of Austrian population. **e:** Australian specimen. **h, i:** Ventrolateral and oblique posterior polar view. **j–l:** Silverline system of Australian specimens. Figure (j) is a right-ventral view showing the irregular silverline pattern in the preoral area (asterisk). Figure (k) is a left-ventral view showing a platyophryid silverline pattern below a shortened ciliary row (arrowhead). Figure (l) is a left side view. **m:** Scheme of ciliary rows (numbers) and preoral area (dotted). CV – contractile vacuole, DF – dense ciliary field, LP – left oral polykinetid, MA – macronucleus, OA – oral apparatus, RP – right oral polykinetid. Scale bars 15 µm.

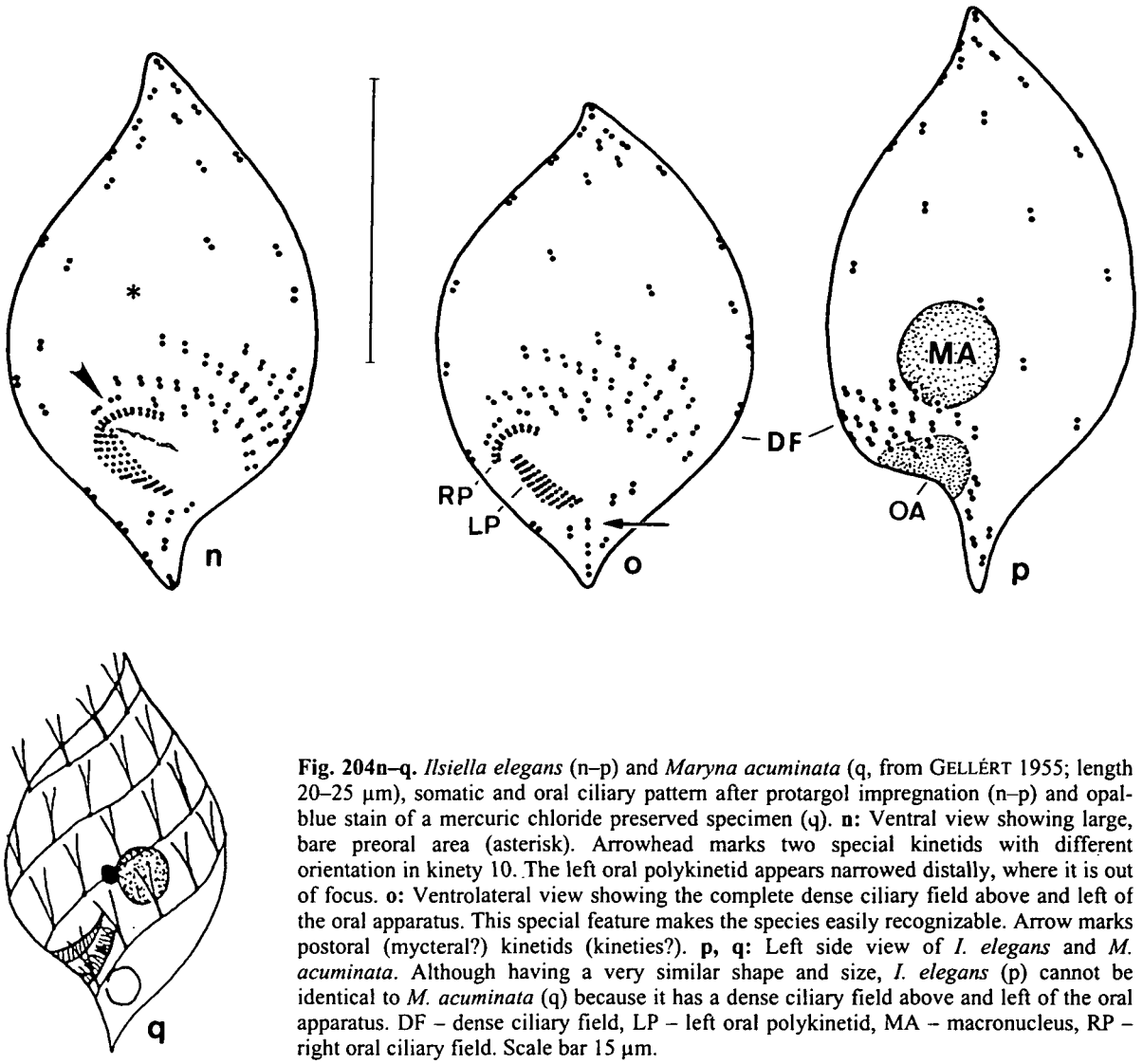


Fig. 204n–q. *Ilsiella elegans* (n–p) and *Maryna acuminata* (q, from GELLÉRT 1955; length 20–25 µm), somatic and oral ciliary pattern after protargol impregnation (n–p) and opal-blue stain of a mercuric chloride preserved specimen (q). **n:** Ventral view showing large, bare preoral area (asterisk). Arrowhead marks two special kinetids with different orientation in kinety 10. The left oral polykinetid appears narrowed distally, where it is out of focus. **o:** Ventrolateral view showing the complete dense ciliary field above and left of the oral apparatus. This special feature makes the species easily recognizable. Arrow marks postoral (mycteral?) kinetids (kineties?). **p, q:** Left side view of *I. elegans* and *M. acuminata*. Although having a very similar shape and size, *I. elegans* (p) cannot be identical to *M. acuminata* (q) because it has a dense ciliary field above and left of the oral apparatus. DF – dense ciliary field, LP – left oral polykinetid, MA – macronucleus, RP – right oral ciliary field. Scale bar 15 µm.

body. Macronucleus spherical to slightly ellipsoidal (6 × 5 µm), with many small nucleoli. Micronucleus attached to macronucleus, about 2 µm across, impregnates only faintly with protargol. Cortex colourless, flexible, thin; extrusomes recognizable neither in vivo nor in protargol preparations. Cytoplasm with many minute (≤ 1 µm) crystals sparkling under interference contrast illumination, especially in posterior body third; and up to 5 µm long bacterial rods, possibly parasites or symbionts. Cells usually packed with 3–5 µm-sized food vacuoles containing bacteria. Swims rather rapidly in narrow spirals rotating about main body axis, but also attaches to soil particles with the anterior body end (Fig. 428k).

Organization of somatic ciliary pattern similar to that of *Maryna antarctica* FOISSNER, 1993c and rather simple because of lacking diagonal groove and caudal cilia. Row pattern, on the other hand, difficult to follow because of sparse ciliation and broad, triangular, unciliated preoral area (Fig. 204a–c, h–p; Table 186). Invariably 10 kineties: right of preoral area and on dorsal surface five loosely ciliated (6–11 dikinetids/row), bipolar kineties, whose oblique

orientation gradually increases from ventral to dorsal side; left lateral rows 6 and 7 posteriorly continue as short preoral kineties; preoral kineties 8–10 strongly shortened and obliquely arranged above and left of oral apparatus, composed of closely spaced dikinetids producing rather distinct ciliary tuft left of oral opening. First preoral kinety (kinety 10 in Fig. 204m) composed of 5–6 dikinetids, with rightmost two kinetids not obliquely but transversely orientated, as in *M. antarctica*; second preoral kinety composed of 7–11 dikinetids; third of 9–10; fourth of 7–8; and fifth of 4–5 dikinetids. Some scattered dikinetids postorally, possibly remnants of mycteral (postoral groove) kineties.

Oral opening at base of subterminal body indentation, that is, right oral ciliary field 30% back from rear body end on average (Fig. 204a, b, h, i, m–o; Table 186). Vestibulum small, conical, with fine pharyngeal fibres extending anteriorly and impregnating only occasionally. Left oral ciliary field (polykinetid) on (dorsal) vestibular bottom, elongate rectangular, consists of an average of nine kineties each composed of five basal bodies having 4 µm long cilia; kineties at ends of field with three to four cilia only. Right oral ciliary field extends along upper vestibular entrance, composed of an average of 10 dikinetids forming a slightly curved row, as is typical for *Ilsiella*.

Occurrence and ecology: To date found in three contrasting terrestrial habitats which, however, agree in their extremely ephemeric nature: *Colophospermum* bark in Namibia (type location), soil from the Murray River floodplain in Australia, and leaf litter from

Table 186. Morphometric data on *Ilsiella elegans*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	29.3	28.0	4.2	1.0	14.2	23.0	38.0	17
Body, width	18.7	18.0	2.6	0.6	14.2	15.0	24.0	17
Anterior body end to macronucleus, distance	13.6	14.0	3.9	0.9	28.6	6.0	20.0	17
Anterior body end to right oral ciliary field, distance	21.0	19.0	3.8	0.9	18.1	17.0	29.0	17
Oral opening, width at distal end of ciliary fields	4.6	5.0	0.8	0.2	17.3	3.0	6.0	17
Macronucleus, length	5.9	6.0	0.5	0.1	8.3	5.0	7.0	17
Macronucleus, width	5.4	5.0	–	–	–	5.0	6.0	17
Micronucleus, length	1.7	1.5	–	–	–	1.5	2.0	17
Micronucleus, width	1.6	2.0	–	–	–	1.0	2.0	17
Right oral field, length	3.9	4.0	–	–	–	3.0	4.0	17
Right oral field, number of dikinetids	9.4	10.0	0.9	0.2	10.0	8.0	11.0	17
Left oral ciliary field, length	4.9	5.0	0.4	0.1	8.7	4.0	6.0	17
Left oral ciliary field, width	1.5	1.5	0.3	0.1	18.2	1.0	2.0	17
Left oral ciliary field, number of kineties	9.4	9.0	0.6	0.2	6.5	8.0	10.0	17
Somatic ciliary rows, number	10.0	10.0	0.0	0.0	0.0	10.0	10.0	17
Kinetids in 1st kinety right of oral opening, number	9.4	9.0	0.7	0.2	7.6	8.0	11.0	17

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected, ventrally orientated specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

a beech forest in Salzburg, Austria. The species is moderately abundant at all sites and of very similar morphology: for instance, the left oral polykinetid is composed of about ten kineties in both the African and Australian population. The ephemeric nature of *I. elegans* is emphasized by the observation that it is present only during the first days after rewetting the samples, and in Salzburg it occurs only in the fresh, rain-wet litter. Thus, it is likely that the species is more common than indicated by the few records, as we usually investigate only air-dried, rewetted samples. Obviously, *I. elegans* is a cosmopolitan preferring extremely ephemeric habitats.

Comparison with related species: *Ilsiella elegans* has a highly characteristic shape distinctly different from that of the two congeners, which are globular (FOISSNER 1993c). First, we identified our populations as *Maryna acuminata* (GELLÉRT, 1955) FOISSNER, 1993c, which has a similar shape. Unfortunately, GELLÉRT (1955) illustrated only a single, mercuric chloride and opal blue-prepared cell, although he studied live specimens, as evident from the text. According to GELLÉRT (1955), *M. acuminata* is only 20–25 µm long, leaf-like flattened ("a leaf-shaped organism pointed at both ends"), and has four ciliary rows with widely and equidistantly spaced, paired cilia (Fig. 204q). Although the number of ciliary rows is subject to different interpretations in marynids, the conspicuous field of ventrolateral ciliary rows of *I. elegans* is not, because it is easily recognizable both in vivo and preparations. Thus, our species cannot be classified with *M. acuminata*. Whether *M. acuminata* belongs to *Maryna* or *Ilsiella* needs reinvestigation of silvered specimens.

At first glance, the condensed ciliary rows of *I. elegans* look like ordinary mycteral (postoral groove) kineties. However, they are above the oral apparatus and thus must be ventrolateral ciliary rows, as in other marynids, where they are less conspicuous because the other kineties are also densely ciliated. There is a line of transitions from very distinct (*I. elegans*) to distinct (*I. palustris*, *I. terricola*, *Maryna antarctica*) through indistinct (→ *M. umbrellata*) to absent (→ *M. namibiensis*). Thus, the feature hardly can be used to split the genus at the present state of knowledge.

Nivaliella plana FOISSNER, 1980 (Fig. 205a–g; 428a–i; Table 187)

Nivaliella plana, as described by FOISSNER (1980b) and reviewed in FOISSNER (1993c), is a minute (10–25 × 6–20 µm in vivo), flattened ciliate with a somewhat quadrangular outline. Over the years, we found it in hundreds of soil samples from all continents (FOISSNER 1998a). The populations formed two groups, viz., one with a smooth surface (cortex), as stated in the original description, and another with a ribbed appearance. Often, both types occurred in the same sample and were connected by more or less distinct transitions. Thus, we studied in detail a North American population, in which the ridges were especially prominent. This showed that the ciliary pattern is as in the Australian *N. plana* population described in FOISSNER (1993c). Accordingly, the ribbed specimens/populations are very likely ecovariants of *N. plana*. However, a detailed description of this variety is warranted because it looks rather different from the smooth variety and is thus easily mistaken for a distinct species. Furthermore, some specimens are often difficult to distinguish from small individuals of *Pseudoplatyophrya nana* and *P. saltans*.

The ribbed population described now is from a coastal grassland with halophytes south of San Francisco, USA. The sample was a mixture of fine roots and slightly saline, acidic (pH 5.5) rhizosphere soil.

Size 18–27 × 10–15 µm, usually about 20 × 13 µm, that is, slightly larger than the smooth variety. Shape highly variable, often as shown in figures 205a, b, that is, bursiform or ovate like a small, fat *Pseudoplatyophrya nana* or *P. saltans*, occasionally broader and more distinctly quadrangular looking, like the smooth variety, or more slender resembling an ordinary *P. nana*; slightly to up 2:1 flattened laterally. Nuclear apparatus near body centre. Macronucleus globular, hyaline with very pale nucleoli. Micronucleus conspicuous in vivo because compact and about 3 × 1 µm in size, attached to macronucleus, discoidal; ellipsoidal in protargol preparations. Contractile vacuole in posterior body end, excretory pore not seen.

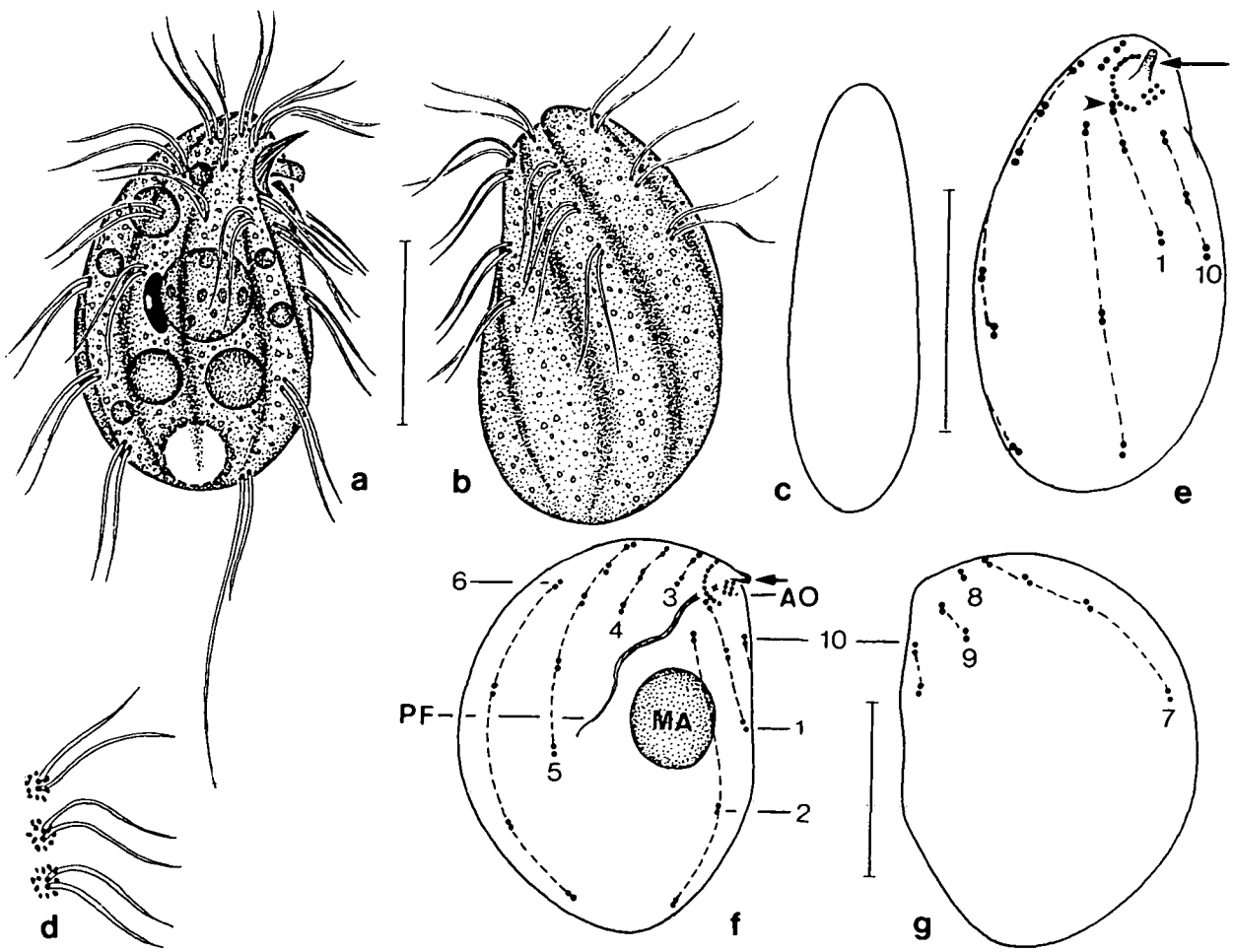


Fig. 205a–g. *Nivaliella plana*, ribbed North American variety from life (a–c) and after protargol impregnation (d–g). **a, b:** Right and left side view of representative specimens. **c:** Dorsal view showing lateral flattening. **d:** Argyrophilic granules, very likely some sort of mucocysts, surround the somatic dikinetids. **e:** Ciliary pattern of ventral side. Arrowhead marks first dikinetid of ciliary row 1; very likely, this kinetid has been overlooked in previous descriptions because it is so close to the paroral membrane. The arrow denotes the feeding tube, which is the main ordinal feature. **f, g:** Ciliary pattern of right and left side of same specimen. Arrow marks feeding tube. Numbers denote ciliary rows (invariably 10, Table 187). AO – adoral organelles(s), MA – macronucleus, PF – pharyngeal fibres. Scale bars 10 µm.

Cortex bright, rigid, and more or less distinctly ribbed along ciliary rows; ribbing usually well recognizable at a magnification of ≥ ×100, even if well-fed. Extrusomes hardly recognizable in vivo; however, the dikinetids are surrounded by minute granules, very likely some sort of mucocysts, in protargol preparations, providing the specimens with a characteristic appearance (Fig. 205d; 428f, i). Cytoplasm usually rather hyaline, contains some 0.5–3 µm-sized fat globules and many minute (~ 0.2 µm) crystals sparkling under interference contrast illumination. Glides quickly on microscope slide and soil particles.

Somatic cilia paired and about 8 µm long in vivo, that is, large compared to size of cell. A distinctly elongated caudal cilium, accompanied by an ordinary cilium, on ventral posterior end of cell. Arrangement of cilia very similar as described by FOISSNER (1993c). Briefly, there are 30 dikinetids on average invariably forming ten ciliary rows, which are distinctly shortened posteriorly, except for rows 2 and 6; thus, the central portion of the right and left side lacks cilia. The first dikinetid of row 10, not mentioned in FOISSNER (1993c), is difficult to recognize because it is close to the paroral membrane (Fig. 205a, b, e–g); see table 187 for numbers of dikinetids in individual kineties.Oral apparatus subapical on ventral side of cell, as minute as in most other members of order, details thus difficult to recognize. Feeding tube about 2 µm long in vivo. Cilia of paroral membrane and adoral organelle(s) each about 3 µm long in vivo, form rigid bundles. Adoral organelle(s) likely composed of six basal bodies, associated with long pharyngeal fibres (Fig. 205a, e, f).

Table 187. Morphometric data on a North American population of *Nivaliella plana*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	18.7	18.0	2.8	0.8	15.0	15.0	24.0	11
Body, width	12.3	12.0	2.2	0.7	18.2	9.0	17.0	11
Anterior body end to proximal end of paroral, distance	3.5	4.0	0.6	0.2	17.4	2.0	5.0	11
Anterior body end to macronucleus, distance	6.8	7.0	2.5	0.8	37.2	3.0	13.0	11
Macronucleus, length	4.9	5.0	1.0	0.3	19.4	4.0	7.0	11
Macronucleus, width	4.6	5.0	0.9	0.3	19.5	4.0	7.0	11
Somatic ciliary rows, number	10.0	10.0	0.0	0.0	0.0	10.0	10.0	11
Somatic dikinetids, total number	29.5	29.0	3.3	1.0	11.1	24.0	38.0	11
Dikinetids in ciliary row 1, number	3.1	3.0	–	–	–	3.0	4.0	11
Dikinetids in ciliary row 2, number	3.1	3.0	–	–	–	3.0	4.0	11
Dikinetids in ciliary row 3, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
Dikinetids in ciliary row 4, number	2.9	3.0	0.5	0.2	18.6	2.0	4.0	11
Dikinetids in ciliary row 5, number	4.1	4.0	0.7	0.2	17.1	4.0	6.0	11
Dikinetids in ciliary row 6, number	5.1	5.0	1.0	0.3	20.5	4.0	8.0	11
Dikinetids in ciliary row 7, number	3.4	3.0	0.7	0.2	19.8	2.0	4.0	11
Dikinetids in ciliary row 8, number	1.3	1.0	–	–	–	1.0	2.0	11
Dikinetids in ciliary row 9, number	1.8	2.0	–	–	–	1.0	2.0	11
Dikinetids in ciliary row 10, number	2.7	3.0	–	–	–	2.0	3.0	11

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Parabryophrya etoschensis nov. spec. (Fig. 206a–d; Table 188)

Diagnosis: Size about 110 × 30 µm; reniform. Macronucleus ellipsoidal. Food vacuoles elongate ellipsoidal, near 10 × 4 µm. About 25 ciliary rows. Two adoral organelles, proximal end of right oral ciliary field broadly rounded.

Type location: Soil from the ghost tree forest (*Moringa ovalifolia*) in the Etosha National Park, Namibia, 19°S 15°40'E (site 56 in figures 2, 3 and chapter 2.1.2).

Etymology: Named after the region discovered.

Description: Size 100–130 x 25–35 µm in vivo, usually about 110 x 30 µm, length:width ratio moderately variable, on average 3.5:1 (Table 188). Shape reniform in ventral and lateral view because more or less distinctly concave postorally, anterior end more narrowly rounded than posterior (Fig 206a, b); unflattened. Macronucleus in or near body centre, broadly ellipsoidal to almost semicircular, on average 26 × 13 µm. Micronucleus, possibly two in some specimens, in indentation of macronucleus, ellipsoidal. Contractile vacuole in posterior body end, with two collecting canals extending anteriorly and an excretory pore in centre of posterior pole. Cortex distinctly furrowed by ciliary rows in anterior body third, contains many bright granules (extrusomes?), which do not impregnate with the protargol method used. Cytoplasm colourless, usually contains a dozen, 8–12 × 3–6 µm-sized food vacuoles with remarkably regularly packed bacteria; when bacteria break during digestion, vacuoles round up (Fig. 206a). Swims rather rapidly by rotation about main body axis.

Cilia paired, closely spaced anteriorly, arranged in about 20–30 strongly spiralling rows commencing left of oral opening and preorally along a narrow suture (Fig. 206b, c; Table 188). Oral apparatus subapical in anterior 20% of cell, auricular with conspicuous, semi-circular right ciliary field composed of many short, radial rows and two inconspicuous adoral organelles at left mouth margin; anterior adoral organelle composed of 10–20 scattered basal bodies, posterior of about four dikinetids likely at strongly curved anterior end of a postoral kinety. Anterior portion of right ciliary field narrowed or even pointed and merging into somatic kineties, posterior end broad, forming conspicuous ciliary patch when viewed ventrolaterally (Fig. 206a, b, d; Table 188).

Occurrence and ecology: To date found only at type location. The species was very rare in the non-flooded Petri dish culture and did not occur in two samples taken from the same area in the year 2001.

Comparison with related species: *Parabryophrya etoschensis* differs from *P. penardi* (KAHL, 1931b), the sole congener reviewed in FOISSNER (1993c), by the macronucleus (ellipsoidal vs. globular), the food vacuoles (narrowly vs. broadly ellipsoidal), the number of ciliary rows (about 25 vs. ≤ 20), the number of adoral organelles (two vs. one), and the shape of the right oral ciliary field (proximal end broad vs. bluntly pointed; thus the field is **auricular** in *P. etoschensis* and **crescentic** in *P. penardi*). Certainly, these differences, especially in the oral structures, are sufficient to classify the Namibian population as a new species. However, the genus and the variability of the species are poorly known, but we have at least two further undescribed species in our notebook.

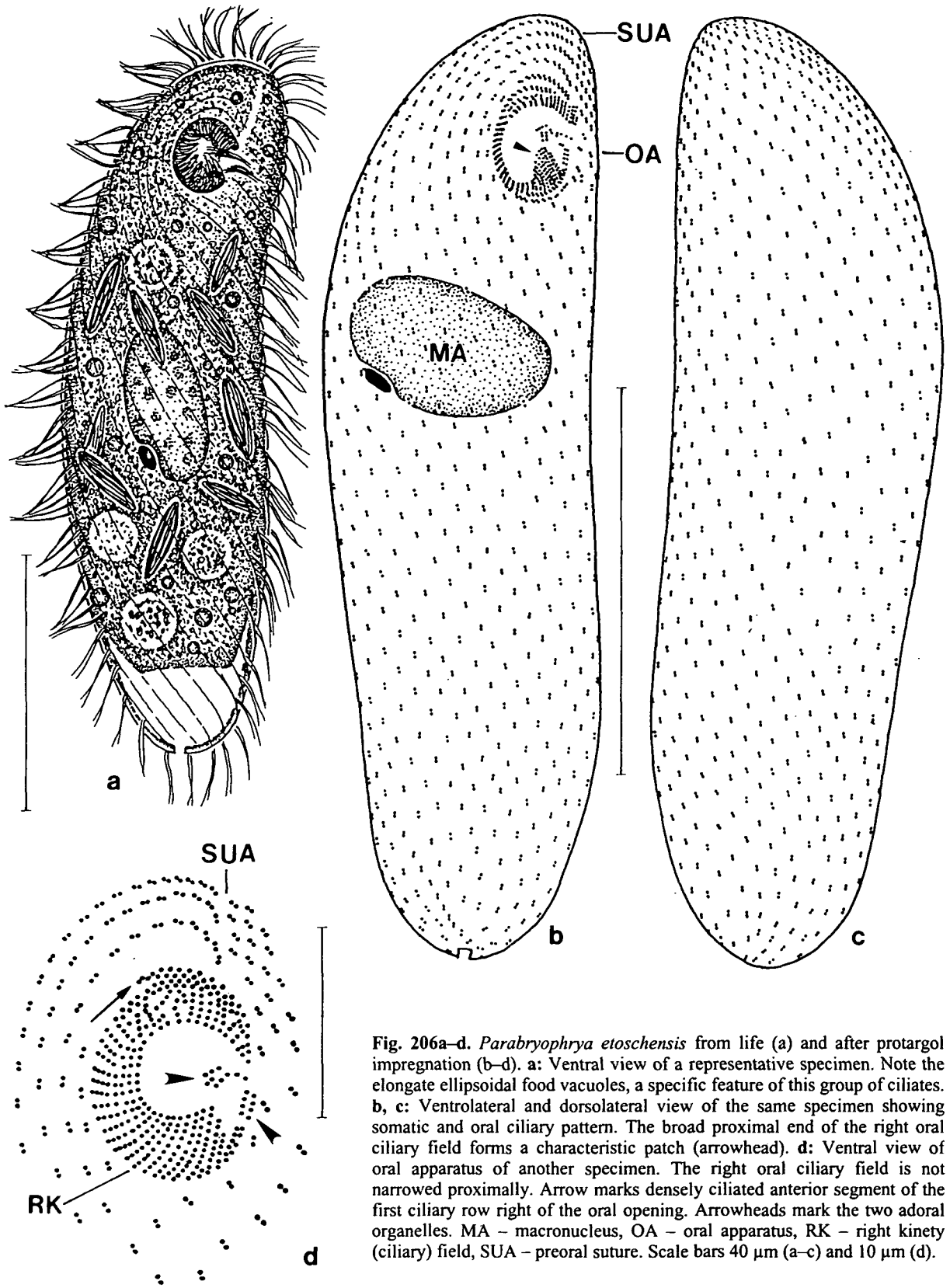


Fig. 206a–d. *Parabryophrya etoschensis* from life (a) and after protargol impregnation (b–d). **a:** Ventral view of a representative specimen. Note the elongate ellipsoidal food vacuoles, a specific feature of this group of ciliates. **b, c:** Ventrolateral and dorsolateral view of the same specimen showing somatic and oral ciliary pattern. The broad proximal end of the right oral ciliary field forms a characteristic patch (arrowhead). **d:** Ventral view of oral apparatus of another specimen. The right oral ciliary field is not narrowed proximally. Arrow marks densely ciliated anterior segment of the first ciliary row right of the oral opening. Arrowheads mark the two adoral organelles. MA – macronucleus, OA – oral apparatus, RK – right kinety (ciliary) field, SUA – preoral suture. Scale bars 40 µm (a–c) and 10 µm (d).

Table 188. Morphometric data on *Parabryophrya etoschensis*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	102.7	103.0	6.7	1.9	6.5	90.0	112.0	13
Body, width	29.3	30.0	3.6	1.0	12.3	22.0	35.0	13
Body length:width, ratio	3.5	3.5	0.4	0.1	11.0	2.9	4.2	13
Anterior body end to oral opening, distance	7.3	7.0	1.0	0.3	13.3	6.0	9.0	13
Anterior body end to macronucleus, distance	39.8	41.0	12.5	3.5	31.3	13.0	55.0	13
Oral apparatus, length	11.8	11.5	1.1	0.3	9.7	10.0	14.0	12
Oral apparatus, width	9.9	10.0	0.7	0.2	7.5	9.0	11.0	10
Macronucleus, length [b]	26.2	25.0	–	–	–	21.0	40.0	13
Macronucleus, width	12.8	13.0	1.9	0.5	14.7	10.0	16.0	13
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	13
Micronucleus, length	4.3	4.0	–	–	–	4.0	5.0	6
Micronucleus, width	2.3	2.0	–	–	–	2.0	3.0	6
Somatic ciliary rows, number [c]	24.8	25.0	–	–	–	22.0	27.0	4
Kinetids in 10 µm of a kinety, number [d]	3.9	4.0	0.7	0.3	17.9	3.0	5.0	7

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Artificially spread, if curved; values thus approximate.

[c] Counted across diagonal; values thus approximate.

[d] Counted at mid-body.

Platyophrya spumacola KAHL, 1927

We split this species into two subspecies according to distinct differences in the number of adoral organelles. The following diagnosis is based on the revision of FOISSNER (1993c).

Improved diagnosis: Average size about 70–100 × 30–40 µm in vivo. Usually slightly reniform and 20–30 somatic ciliary rows with about 50 dikinetids in a right lateral kinety and 40 in a left lateral. Oral apparatus subapical on ventral side, 6–10 adoral organelles on average. Prefers terrestrial habitats.

Platyophrya spumacola spumacola KAHL, 1927b **nov. stat.**

Diagnosis: Usually about 25 ciliary rows and 10 adoral organelles.

Locus classicus: *Cicada* foam attached to plants in Hamburg, Germany.

Remarks: See FOISSNER (1993c) for a detailed review on this subspecies.

Platyophrya spumacola hexasticha nov. sspec. (Fig. 207a–e; Table 189)

Diagnosis: On average 21 ciliary rows and 6 adoral organelles.

Type location: Soil from *Aloe dichotoma* forest near the Gariganus Guest Farm, Namibia, 26°30'S 18°25'E (site 5 in figure 2 and chapter 2.1.2).

Etymology: Composite of the Greek words *hexa* (six) and *sticha* (row of things), referring to the row of six adoral organelles.

Description: In vivo indistinguishable from *P. spumacola spumacola*. Thus, we refer the reader to FOISSNER (1993c), who describes and illustrates the live aspect of *P. spumacola* in detail. Briefly, cells have a size of 60–120 × 25–50 µm and are often slightly reniform due to an indistinct ventral indentation. Macronucleus with distinct membrane. Micronucleus not recognizable, likely in perinuclear space of macronucleus. Contractile vacuole distinctly subterminal, with ventrolaterally located excretory pore at end of shortened kineties 6 and 7 or 7 and 8. Mucocysts numerous, bulbous, 1 µm across, and rather strongly impregnated, often covering infraciliature in protargol preparations (Fig. 207e). Cytoplasm with some large, empty-appearing vacuoles and food vacuoles containing the heterotrophic flagellate *Polytomella*.

Somatic ciliature as in *P. spumacola spumacola* (FOISSNER 1993c). Briefly, the slightly spiralling ciliary rows are more closely spaced and ciliated on right than left side of cell and form a rather distinct suture extending from the excretory pore over the posterior pole to the subterminal dorsolateral surface; most left side dikinetids have ciliated only the posterior basal body. Postoral pseudomembrane distinct, consists of about 25 basal body quadruplets (Fig. 207a–c).

Oral apparatus basically as in *P. spumacola spumacola* (FOISSNER 1993c), but smaller and thus less conspicuous (Fig. 207a, c, d, f). Oral area extends from anterior body end back on ventral side, elliptical. Paroral membrane C-shaped, composed of about 20 dikinetids associated with many fine fibres forming right half of pharyngeal basket; anterior portion of fibres not impregnated causing blank stripe between paroral and right pharynx half. At left mouth margin five to seven, usually six minute, brick-shaped, obliquely orientated adoral organelles associated with thick, but short rods forming left half of pharyngeal basket. Oral slit supported by fine fibres of unknown origin. Pharyngeal basket cylindroidal, extends to mid-body, not bifurcated proximally, as in → *Platyophryides latus*.

Occurrence and ecology: The type location is an extraordinary place, namely, a small forest of the giant Liliaceae, *Aloe dichotoma*. Eleven new taxa were discovered in this sample and several others in two further samples from neighbouring habitats, indicating that this area is a local diversity centre (detailed discussion, see general part). *Platyophrya spumacola hexasticha* occurs also at Namibian sites (43, 52, 54), and recently we found it in forest soil from Austria, indicating a wide geographical range. Likely, we saw this species also in other soil samples, but did not distinguish it from *P. spumacola spumacola*.

Comparison with related species: This population is difficult to assign because its main features overlap with those of *P. spumacola*, *P. sphagni*, and *P. vorax*. The number of ciliary rows and adoral organelles matches *P. sphagni* which, however, is a limnetic

species with symbiotic green algae; furthermore, it is distinctly smaller, viz., 60 x 25 µm vs. 90 x 35 µm (FOISSNER 1993c, FOISSNER & KREUTZ 1996). *Platyophrya vorax* is even smaller (usually 50 x 25 µm) than *P. sphagni* and has only 11 ciliary rows and four adoral organelles. Thus, we classify the Namibian site (5) population as a subspecies of *P. spumacola*, differing mainly by the lower number of adoral organelles (6 vs. 10). Interestingly, the slides contain also a few ordinary *P. spumacola* with a size of about 100 x 40 µm, 32 ciliary rows, and 13 adoral organelles.

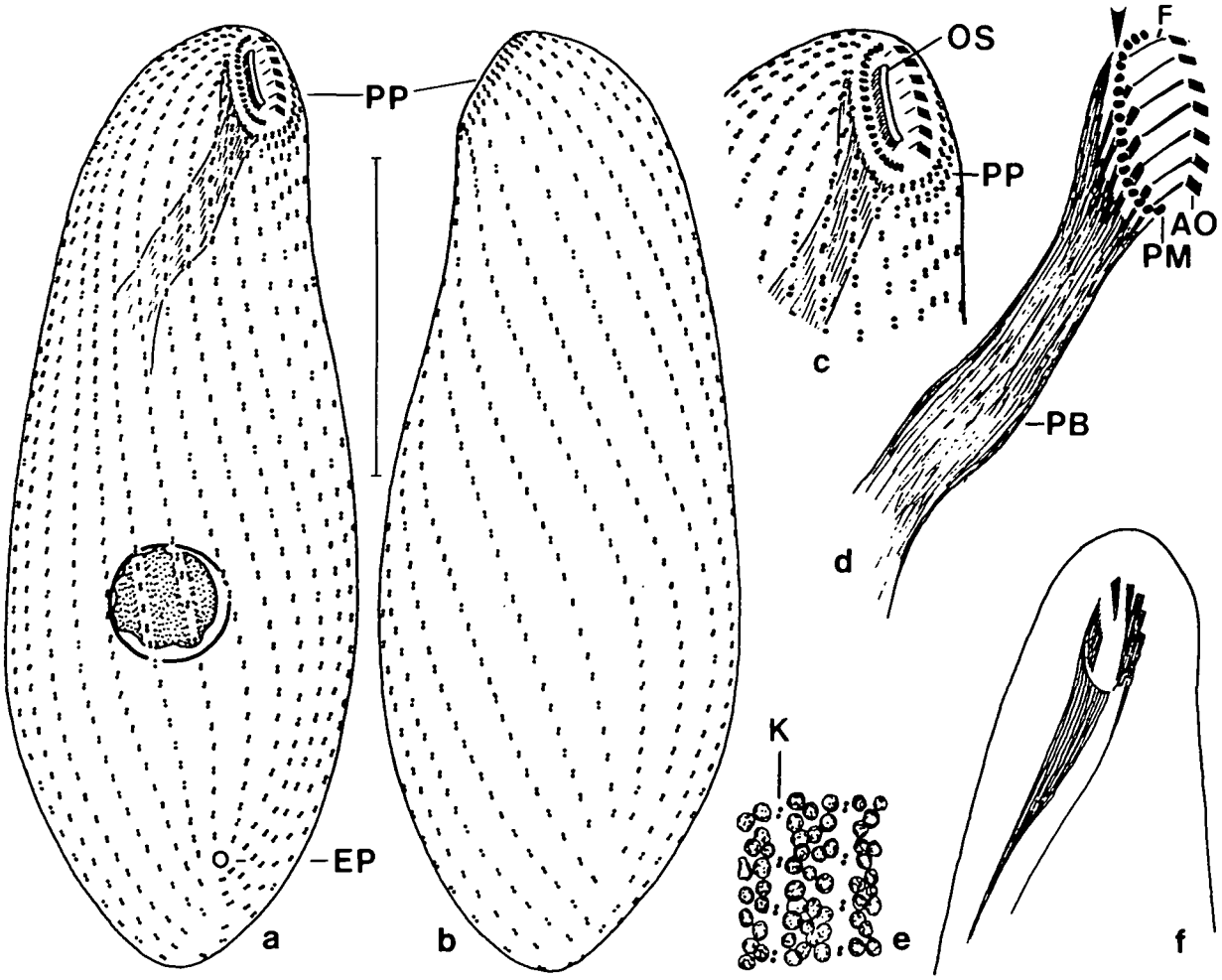


Fig. 207a–f. *Platyophrya spumacola hexasticha*, oral and somatic infraciliature after protargol impregnation. **a, b:** Right and left side view of holotype specimen. A suture extends from the excretory pore over the posterior pole onto the left side. **c, d, f:** Oral structures; oral slit shown only in figure (c). Figure (f) is a ventral view showing that the pharyngeal basket is composed of two halves: the right half is formed by very fine fibres originating from the paroral membrane, while the left half is formed by short, thick rods each connected via a fine fibre (F) with an adoral organelle. The anterior portion of the fibres building the right basket half does not impregnate producing a blank stripe (arrowhead). **e:** Surface view showing inflated mucocysts between ciliary rows. AO – adoral organelles, EP – excretory pore of contractile vacuole, F – fine fibres connecting adoral organelles with left side pharyngeal rods, K – kinety, OS – oral slit, PB – pharyngeal basket, PM – paroral membrane, PP – postoral pseudomembrane. Scale bar 25 µm.

Table 189. Morphometric data on *Platyophrya spumacola spumacola* (PSS, from FOISSNER 1985) and *P. spumacola hexasticha* (PSH).

Characteristics [a]	Species	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	PSS	74.2	74.0	9.8	3.1	13.2	58.0	93.0	10
	PSH	84.1	84.0	13.6	3.2	16.1	55.0	113.0	18
Body, width	PSS	28.8	28.0	5.1	1.6	17.6	23.0	39.0	10
	PSH	32.1	30.0	6.3	1.5	19.6	24.0	47.0	18
Anterior body end to proximal end of paroral membrane, distance	PSH	9.2	9.0	2.8	0.7	30.8	6.0	20.0	18
Anterior body end to macronucleus, distance	PSH	45.5	46.0	10.0	2.4	22.1	25.0	66.0	18
Macronucleus, length	PSS	8.5	8.0	0.8	0.2	9.0	8.0	10.0	10
	PSH	11.3	11.0	0.8	0.2	7.3	10.0	13.0	18
Macronucleus, width	PSH	10.5	11.0	1.3	0.3	12.3	8.0	13.0	18
Right lateral kineties, distance between	PSS	2.9	3.0	0.7	0.2	23.5	2.0	4.0	10
	PSH	3.7	4.0	0.4	0.1	10.5	3.0	4.0	18
Left lateral kineties, distance between	PSS	3.9	4.0	0.9	0.3	23.6	3.0	5.0	10
	PSH	5.4	5.0	0.8	0.2	14.9	4.0	7.0	18
Somatic ciliary rows, number	PSS	23.4	23.0	3.5	1.1	14.8	17.0	30.0	10
	PSH	20.8	21.0	1.1	0.3	5.0	19.0	22.0	16
Kinetids in a right lateral kinety, number	PSS	48.1	50.0	4.4	1.4	9.2	41.0	52.0	10
	PSH	48.8	50.0	3.7	1.2	7.7	42.0	54.0	9
Kinetids in a left lateral kinety, number	PSS	38.2	38.0	5.8	1.8	15.3	30.0	50.0	10
	PSH	36.9	35.0	4.7	1.5	12.7	30.0	45.0	10
Paroral membrane, length	PSS	9.6	9.0	1.2	0.4	12.8	8.0	12.0	10
	PSH	7.6	8.0	0.9	0.2	12.2	5.0	9.0	18
Oral apparatus, width [b]	PSS	4.9	5.0	0.8	0.3	16.6	4.0	7.0	10
	PSH	4.7	5.0	0.6	0.1	12.2	4.0	6.0	18
Pharyngeal basket, width at mid-portion	PSH	3.8	4.0	1.2	0.3	32.2	3.0	8.0	18
Adoral organelles, number	PSS	9.8	10.0	1.0	0.3	9.9	8.0	12.0	12
	PSH	5.7	6.0	0.6	0.1	10.3	5.0	7.0	17

[a] Data on *P. spumacola spumacola* based on cultivated, CHATTON-LWOFF silver nitrate-impregnated, and randomly selected specimens. Data on *P. spumacola hexasticha* based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] From outer margin of paroral to outer margin of adoral organelles.

Plesiocaryon nov. gen.

Diagnosis: Small, flattened, completely ciliated Cyrtolophosididae (?) with macronucleus and micronucleus each in separate nuclear membrane. Silverline system colpodid. A short, oblique kinety at anterior margin of buccal cavity.

Type species: *Balantiophorus elongatus* SCHEWIAKOFF, 1892.

Etymology: Composite of the Greek *plesio* (related) and the Latin noun *caryon* (nucleus), referring to the plesiomorphic state of the nuclear apparatus. Neuter gender.

Comparison with related genera: The diagnosis is based on FOISSNER (1993c) and DIAZ et al. (2000). *Balantiophorus elongatus* SCHEWIAKOFF, 1892 looks rather similar to *Cyrtolophosis mucicola* STOKES, 1885 and was thus transferred to this genus by KAHL (1931b); a decision accepted by all later authors (FOISSNER 1993c).

However, very recently DIAZ et al. (2000) performed a detailed study on *C. elongata* showing by transmission electron microscopy that, contrary to *C. mucicola*, the micronucleus does not reside in the perinuclear space of the macronucleus. This is a rather fundamental difference because the macro-micronuclear complex is considered as the main apomorphy of the order Cyrtolophosidida, although some exceptions are now known (FOISSNER 1993c, LYNN et al. 1999).

Certainly, the ordinary nuclear apparatus of *C. elongata* must be credited by at least genus level. Accordingly, we combine *Cyrtolophosis elongata* with *Plesiocaryon*: *P. elongatum* (SCHEWIAKOFF, 1892) nov. comb. We cannot even exclude that this species and other "deviating" cyrtolophosidids belong to an entirely different group (Sorogenida?), which convergently developed similar oral structures (see also → *Platyophryides*).

Nomenclature: The type species of *Balantiophorus* SCHEWIAKOFF, 1889 is *B. minutus* SCHEWIAKOFF, 1889, which, however, is a junior, subjective synonym of *Cyrtolophosis mucicola* STOKES, 1885 (FOISSNER 1993c). Thus, *Balantiophorus* is not available, and *B. elongatus* SCHEWIAKOFF, 1892 must be classified in a new genus, *Plesiocaryon*. See FOISSNER (1993c) for the literature cited.

Plesiocaryon elongatum (SCHEWIAKOFF, 1892) **nov. comb.**

Based on the investigations of DIAZ et al. (2000), we reinvestigated the preparations from Kenya, used by FOISSNER (1993c; Fig. 218d, e) to illustrate the infraciliature. This showed that FOISSNER over-interpreted his preparations. Very likely, the Kenyan population has monokinetids, except for the oral region, quite similar as shown by DIAZ et al. (2000) and in → *Plesiocaryon terricola*. Actually, the infraciliature is as shown in the in vivo illustration and in micrograph 218.1 of FOISSNER (1993c).

Plesiocaryon terricola **nov. spec.** (Fig. 208a–m; 412f-i; Table 190)

1993 *Cyrtolophosis acuta* KAHL, 1926 – FOISSNER, Colpodea, p. 543 (partim).

Diagnosis: Size about 85 × 9 µm in vivo; more or less distinctly vermiform. Contractile vacuole subterminal. On average 10 loosely ciliated somatic kineties, 4 adoral organelles, and 9 paroral dikinetids.

Type location: Soil from the ghost tree forest (*Moringa ovalifolia*) in the Etosha National Park, Namibia, 19°S 15°50'E (site 56 in figures 2, 3 and chapter 2.1.2).

Etymology: The Latin adjective *terricola* (living in soil) indicates that it is likely confined to terrestrial habitats.

Description: Size 60–120 × 8–12 µm in vivo, usually near 85 × 9 µm; length:width ratio also highly variable, viz., 5–14:1, on average near 10:1 both in vivo and protargol preparations (Table 190). More or less distinctly rod-shaped and curved ventrally when swimming, while vermiform when creeping serpentinely on and between soil particles, both ends gradually narrowed and rounded, never pointed; laterally flattened up to 2:1, especially in oral area (Fig. 208a, e, f, k, m; 412f, g). Macronucleus near body centre on average, broadly (1.5:1) to slenderly (3:1) ellipsoidal, very hyaline with few, pale nucleoli. Micronucleus broadly to slenderly ellipsoidal, invariably attached to posterior end of macronucleus, but not very tightly so that both are recognizable as separate structures. Contractile vacuole distinctly subterminal, that is, excretory pore on right side about 10 µm above body end (Fig. 208a, e, k, m; 412h). Cortex highly flexible, contains loose rows of granules 0.5–1 µm across, likely some sort of mucocysts. Cytoplasm finely granulated, contains some lipid droplets 0.5–2 µm across and up to 12 µm-sized food vacuoles with bacterial remnants. Swims and crawls rather rapidly showing great flexibility, usually distinctly curved ventrally when swimming (Fig. 208a, f); never rests or build a dwelling-tube. Division occurs in freely motile (non-encysted) condition.

Cilia in oral region about 7 µm, postorally only 5 µm long in vivo, arranged in an average of 10 equidistant rows very loosely ciliated throughout, that is, with average in vivo distances of about 6 µm among individual kinetids (Fig. 208a, h–l; Table 190). Ciliary rows commence postorally, except for three to four bipolar dorsolateral kineties; accompanied by a rather distinct fibre at left. Cilia ventrally paired only in oral area, while dorsally up to mid-body with kinetids so regularly spaced that short, oblique rows are formed (Fig. 208 l); monokinetids occur on postoral ventral side and in posterior half of dorsal side, while dikinetids with barren anterior basal body occur in the transition zone (Fig. 208a, j, k), indicating that *P. terricola* has true monokinetids, which is unusual for colpodids (FOISSNER 1993c), but likely occurs also in *P. elongatum* (DIAZ et al. 2000).

Oral apparatus occupies ventral anterior 10 µm of cell, rounded triangular oral opening about 5 × 3 µm in vivo, and thus, very small compared to body length (Fig. 208a–c; 412f, g; Table 190). Vestibulum extends to cell's midline, making oral area thin and bright at low magnification (Fig. 208e). Right half of vestibulum covered by a sigmoidal, hyaline lip bearing four minute, oblique thickenings posteriorly, likely corresponding to the barren monokinetids in the posterior half of the paroral membrane (Fig. 208b, i). Pharyngeal fibres very fine and recognizable only after protargol impregnation, but a surprisingly large pharynx, forming a tubular structure extending to mid-body, becomes recognizable in feeding specimens (Fig. 208a, f). Left half of vestibulum occupied by four minute adoral organelles increasing in size from anterior to posterior, each composed of two kineties bearing 3–4 µm long cilia in vivo, except for anterior organelle likely consisting of only a single ciliary row in most specimens. Along right margin of organelles a C-shaped fibre posteriorly extending into ventral margin of vestibular entrance, while anteriorly possibly contacting two to four granules (basal bodies? "oblique kinety" mentioned in genus diagnosis; see also FOISSNER 1993c) at margin of vestibulum (Fig. 208a, b, d, h-k). Paroral membrane comparatively large,

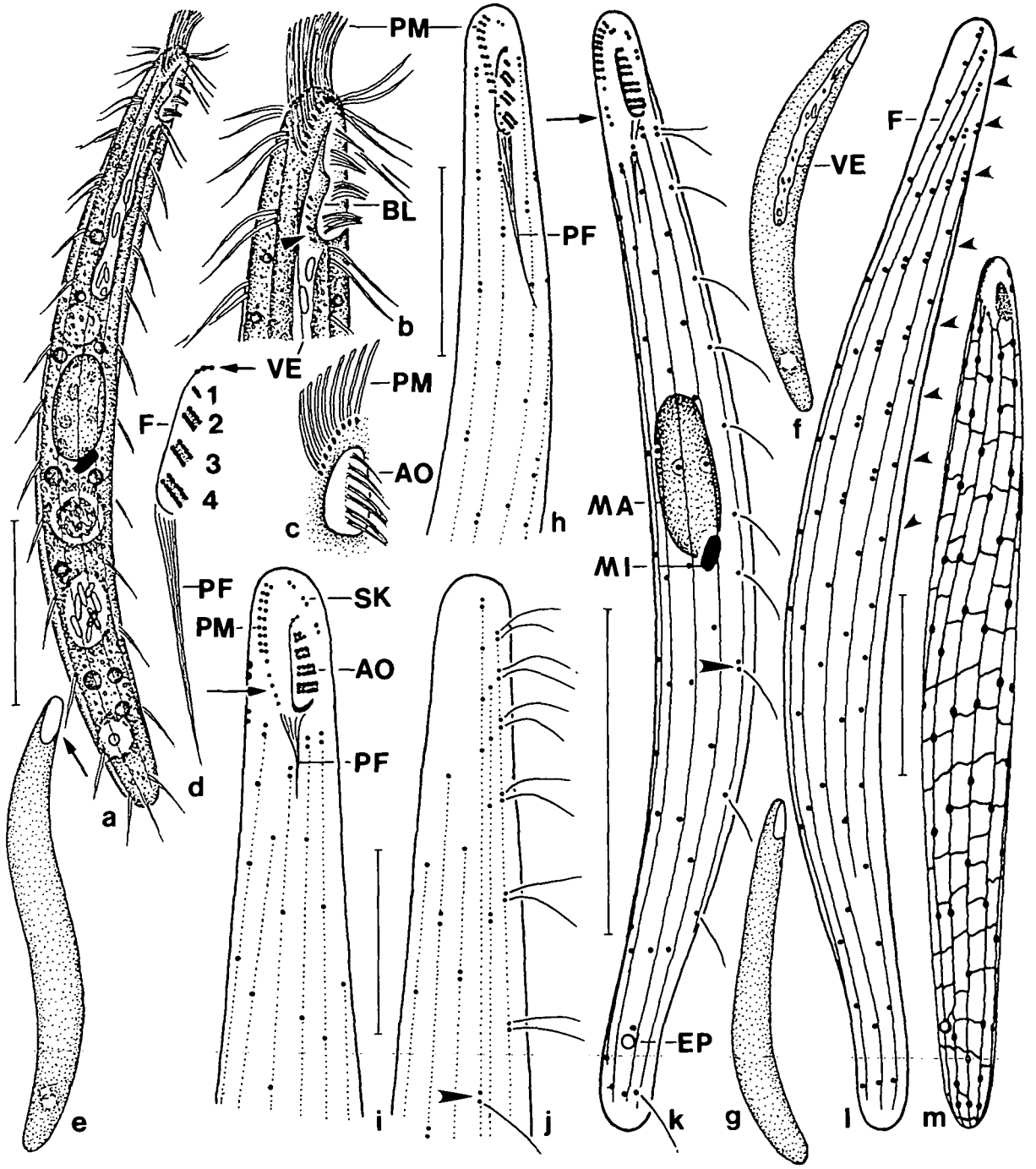


Fig. 208a–m. *Plesiocaryon terricola* from life (a–c, e–g) and after protargol (h–l) and silver nitrate impregnation (m). **a, b, f:** Right side views. Note the curved buccal lip and the tubular vestibulum. Arrowhead in (b) marks minute thickenings in posterior half of buccal lip. **c:** Ventral view. Right of the adoral organelles is the about 3 µm deep vestibular entrance. **d:** Summary of observations on adoral structures; numbers denote adoral organelles. Arrow marks granules ("oblique kinety") at upper margin of buccal cavity. **e–g:** Shape variants. Arrow marks oral area, which is flat and thus bright. **h–l:** Ventral and ventrolateral views of somatic and oral somatic ciliary pattern. Arrows mark posterior portion of paroral membrane, which consists of barren monokinetids. Arrowheads denote dikinetids having ciliated only the posterior basal body. Small arrowheads in (l) mark oblique kineties formed by the regularly spaced kinetids. **m:** Silverline pattern. AO – adoral organelles, BL – buccal lip, EP – excretory pore, F – fibres, MA – macronucleus, MI – micronucleus, PF – pharyngeal fibres, PM – paroral membrane, SK – somatic kinety, VE – vestibular tube. Scale bars 10 µm (h–j) and 20 µm (a, k–m).

extends from anterior body end to vestibular vertex, consists of two parts: anterior portion composed of an average of nine closely spaced, obliquely arranged dikinetids producing a distinct, about 7 µm long ciliary tuft; posterior portion composed of an average of four widely spaced, barren monokinetids appearing as minute thickenings in vivo (Fig. 208b, c, h–k; Table 190).

Silverline pattern colpodid, that is, composed of rather wide and regular meshes produced by short, transverse silverlines connecting the longitudinal silverlines extending among the kinetids of a kinety (Fig. 208m; 412h, i).

Table 190. Morphometric data on *Plesiocaryon terricola*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	72.6	71.0	13.4	2.9	18.5	51.0	100.0	21
Body, width	7.4	7.0	0.9	0.2	11.7	6.0	10.0	21
Body length:width, ratio	9.7	10.0	2.1	0.5	21.4	5.2	13.9	21
Anterior body end to end of oral apparatus, distance	7.1	7.0	0.6	0.1	8.0	6.0	8.0	21
Anterior body end to macronucleus, distance	28.9	30.0	5.0	1.1	17.4	22.0	43.0	21
Posterior body end to excretory pore, distance	5.7	6.0	1.7	0.4	29.2	3.0	9.0	21
Macronucleus, length	9.8	10.0	1.3	0.3	13.3	7.0	12.0	21
Macronucleus, width	4.3	4.0	0.7	0.1	15.7	3.0	5.5	21
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Micronucleus, length	2.7	3.0	–	–	–	2.0	3.0	21
Micronucleus, width	1.8	2.0	–	–	–	1.0	2.5	21
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Somatic ciliary rows, number	9.5	10.0	0.8	0.2	7.9	8.0	10.0	21
Kinetids in a dorsal ciliary row, number [b]	14.2	14.0	–	–	–	10.0	18.0	21
Adoral organelles, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21
Paroral kinetids, number	9.3	9.0	0.9	0.2	9.2	8.0	11.0	21
Paroral monokinetids, number	4.5	4.0	1.1	0.3	25.1	3.0	7.0	21

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Dikinetids counted as 1 kinetid. Values rough because difficult to count due to the large distances between individual kinetids.

Occurrence and ecology: *Plesiocaryon terricola* was discovered in a sample taken at Namibian site (56) in January 2001. However, it was also observed in the sample taken in 1994, but misidentified as *Cyrtolophosis acuta*. *Plesiocaryon terricola* became numerous three weeks after rewetting the sample and stayed for further three weeks, although the culture was sampled twice for preparations. During this period, no other *Cyrtolophosis* or *Plesiocaryon* species was present in the culture, at least, we could not find a single specimen resembling *C. acuta* or *P. elongatum* in vivo and the silver preparations. *Plesiocaryon terricola* is cosmopolitan because we have indisputable records from Austria (Fig. 219o in FOISSNER 1993c) and soils globally. Indeed, most of our "*Cyrtolophosis acuta*" records are *P.*

terricola. We never found *P. terricola* in any of over 1000 freshwater samples investigated during the past 30 years. Thus, this species must be confined to terrestrial habitats. This is emphasized by the flexible and narrow body adapted for exploiting even very fine soil pores.

Generic classification and comparison with related species: The micronucleus of this "*Cyrtolophosis*" is sometimes rather distant from the macronucleus and thus very likely not in its perinuclear space, as is typical for *Cyrtolophosis* (FOISSNER 1993c). Accordingly, we assign this species to *Plesiocaryon*, although indisputable evidences from electron microscopical investigations are lacking.

We know *P. terricola* since the eighties, but mixed and/or misidentified it occasionally as *Cyrtolophosis acuta* and/or *C. elongata* (FOISSNER 1980b, 1993c). This became evident from an examination of the original notes. Indeed, these species are not easily to distinguish, especially for the beginner FOISSNER was in 1980, because the original descriptions are rather incomplete and good redescriptions were not available. Thus, FOISSNER's (1980b, 1993c) data on "*Cyrtolophosis acuta*" should be abandoned and investigation commence again, using well-defined populations as described above.

Plesiocaryon terricola differs from *Cyrtolophosis acuta* in size (85 × 9 µm vs. 25 × 5 µm), length:width ratio (10:1 vs. 5:1), body shape (vermiform vs. fusiform), and habitat (terrestrial vs. limnetic). Unfortunately, possible further differences remain obscure because the original description is meagre (KAHL 1926, 1931b) and the redescription doubtful (FOISSNER 1980b, 1993c). However, the differences in size, shape and habitat are so pronounced that conspecificity is highly unlikely. Whether *C. acuta* is identical to *P. elongatum*, as supposed by FOISSNER (1993a) and DIAZ et al. (2000), needs further investigation.

Plesiocaryon terricola differs also distinctly from *P. elongatum* by body size (60–120 × 8–12 µm, usually 85 × 9 µm vs. 15–25 × 5–15 µm, usually 25 × 10 µm), length:width ratio (10:1 vs. 2.5:1), body shape (vermiform vs. elongate ellipsoidal), location of contractile vacuole (subterminal vs. terminal), and the number of ciliary rows (8–10 vs. 7–8).

We emphasize that there was not a single specimen resembling *C. acuta* or *P. elongatum* in the abundant population from Namibian site (56), neither in vivo or silver preparations.

Ottowphrya nov. gen.

Before defining *Ottowphrya*, the senior author takes the opportunity to portray the interesting events guiding to the discovery of this new genus, a long story indeed, which commenced in 1930 when KAHL described *Platyophrya lata*, differing from the "otherwise very similar *P. spumacola*" by the projecting oral area and five to six cirri-like organelles along the left mouth margin (Fig. 210a). It was only in 1979 that DRAGESCO & DRAGESCO-KERNÉIS published details on the ciliary pattern of an organism they believed to be *P. lata* KAHL, 1930a (Fig. 209k–q). This well-done redescription hardly left doubts about the identification and identity of the species because the specimens were of similar size and shape and possessed six to eight rather conspicuous adoral organelles at the left mouth margin, that is, "cirri" as emphasized by KAHL (1930a).

Later, FOISSNER (1987c) established a new species, *P. dragescoi*, for a ciliate differing from *P. lata* by a lower number of adoral organelles (3–4 vs. 5–8) and somatic ciliary rows (19–22 vs. 28–37). He also recognized that ciliates of this type do not belong to *Platyophrya* because of distinct differences in the shape and orientation of the adoral organelles. Accordingly, FOISSNER (1987c) established the genus *Platyophryides*, with → *Platyophrya lata* KAHL, 1930a as the type species. This rather unconventional decision was confirmed by an electron microscopical investigation of the nuclear apparatus, which showed that, in contrast to the other members of the order, the micronucleus is not in the perinuclear space of the macronucleus (PUYTORAC et al. 1992). In 1993, when FOISSNER revised the class Colpodea, he added a third species, *P. magnus*, and classified the investigation of *P. lata* by DRAGESCO & DRAGESCO-KERNÉIS (1979) as an "authoritative redescription", that is, without any doubts about the identification.

In the years following the revision of the class, I recognized that there are *P. latus* populations with a body shape either more similar to that depicted by KAHL (1930a) or DRAGESCO & DRAGESCO-KERNÉIS (1979). However, differences were never so distinct that I got the impression of two reliable taxa, not even after silver carbonate impregnation of a "Kahlian-shaped" population (Fig. 430q–u), but I became increasingly confused about this species. This encouraged me to prepare silver nitrate slides from various populations, and those from the "Kahlian-shaped" specimens of Jordan and Venezuela were a great surprise: they showed silverlines in *Colpoda* pattern, while all "Dragescoan-shaped" populations possessed a *Platyophrya* pattern (FOISSNER 1993c).

Now it was clear that the two "shape variants" were not only different species, but even different genera, and DRAGESCO & DRAGESCO-KERNÉIS (1979) and FOISSNER (1993c) misidentified the Kahlian *P. lata*, which we shall redescribe in detail below.

Diagnosis: Moderately small, platyophryid Colpodea incertae sedis with silverlines in *Platyophrya* pattern and conspicuous adoral organelles parallel to paroral membrane.

Type species: *Platyophryides dragescoi* FOISSNER, 1987c.

Dedication: Wilhelm FOISSNER dedicates this new genus to his friend and colleague, Prof. Dr. J.C.G. OTTOW (Giessen University, Germany), on the occasion of his retirement.

Remarks: The ordinal classification of this kind of colpodid is open since PUYTORAC et al. (1992) showed that they lack the main ordinal character, viz., a micronucleus within the perinuclear space of the macronucleus. Although not proven by electron microscopy, silver carbonate impregnation suggests that *Ottowphrya dragescoi* has the micronucleus also outside the macronucleus (Fig. 429m). Thus, *Platyophryides* and *Ottowphrya* possibly belong to the Sorogenida, as defined by FOISSNER (1993c), and should be checked for the ability to aggregate and produce aerial sorocarps. Both differ from *Sorogena* mainly by the shape and orientation of the adoral organelles and the inconspicuous oral dome. Furthermore, *Ottowphrya* has silverlines in *Platyophrya* pattern.

The occurrence of an ordinary macro-micronucleus pattern in seemingly "typical" cyrtolophosidid colpodids, such as → *Plesiocaryon* and → *Platyophryides*, makes classification of colpodids very difficult. When FOISSNER (1993c) suggested the conspicuous macro-micronucleus complex of several colpodids as an ordinal character, most exceptions were not known.

Ottowphrya dragescoi (FOISSNER, 1987) **nov. comb.** (Fig. 209a–v, 210q; 429a–y; Table 191)

1979 *Platyophrya lata*, KAHL, 1930 – DRAGESCO & DRAGESCO-KERNÉIS, Acta Protozool., 18:402 (misidentification).
1987 *Platyophryides dragescoi* FOISSNER, Zool. Beitr., 31: 243.
1993 *Platyophryides dragescoi* FOISSNER, 1987 – FOISSNER, Colpodea: 603 (revision).

Synonymy: A reinvestigation of the Finnish population mentioned in FOISSNER (1993c) and presented here in detail showed that *Platyophrya lata*, as described by DRAGESCO & DRAGESCO-KERNÉIS (1979), and *Platyophryides dragescoi* FOISSNER, 1987c are very likely the same species. Many intermediate forms were found in this (Table 191) and some other populations. However, none of these populations ever reached the giant → *P. magnus* FOISSNER, 1993c, which is thus very likely a reliable species. The following diagnosis summarizes the previous data and the new observations described below.

Improved diagnosis: Size about 90 × 50 µm in vivo. Broadly bursiform with slightly narrowed, ventrally curved oral portion. About 20–40 ciliary rows, depending on population. Oral apparatus occupies conspicuously broad, anterior body end, consists of 3–8, usually 5–6 adoral organelles and an about 20–30 µm long paroral membrane comprising 35–70 kinetids, depending on population.

Type material: Type slides of the German *Platyophryides* (now *Ottowphrya*) *dragescoi* are deposited at the Biologiezentrum in Linz, Austria (FOISSNER 1987c). These specimens have only three adoral organelles, while the Finnish population, of which we deposit voucher slides at the same locality (Table 1), has three to seven, usually five organelles.

Description: The following description summarizes the data from DRAGESCO & DRAGESCO-KERNÉIS (1979) and FOISSNER (1987c), who studied mainly a German population and mentioned observations from Austrian and Australian specimens. Furthermore, we present detailed data from a Finnish population, already mentioned in FOISSNER (1993c), and excellent scanning electron micrographs of specimens from Mount Kenya in Africa.

Size in vivo 80–120 µm (DRAGESCO & DRAGESCO-KERNÉIS 1979), 70–100 × 40–60 µm (FOISSNER 1987c), and 60–110 × 30–65 µm in Finnish population; in silver preparations 45–88 × 34–58 µm ($\bar{x}$ = 70 × 47 µm; DRAGESCO & DRAGESCO-KERNÉIS 1979), 63–91 × 27–45 µm ($\bar{x}$ = 76 × 38 µm; FOISSNER 1987c), and 59–101 × 31–64 µm ($\bar{x}$ = 81 × 52 µm) in Finnish population (Table 191); acontractile but highly flexible. Shape fairly variable, usually distinctly bursiform with obliquely truncate, slightly narrowed oral portion projecting ventrally; ventral contour thus sigmoidal, dorsal convex; posterior end invariable broadly rounded with a more or less distinct subterminal indentation at site of contractile vacuole. Laterally flattened up to 2:1, depending on nutrition state (Fig. 209a, d, e, g, k–o, 210q; 429i, n–v). Nuclear apparatus slightly underneath mid-body on average. Macronucleus about 15 µm in vivo, slightly ellipsoidal, contains some medium-sized nucleoli. Micronucleus in small indentation of macronucleus, possibly even in its perinuclear space (DRAGESCO & DRAGESCO-KERNÉIS 1979, FOISSNER 1987c; but see Fig. 429m). Contractile vacuole subterminal with excretory pore at margin of ventral and right side. Cytopyge in small suture

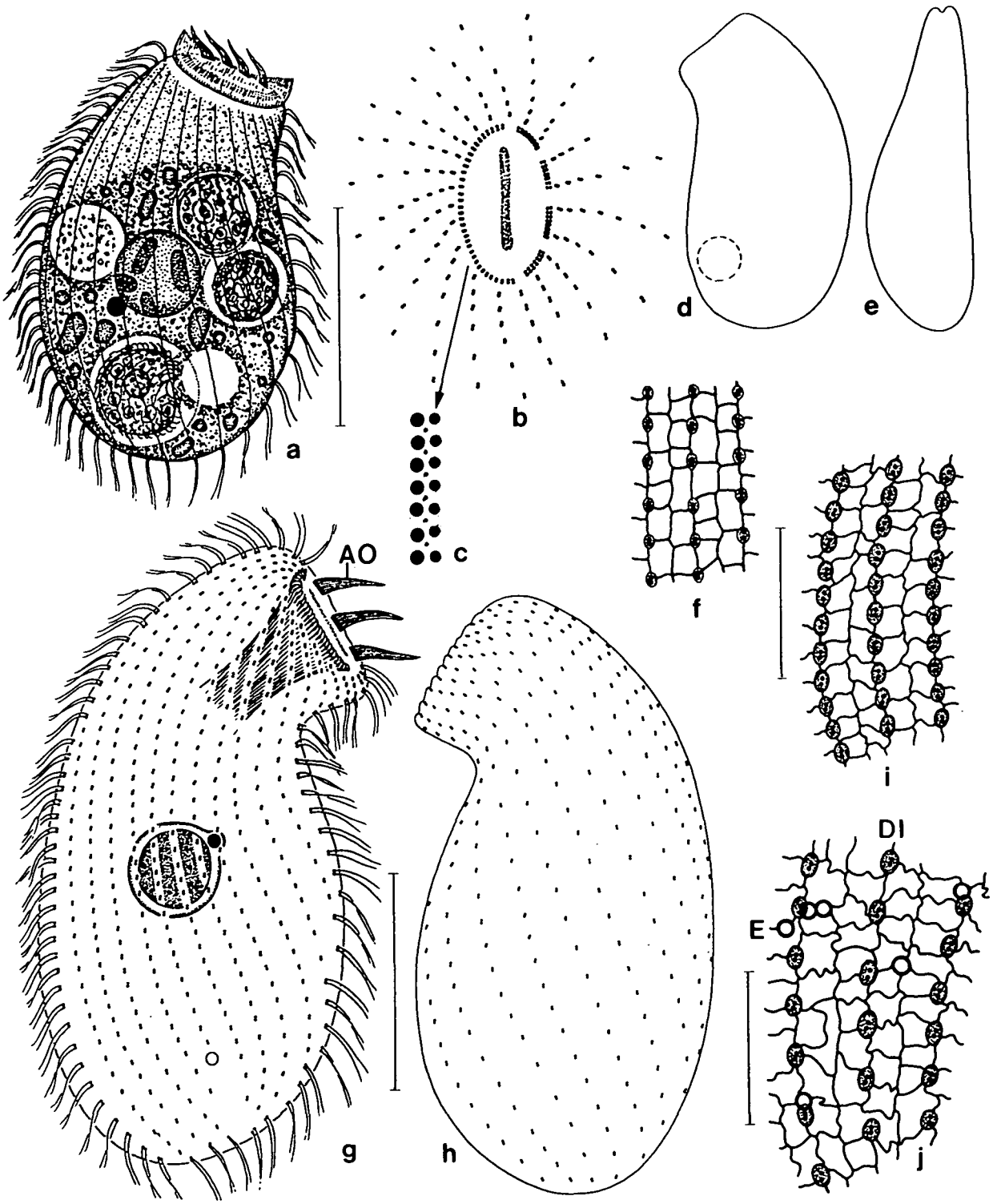


Fig. 209a–j. *Ottowphrya dragescoi*, German type (f–h), Austrian (a–e), and Finnish (i, j) specimens from life (a, d, e) and after silver carbonate (b, c), protargol (g, h), KLEIN-FOISSNER (f), and CHATTON-LWOFF (i, j) silver nitrate impregnation. **a:** Right side view of a representative specimen packed with food vacuoles. **b, c:** Oral structures. Both the paroral and the adoral organelles are dikinetidal. The inner row of paroral basal bodies impregnates more lightly. **d, e:** Shape variant in left side and ventral view. **f–j:** Ciliary pattern (g, h) and silverline system (f, i, j) of right and left side. AO – adoral organelles, DI – dikinetids of a ciliary row, E – docked extrusome. Scale bars 30 µm (a, g, h) and 10 µm (i, j).

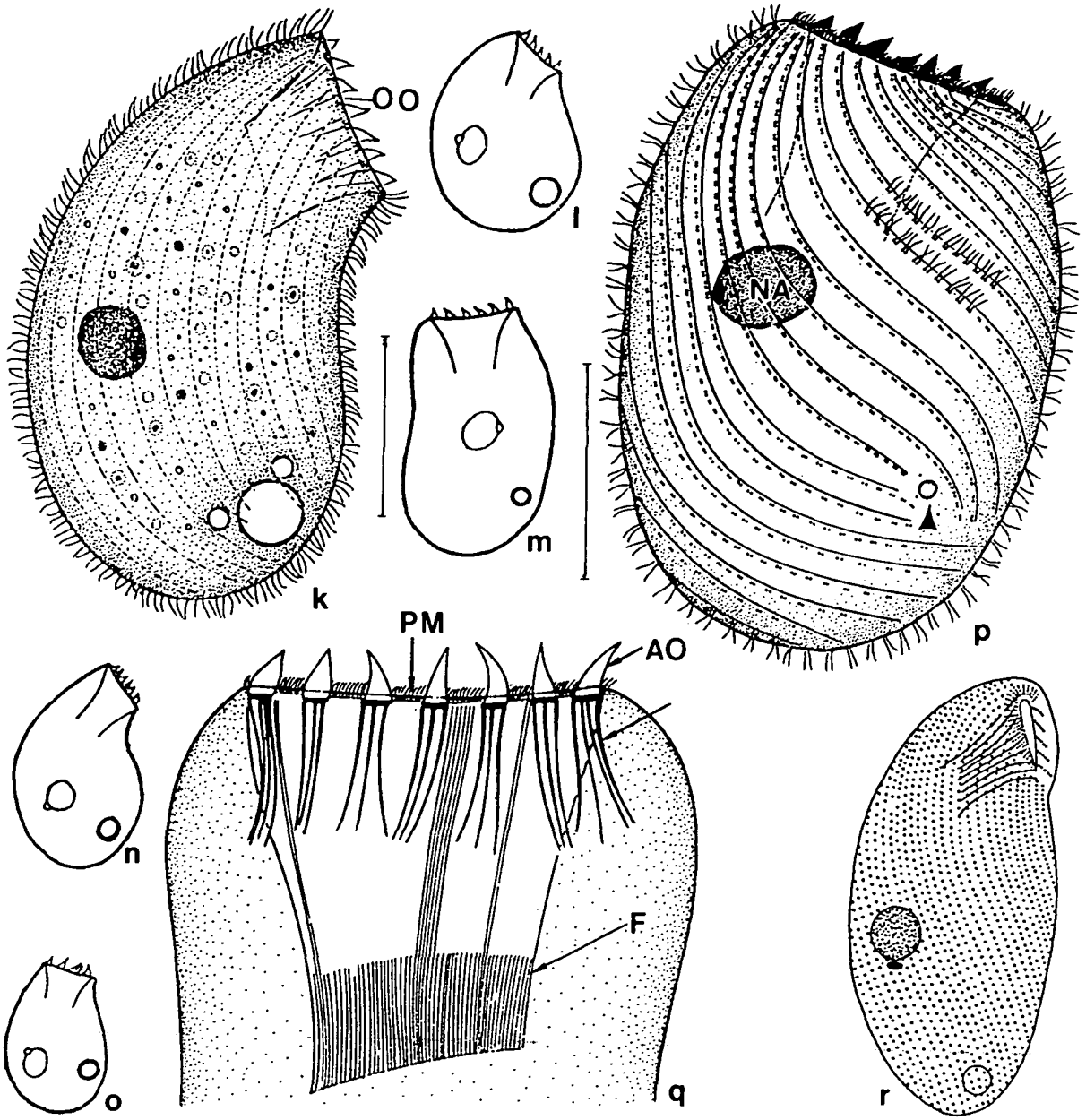


Fig. 209k–q. *Ottowphrya dragescoi* (from DRAGESCO and DRAGESCO-KERNÉIS 1979) from life (k–o) and after protargol impregnation (p, q). **k:** Right side view of a representative specimen. Note the huge oral opening. **l–o:** Shape variants. The specimen shown in (o) is highly similar to the Austrian specimen shown in figure 209a. **p:** Ciliary pattern of ventral side. The kineties are accompanied by a fibre bundle. The arrowhead marks the excretory pore of the contractile vacuole. **q:** Fine structure of oral apparatus. The adoral organelles have attached short, conspicuous fibres (arrow), while the right half of the pharyngeal basket is lined by many long, fine fibres, likely originating from the paroral membrane. AO – adoral organelles, F – fibres, NA – nuclear apparatus, OO – oral opening, PM – paroral membrane. Scale bars 30 μm.

Fig. 209r. *Woodruffia lichenicola* GELLÉRT, 1955 is likely a junior synonym of → *Platyophryides latus*. The figure is a composite from mercuric chloride-fixed and opal blue-stained or silver-impregnated cells; length 60–70 μm.

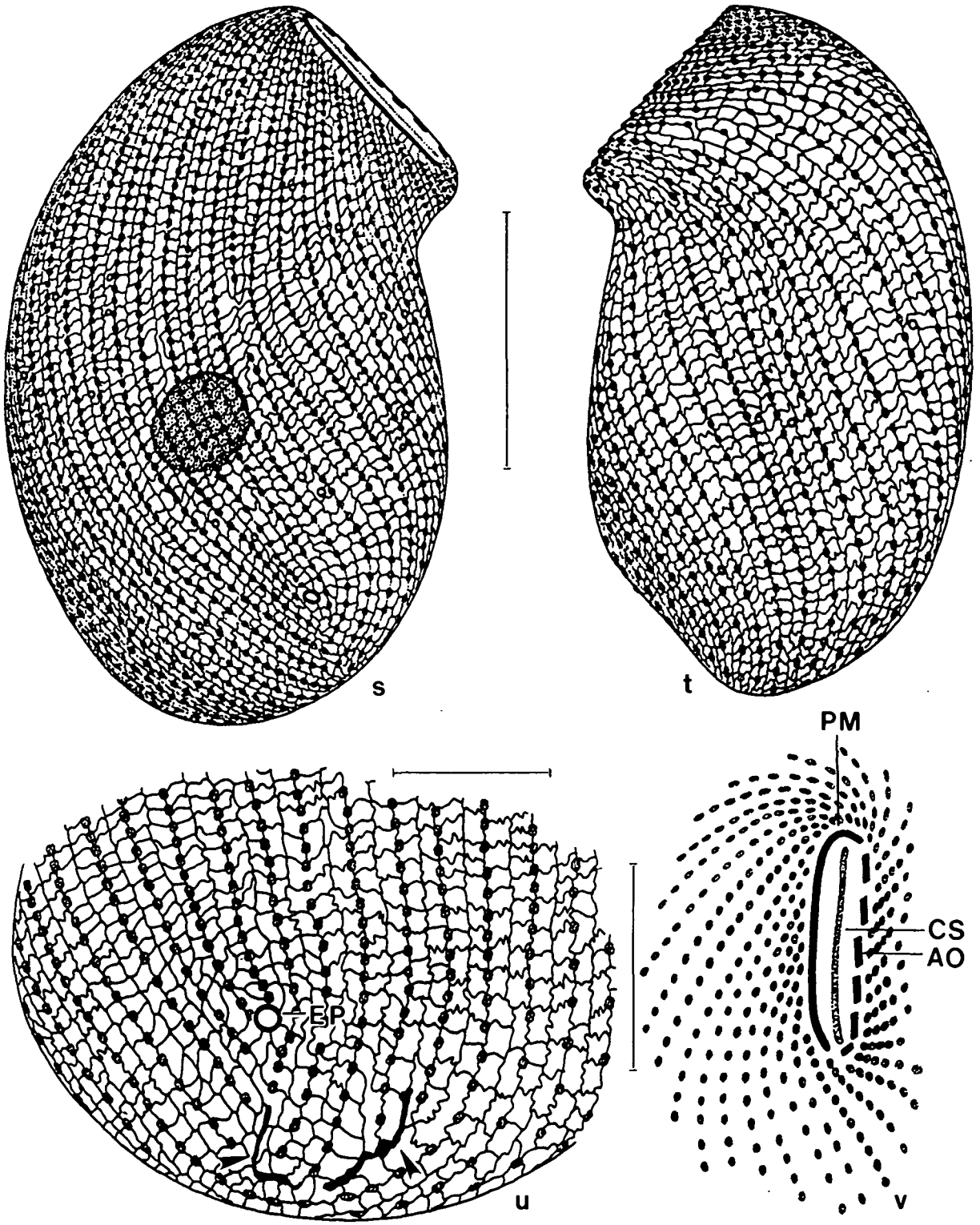


Fig. 209s–v. *Ottowphrya dragescoi*, cultivated specimens from a Finnish population after CHATTON-LWOFF silver nitrate impregnation. **s, t:** Ciliary pattern and silverline system of right and left side. **u:** Posterior pole area showing the U-shaped cytopyge (arrowheads). **v:** Anterior polar view. Note that the posterior adoral organelle is distinctly smaller. AO – adoral organelles, CS – cytostome slit, EP – excretory pore, PM – paroral membrane. Scale bars 30 µm (s, t) and 15 µm (u, v).

underneath excretory pore, marked by a thick, roughly U-shaped silverline (Fig. 209u). Cortex inconspicuous, slightly furrowed by ciliary rows, contains many 1–1.5 µm-sized extrusomes surrounded by a silverline and forming a voluminous, slimy coat in encysting specimens (Fig. 209j; 429j, k). Cytoplasm hyaline in oral portion, packed with food vacuoles and up to 10 µm-sized fat globules in posterior two thirds. Feeds on small and medium-sized colpodids and tetrahymenids ingested whole and slowly disintegrating in the food vacuoles. Usually glides slowly on microscope slide and soil particles showing considerable flexibility.

Somatic ciliature composed of dikinetids, some of which, however, have ciliated only one basal body with an about 8 µm long cilium. Number of ciliary rows highly variable: 19–22 ($\bar{x}$ = 21) in German type population (FOISSNER 1987c); 21–30 ($\bar{x}$ = 24) in Finnish specimens (Table 191); 33–37 in French and Australian specimens (DRAGESCO & DRAGESCO-KERNÉIS 1979; Fig. 429e); and 20–30 in Kenyan population. Ciliary rows basically bipolar and slightly to distinctly spiralized, especially on right side, where some shortened rows form a minute suture underneath the excretory pore of the contractile vacuole; more closely spaced and denser ciliated on right than central area of left side. Cilia closely spaced at anterior end of kineties, seemingly producing a platyophryid postoral pseudomembrane; however, most ciliary rows extend to posterior region of cell, only some are strongly and irregularly shortened (Fig. 209a, b, g, h, p, s–u; 429a–v). Silverlines in *Platyophrya* pattern throughout; individual silverlines only slightly undulating and somewhat narrower spaced than dikinetids, surround docked extrusomes and dikinetids (Fig. 209f, i, j, s–u; 429i–k).

Oral apparatus occupies almost entire anterior body end, conspicuous because large and on a flat dome supported by fibres originating from paroral dikinetids (Fig. 209a–c, g, k, q, s, v; 429a–c, e–i, l–p, t, w–y). Paroral membrane at right mouth margin, elongate C-shaped, composed of about 35 rather widely spaced dikinetids in Austrian and German specimens and of approximately 50–70 dikinetids in Australian and Kenyan cells; inner basal body of dikinetids more lightly impregnated than outer; a minute, argyrophilic granule between each two dikinetids. Both paroral basal body rows bear about 5 µm long cilia forming two different membranes, as in → *Reticulowoodruffia terricola*: outer (right) row cilia appear thinner and wider spaced than these of inner row, beat distinctly and individually in vivo; inner (left) row cilia likely almost or entirely immobile and so close together that a ribbon-like structure is formed appearing as a broad, bright wall in vivo (Fig. 429w-y). Adoral organelles at left mouth margin in small grooves, orientated almost parallel to oral slit, tongue-shaped both in the light and electron microscope; individual organelles composed of two rows of basal bodies, however, only one of the rows has cilia increasing in length from about 2–4 µm anteriorly to 5–7 µm posteriorly within each organelle; posteriormost organelle almost invariable half the size of other organelles, as in → *Platyophryides latus*. Two to four thick rods with a length of 7–20 µm originate from each organelle and extend posteriorly in the pharyngeal wall. Number of adoral organelles rather variable: 3 in German type population; 3–4 in Austrian specimens; 6–8 in French specimens; 3–7, usually 5 in Finnish specimens; 7 in Australian specimens; and 4–6, usually 5 in Kenyan specimens. Likewise, the number of basal bodies comprising a row within an organelle varies between 5 to 12. Oral opening slit-like, pharynx cylindroidal and supported by many fine fibres likely originating from paroral membrane and adoral organelles.

Occurrence and ecology: FOISSNER (1987c) discovered *O. dragescoi* in soil and needle litter from a spruce forest near Ulm/Danube, Germany. Another population occurred in mosses growing on spruce trunks in Salzburg, Austria. The Australian population was found

in bark of an *Eucalyptus* tree in the rain forest near Cairns (BLATTERER & FOISSNER 1988). In Finland, we found *O. dragescoi* in the litter of a coniferous forest near the town of Savonlinna (61°50'N 29°E). The African population used for the scanning electron microscopical investigations was collected by Mag. Aline BERTHOLD on Mount Kenya at about 3300 m sea level. This sample (pH 5.1) consisted mainly of *Hagenia* and grass litter, mixed with some *Sphagnum* and soil. The Kenyan population was cultivated in Eau de Volvic with small colpodids as food supply. DRAGESCO & DRAGESCO-KERNÉIS (1979) did not provide the source of their moss, likely it was from France. The reliable records, that is, those substantiated by illustrations, indicate that *O. dragescoi* is a cosmopolitan species preferring terrestrial habitats, especially moss and coniferous litter.

Comparison with related species: See detailed discussion under → *Platyophryides latus*. Basically, *O. dragescoi* is easily identified by the stout shape and the long oral slit occupying the anterior body end. Only extreme shape variants can be mixed with *P. latus* or *Platyophrya similis* (Fig. 210o–q).

Table 191. Morphometric data on a Jordanian (upper line) and Namibian (middle line) population of → *Platyophryides latus* and a Finnish population of *Ottowphrya dragescoi* (lower line).

Characteristics [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	CHL	63.6	63.0	7.0	1.5	11.0	50.0	78.0	21
	PA	82.0	78.0	14.6	3.2	17.8	63.0	132.0	21
	CHL	81.8	81.0	12.4	2.9	15.2	59.0	101.0	19
Body, width	CHL	34.1	34.0	4.9	1.1	14.5	27.0	48.0	21
	PA	32.4	30.0	6.4	1.4	19.8	25.0	49.0	21
	CHL	49.1	52.0	9.5	2.2	19.4	31.0	64.0	19
Body, width in oral area	CHL	15.7	15.0	1.4	0.3	9.0	13.0	18.0	21
	PA	12.9	13.0	2.1	0.5	16.6	10.0	19.0	21
	CHL	27.9	28.0	6.3	1.5	22.7	18.0	40.0	19
Body width:length of paroral membrane, ratio	CHL	3.2	3.0	0.6	0.1	18.9	2.0	5.0	21
	PA	3.4	3.3	0.6	0.1	17.3	2.5	4.6	21
	CHL	2.4	2.3	0.5	0.1	19.8	2.0	4.0	19
Anterior body end to macronucleus, distance	CHL	28.6	28.0	7.8	1.7	27.2	11.0	40.0	21
	PA	33.7	34.0	5.4	1.2	15.9	24.0	43.0	21
	CHL	43.4	45.0	8.7	2.0	20.0	29.0	60.0	19
Macronucleus, length	CHL	10.7	11.0	1.5	0.3	14.0	8.0	16.0	21
	PA	14.3	13.0	2.7	0.6	19.0	11.0	24.0	21
	CHL	13.1	13.0	1.6	0.4	12.2	10.0	16.0	19
Macronucleus, width	CHL	10.0	10.0	1.2	0.3	11.8	8.0	14.0	21
	PA	12.2	12.0	1.4	0.3	11.6	10.0	15.0	21
	CHL	10.7	10.0	1.3	0.3	12.5	8.0	13.0	19
Micronucleus, largest diameter	CHL	?	?	?	?	?	?	?	
	PA	2.4	2.5	–	–	–	2.0	3.0	21
	CHL	?	?	?	?	?	?	?	
Paroral membrane, length	CHL	10.8	11.0	1.3	0.3	11.6	8.0	14.0	21
	PA	9.4	9.0	1.1	0.2	11.4	7.0	11.0	21
	CHL	20.8	21.0	5.7	1.3	27.4	10.0	32.0	19

(continued)

Characteristics [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Distance between right side ciliary rows at mid-body	CHL	3.2	3.5	0.6	0.1	18.2	2.5	4.0	21
	PA	3.8	4.0	0.8	0.2	22.1	3.0	6.0	21
	CHL	3.9	4.0	0.8	0.2	19.1	2.5	5.0	19
Distance between left side ciliary rows at mid-body	CHL	4.6	4.5	–	–	–	4.0	5.0	21
	PA	4.8	5.0	0.8	0.2	16.0	3.0	6.0	21
	CHL	5.6	5.0	0.8	0.2	15.0	4.0	7.0	19
Excretory pore of contractile vacuole, largest diameter	CHL	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	PA	?	?	?	?	?	?	?	
	CHL	3.1	3.0	0.5	0.1	10.4	2.0	4.0	19
Somatic ciliary rows, number	CHL	22.7	23.0	2.0	0.4	9.0	20.0	27.0	21
	PA	17.4	18.0	1.4	0.3	8.0	15.0	19.0	21
	CHL	24.2	23.0	2.5	0.6	10.4	21.0	30.0	19
Dikinetids in a right side ciliary row, number	CHL	31.2	30.0	3.9	0.9	12.7	26.0	40.0	21
	PA	38.8	40.0	3.9	0.8	9.9	32.0	48.0	21
	CHL	43.1	42.0	6.7	1.5	15.5	30.0	55.0	19
Dikinetids in a left side ciliary row, number	CHL	27.5	28.0	3.8	0.8	13.8	20.0	34.0	21
	PA	30.6	30.0	4.4	1.0	14.5	25.0	40.0	21
	CHL	46.7	45.0	11.4	3.1	24.5	30.0	65.0	19
Adoral organelles, number	CHL	4.4	4.0	–	–	–	4.0	5.0	21
	PA	5.0	5.0	0.4	0.1	8.9	4.0	6.0	21
	CHL	5.0	5.0	1.2	0.3	23.8	3.0	7.0	19

[a] Data based on mounted, silver-impregnated, and randomly selected specimens from non-flooded Petri dish cultures (*Platyophryides*) and a pure culture (*Ottowphrya*). Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, PA – protargol impregnation (FOISSNER's method), SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Ottowphrya magna (FOISSNER, 1993) **nov. comb.** and *Platyophryides* **sp.** of PUYTORAC et al. (1992)

Platyophryides magnus FOISSNER, 1993c has a platyophryid silverline pattern and thus belongs to *Ottowphrya*. It differs from *O. dragescoi* by body size (> 140 µm vs. ≤ 120 µm), number of ciliary rows (50 vs. ≤ 40) and adoral organelles (9–10 vs. ≤ 8, usually 5–6), as well as by the structure of the adoral organelles (composed of 3 vs. 2 basal body rows).

However, PUYTORAC et al. (1992) described a *Platyophryides* which seemingly bridges the gap between *O. dragescoi* and *O. magna*. We give the full description of this interesting isolate because it is important for the systematics of the whole group.

When fed on bacteria and maintained in a culture medium made from a wheat infusion and yeast extract, the protargol-stained ciliates are ovoid, about 85 µm in length (60–110 µm, n = 32) and 68 µm in width (50–90 µm, n = 32). The somatic kineties, composed of dikinetids, are slightly spiralized, numbering 42 (34–48, n = 23), with two to three more right kineties

(16–25) than left kineties (15–22). There are no pre- or postoral sutures and no pseudomembrane formed from the ends of the left somatic kineties. The median macronucleus is ovoid, 17–22 µm in length, and is flanked by a small micronucleus. There is a posterior contractile vacuole.

The subapical buccal region is elongated along the anterior third of the ventral surface. From 30–45 µm (n = 23) in length, it is bordered on its right by a paroral formed from a double row of kinetosomes and five to nine (n = 23) adoral membranelles. The anterior and posterior ends of the paroral curve towards the left at either end of the superficial buccal region. The adoral membranelles are aligned almost parallel to the long axis of the buccal region along its left side.

When these cells have fed, they become immobile after rotating in one place. They secrete a cyst and undergo one or two divisions. Under unfavourable conditions, resting cysts with three wall layers appear.

When the cell density is high or when *Tetrahymena* or, even more effectively, *Colpidium* are introduced, active predatory giants appear. Their size is quite variable, up to 5 times the size of the bacterivorous forms. The number of somatic kineties more than doubles (87–112, n = 19), while the small difference between right kineties (46–58) and left kineties (41–54) is maintained. The buccal region increases to 180–220 µm (n = 8) in length, with the paroral maintaining its position along the right side of the buccal region and the number of adoral membranelles increasing to 15–20 (n = 8). The macronucleus remains ovoid but increases to 50–78 µm (n = 13) in length.

If regularly fed ciliate prey, these giant forms grow and divide within cysts, like the bacterivorous forms. However, if the prey numbers decrease, the cells rapidly become small. In addition to division within cysts, resting cysts of the giant forms have also been observed.

Despite our efforts, we have been unable to observe stomatogenesis within the cysts. Moreover, we have been unable to observe the process of transformation of small forms to giants and the reverse transformation.

Unfortunately, PUYTORAC et al. (1992) do not describe the silverline pattern, which is, as we now know, very important for the classification of this kind of colpodid. Thus, no final conclusion can be drawn. However, we have convincing arguments that the Brazilian species is very near or even is *O. magna*. PUYTORAC et al. (1992) show by transmission electron microscopy that the adoral organelles of the Brazilian population are composed of triads and/or three rows of basal bodies. Indeed, they state this as a unique feature of their isolate. FOISSNER (1993c) stated the same in the diagnosis of *O. magna*: "9–10 adoral organelles consisting of 3 rows of basal bodies each". Thus, the PUYTORAC et al. (1992) population is likely *O. magna*. This is emphasized by the large size of both taxa and their Gondwanan distribution: *O. magna* was discovered in a sand dune near the city of Singapore (FOISSNER 1993c), and PUYTORAC et al. (1992) isolated their species from a freshwater pond in Brasilia. The special life cycle observed by PUYTORAC et al. (1992) does not contradict our proposal because FOISSNER (1993c) could not study the cycle in *O. magna*. On the other hand, the different habitats indicate different species.

Certainly, the Brazilian isolate is not → *Platyophryides latus* or → *Ottowphrya dragescoi*, as proposed by PUYTORAC et al. (1992), because both have two-rowed adoral organelles, a rather fundamental difference emphasized by the fact that the Brazilian isolate has all three rows

ciliated, while *O. dragescoi* has cilia associated only with one of the two rows; each of these features is a species character of its own! Furthermore, we could not observe extreme polymorphism in our cultures of *O. dragescoi*, despite that it was fed with ciliate prey.

Platyophryides FOISSNER, 1987

1987 *Platyophryides* FOISSNER, Zool. Beitr., 31: 240. Type species (original designation): *Platyophrya lata* KAHL, 1930.

Improved diagnosis: Moderately small to medium-sized platyophryid Colpodea incertae sedis with silverlines in *Colpoda* pattern and conspicuous adoral organelles parallel to paroral membrane.

Remarks: See FOISSNER (1993c) and remarks under genus → *Ottowphrya*. The diagnosis was emended with the silverline pattern, the sole but strong difference to → *Ottowphrya* and cleared from a doubtful feature, the postoral pseudomembrane, which is lacking according to our new results in both *Platyophryides* and *Ottowphrya*. The genus is monotypic.

Platyophryides latus (KAHL, 1930) FOISSNER, 1987 (Fig. 210a–q, 211a–l; 430a–u; Tables 191, 192)

1930 *Platyophrya lata* KAHL, Tierwelt Dtl., 18: 65.
1955 *Woodruffia lichenicola* GELLÉRT, Acta biol. hung., 6: 87 (see FOISSNER 1993c for detailed discussion of synonymy; no new aspects emerged since that).
1987 *Platyophryides lata* (KAHL, 1930) – FOISSNER, Zool. Beitr., 31: 240 (combination with *Platyophryides*).
1993 *Platyophryides latus* (KAHL, 1930) – FOISSNER, Colpodea: 598 (revision; mixed with → *Ottowphrya dragescoi*).

Neotype material: Neotypified from Jordanian population for reasons 1, 3, 5, 6 detailed in chapter 2.4.2. Voucher slides from the Namibian site (71) population, where ontogenesis was studied, also have been deposited (Table 1).

Improved diagnosis: Size about 80 × 35 µm in vivo. Bursiform with cylindroidally narrowed, ventrally curved oral portion. About 20 ciliary rows. Oral apparatus occupies anterior body end, consists of 4–5 adoral organelles and an about 10 µm long paroral membrane comprising approximately 26 kinetids.

Redescription: The redescription is based on the Jordanian neotype population and supplemented with data from the Namibian site (71) specimens, which impregnated so well with protargol that ontogenesis could be studied in detail. Both populations agree in all main features, so that conspecificity is beyond reasonable doubt. Morphometric differences, see table 191.

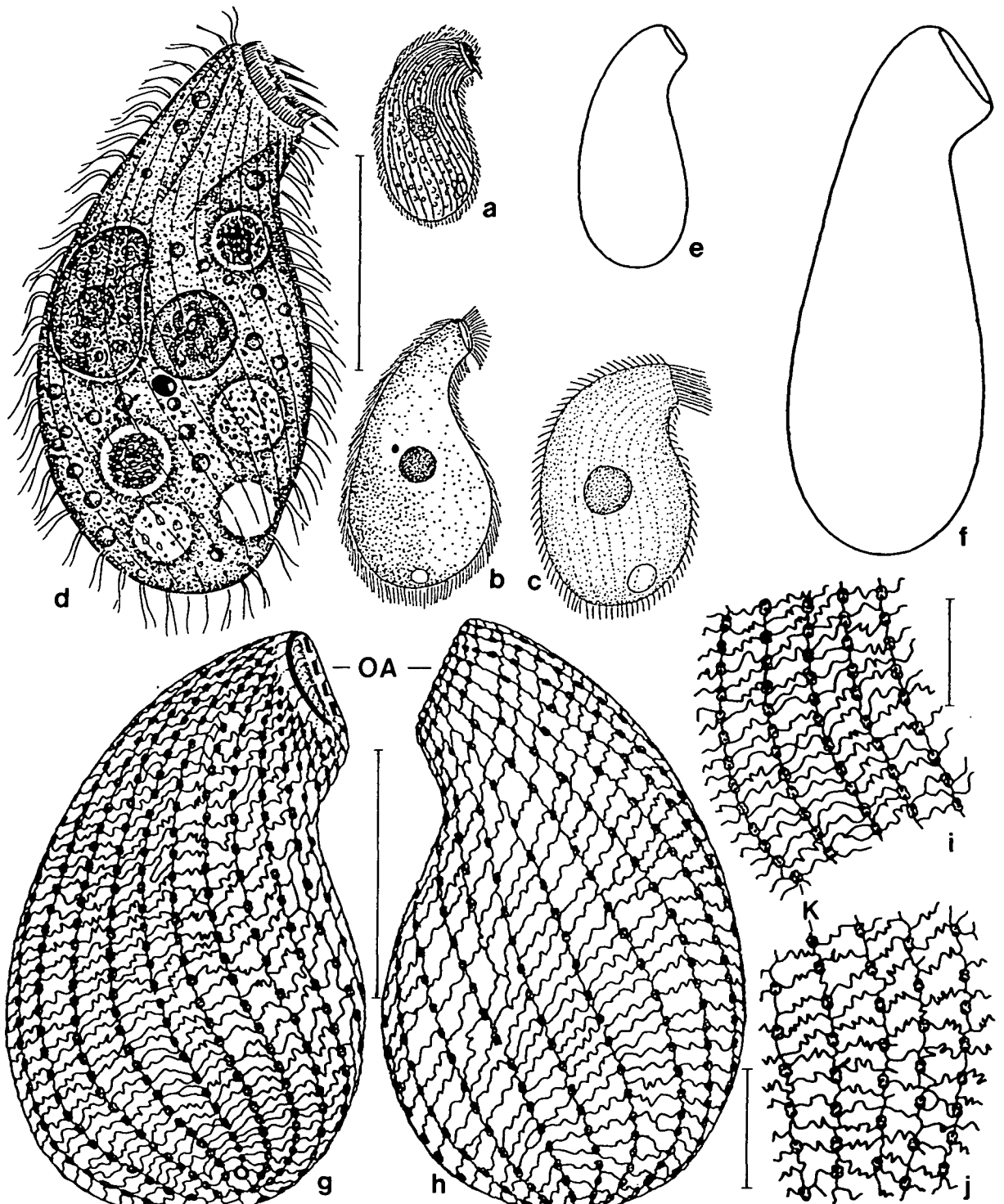


Fig. 210a–j. *Platyophryides latus*, literature figures (a–c), Jordanian neotype specimens (d, g–j), and Venezuelan individuals (e, f) from life (a–f) and after CHATTON-LWOFF silver nitrate impregnation (g–j). **a:** Original illustration, length 100 µm (from KAHL 1930a). **b:** Mexican specimen, 100 µm (from MADRAZO-GARIBAY & LÓPEZ-OCHOTERENA 1973). **c:** North American specimen (from LUNDIN & WEST 1963). **d:** Right side view of a representative specimen having just ingested a *Colpoda maupasi*. **e, f:** Representative specimens from Venezuela, length about 70 µm. **g–j:** Ciliary pattern and silverline system of right (g, i) and left (h, j) side. K – ciliary rows, OA – oral apparatus. Scale bars 25 µm.

Size highly variable within and between populations, in vivo 55–85 × 25–45 µm in Jordanian and Venezuelan specimens, 65–140 × 25–50 µm in Namibian population, where large, slender specimens occur; usually about 70 × 35 µm in Jordanian and 85 × 30 µm in Namibian population; acontractile but highly flexible. Shape, although very variable in all populations and sometimes deformed by large food inclusions, highly characteristic, viz., bursiform with a distinctly narrowed, cylindroidal oral portion (13–15 µm vs. 30–35 µm in mid-body) present in about 70% of specimens; other individuals more or less *Platyophrya*-shaped, that is, bursiform with the oral apparatus located subapically on ventral side (Fig. 210a, d, f, g, o, p; 430a–g). Nuclear apparatus in or near mid-body on average, sometimes dislocated by large food inclusions. Macronucleus about 15 µm across, with long, tortuous nucleolus; nuclear membrane connected to content by fibrous structures in protargol preparations. Micronucleus

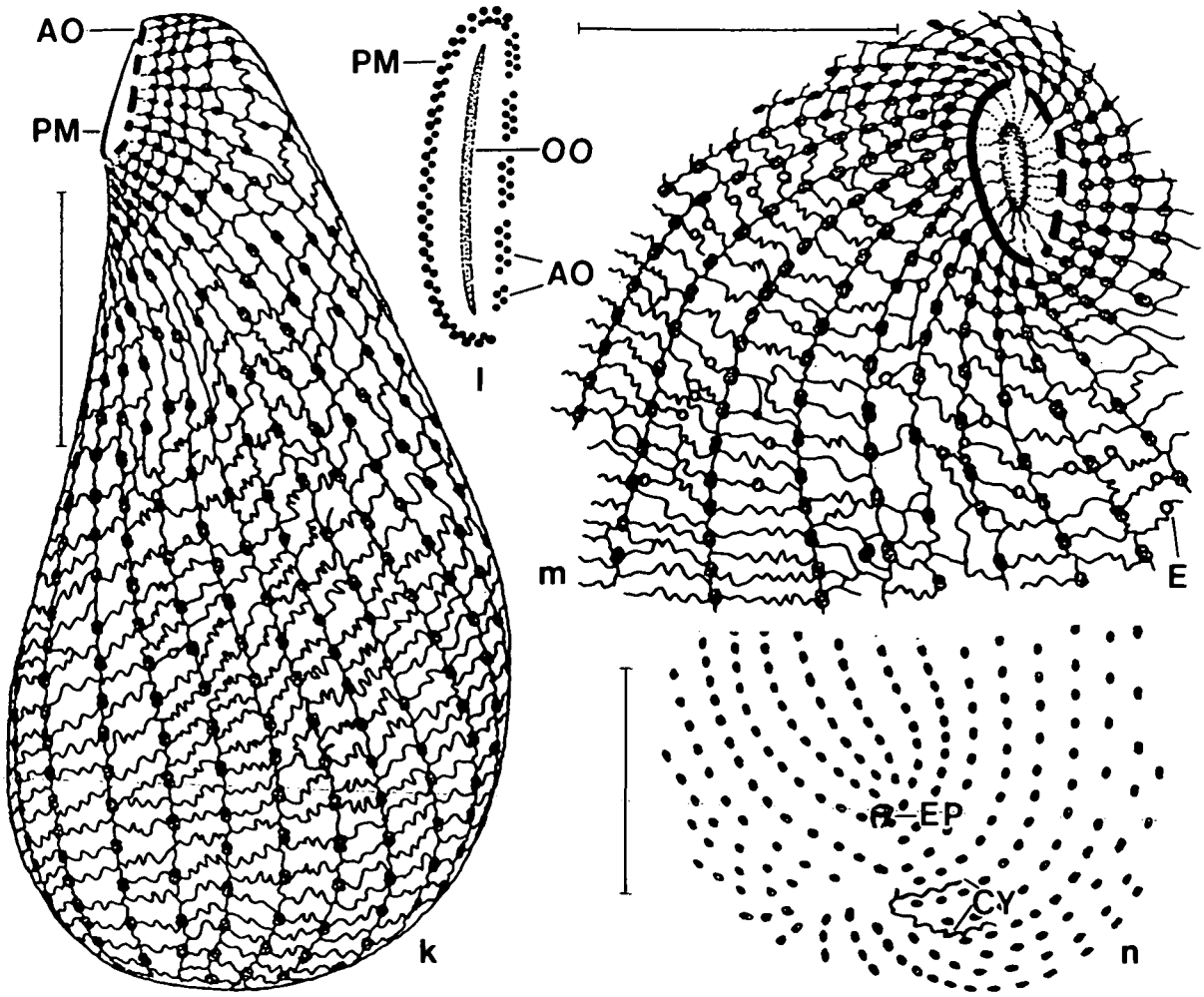


Fig. 210k–n. *Platyophryides latus*, ciliary pattern and silverline system of Jordanian neotype population after CHATTON-LWOFF silver nitrate impregnation. **k:** Left side view showing lack of a postoral pseudomembrane. **l:** Oral structures, schematized. Note that the posterior adoral organelle is only half the size of the other organelles, a specific feature of *Platyophryides* and → *Ottowphrya*. **m:** Oral view. **n:** Posterior pole area showing excretory pore and U-shaped cytopyge. AO – adoral organelles, CY – cytopyge, E – docked extrusome surrounded by a silverline, EP – excretory pore of contractile vacuole, OO – oral opening (slit), PM – paroral membrane. Scale bars 20 µm.

about 3 µm across, surrounded by a distinct membrane in protargol preparations, not in perinuclear space of macronucleus (Fig. 210a, 211a; 430j, q). Contractile vacuole subterminal with excretory pore at margin of ventral and right side. Cytopyge in posterior pole area, marked by a peculiar, U-shaped silverline (Fig. 210d, g, n). Cortex inconspicuous, contains numerous colourless, about 1 µm-sized granules, very likely mucocysts surrounded by a silverline. Cytoplasm without specific inclusions, usually packed with fat globules and large food vacuoles containing remnants of medium-sized ciliates, such as *Colpoda maupasi* and *C. steinii*; the specimens from Marion Island were packed with fungal conidia. Swims and creeps rather rapidly on microscope slide as well as on and between soil particles showing great flexibility.

Somatic cilia about 8 µm long and paired throughout, arranged in 23 (Jordanian specimens) or 18 (Namibian specimens) slightly to distinctly sigmoidal, bipolar rows more closely spaced and densely ciliated on right than left side of cell; a short posterior pole suture is formed by some shortened rows. At left mouth margin kineties commence with two to four, usually three closely spaced kinetids which, however, do not form a postoral pseudomembrane, as explained in figure 216g. Silverlines in *Colpoda* pattern throughout; individual silverlines conspicuously undulating and about one and a half as closely spaced as kinetids, surround docked extrusomes and dikinetids (Fig. 210d, g–k, m, 211a, b; 430a–i, k–s; Table 191).

Oral apparatus occupies anterior body end, rather conspicuous. Paroral membrane at right mouth margin, C-shaped, in Namibian specimens composed of an average of 26 (22–30, n = 5) dikinetids bearing about 5 µm long cilia; inner basal body of dikinetids smaller and more lightly impregnated both in protargol and silver carbonate preparations. On average four (Jordanian specimens) to five (Namibian specimens) adoral organelles on left mouth margin; individual organelles cirrus-like in appropriately orientated specimens, located slightly obliquely to main mouth axis, composed of two rows of basal bodies bearing about 5 µm long cilia; proximal organelle distinctly smaller in most specimens, as in → *Ottowphrya dragescoi*. Oral opening slit-like, pharynx at right bordered by many fine rods originating from paroral kinetids and conspicuously bifurcated proximally; left basket half supported by fine, only occasionally impregnated fibres originating from adoral organelles (Fig. 210a, g, k–m, o, p, 211a, b; 430a, h, k, s–u; Table 191).

Occurrence and ecology: The records known were reviewed by FOISSNER (1993c). Currently, all those not illustrated are questionable because the species was not separated from → *Ottowphrya dragescoi*. Thus, only three reliable literature records remain: roof mosses and *Sphagnum* in Germany (KAHL 1930a; Fig. 210a); San Anton waterfall in Mexico (MADRAZO-GARIBAY & LÓPEZ-OCHOTERENA 1973; Fig. 210b), and Michigan, USA (LUNDIN & WEST 1963; Fig. 210c). We found *P. latus* in a highly saline and slightly acidic (pH 5.4) mixture of grass and soil from the beach of the subantarctic Marion Island (FOISSNER 1996b); in mud (pH 6.6) from rock-pools of the Catanjapo River just before it runs into the Orinoco about 10 km south of Porto Ayachucho, Venezuela; and in the highly saline and slightly acidic (pH 5.4) sample from the Namibian site (71). The neotype population is from the surroundings of Wadi Rum in Jordan (29°30'N 35°E). The sample was a mixture of plant litter and brownish, highly saline (25‰) and circumneutral (pH 7.5) sand. Obviously, *P. latus* is an euryhaline cosmopolitan preferring terrestrial biotopes.

Identification and comparison with related species: The original description of *P. latus* is rather brief, but the figure (Fig. 210a) and the features mentioned match

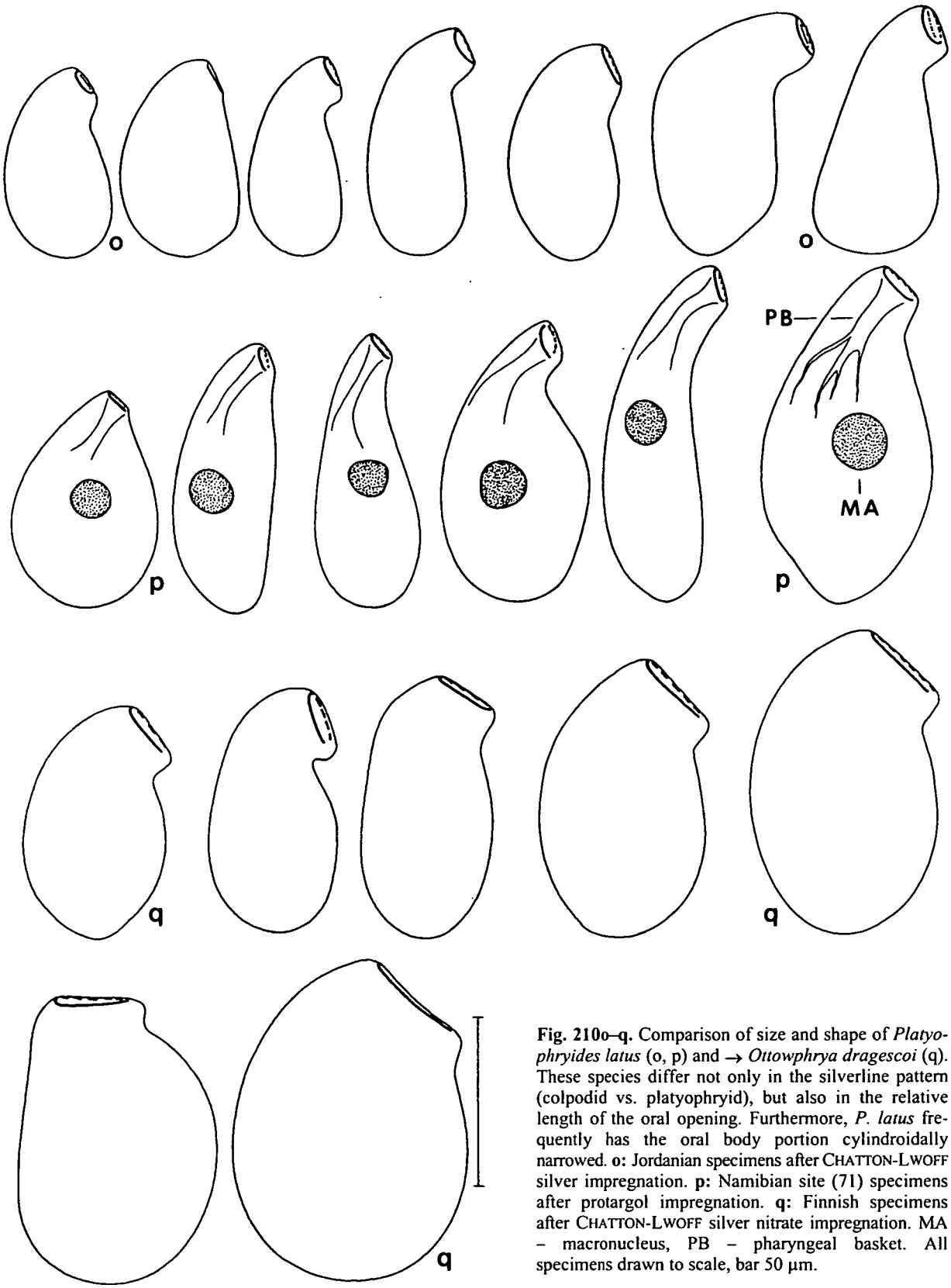


Fig. 210o–q. Comparison of size and shape of *Platyophryides latus* (o, p) and → *Ottowphrya dragescoi* (q). These species differ not only in the silverline pattern (colpodid vs. platyophryid), but also in the relative length of the oral opening. Furthermore, *P. latus* frequently has the oral body portion cylindroidally narrowed. **o:** Jordanian specimens after CHATTON-LWOFF silver impregnation. **p:** Namibian site (71) specimens after protargol impregnation. **q:** Finnish specimens after CHATTON-LWOFF silver nitrate impregnation. MA – macronucleus, PB – pharyngeal basket. All specimens drawn to scale, bar 50 µm.

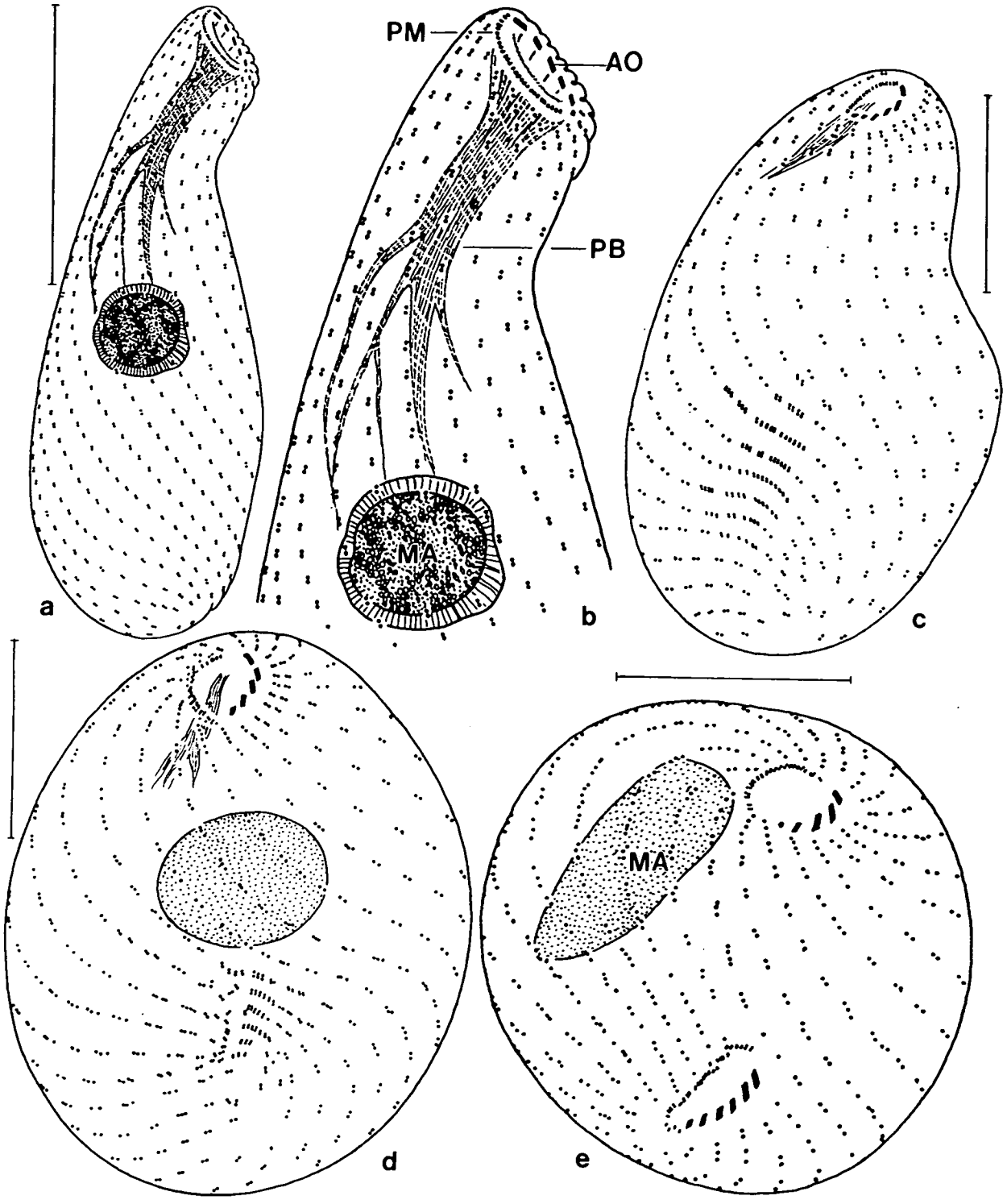


Fig. 211a–e. *Platyophryides latus*, ciliary pattern of morphostatic (a, b) and dividing (c–e) specimens from Namibia after protargol impregnation. **a, b:** Right lateral view of a representative specimen. **c:** Very early divider showing intense duplication of basal bodies in about six ventrolateral kineties. **d:** Early divider showing assemblage of opisthe's oral structures. The parental oral structures appear disorganized. **e:** Early-middle divider. The opisthe oral structures are almost completed. The parental paroral has reorganized, while the pharyngeal basket was resorbed. AO – adoral organelles, MA – macronucleus, PB – pharyngeal basket, PM – paroral membrane. Scale bars 40 μm (a) and 20 μm (c–e).

our population well. Thus, the identification is very likely correct. Original description (translated from German): "Shape broad (2:1), oral area distinctly projecting, ventral contour thus strongly sigmoidal. Length 105 µm, very flat, bright, colourless, narrowly striated by the ciliary rows. At left mouth margin 5–6 cirrus-like structures, at right mouth margin, which has a narrow fringe, closely spaced short bristles; otherwise as *Platyophrya spumacola*. Common, but much rarer than *P. spumacola*".

The most typical feature of *P. latus* is the cylindroidally narrowed, projecting oral area, emphasized also by KAHL (1930a). It makes the species rather easily distinguishable from other platyophryids, at least at population level. However, the *Platyophrya*-shaped specimens are difficult to separate from *P. sphagni*, *P. spumacola*, and *P. similis*. Thus, silver impregnation should be applied to reveal the silverline pattern, which is colpodid in *Platyophryides* and platyophryid in *Platyophrya*. However, the species can be distinguished

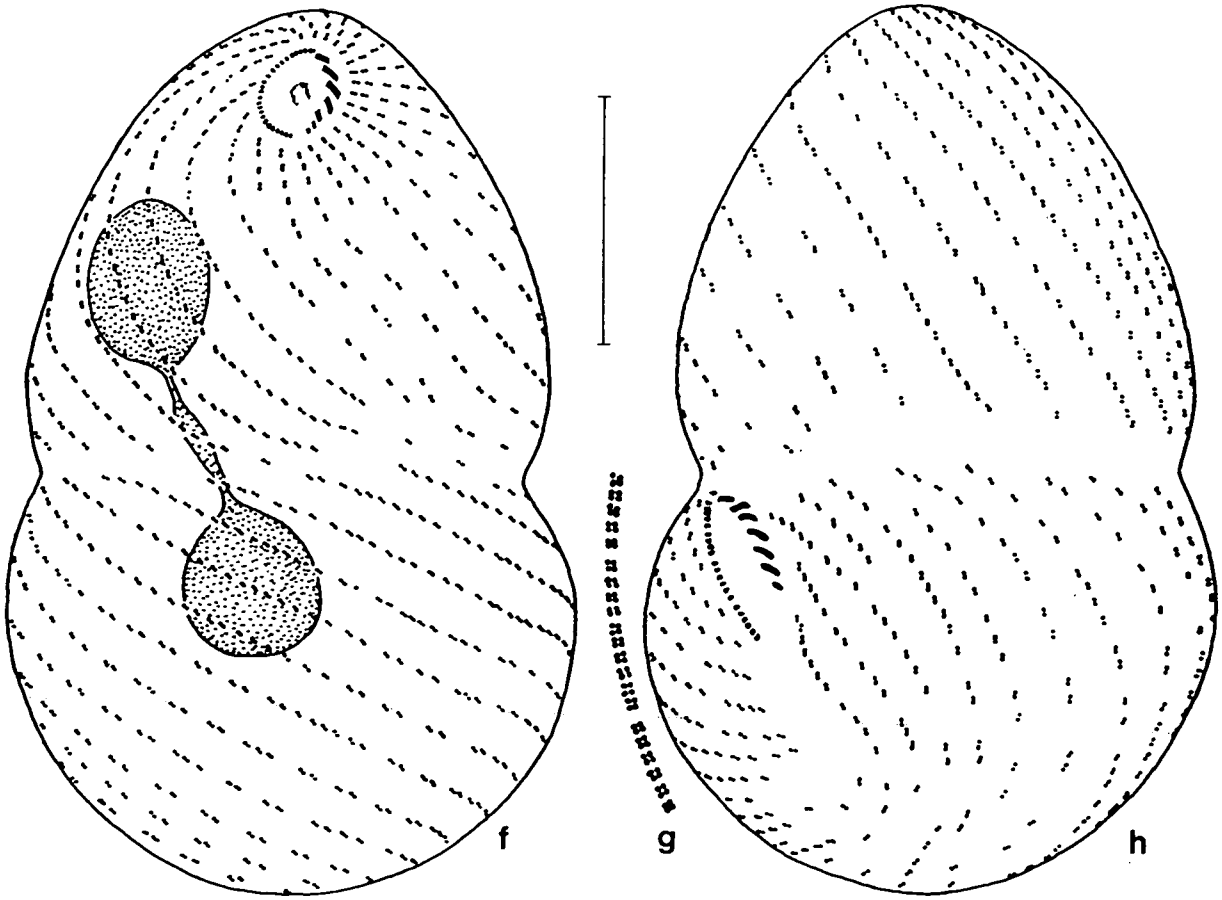


Fig. 211f–h. *Platyophryides latus* from Namibian site (71), ciliary pattern of a middle divider after protargol impregnation. The division furrow is now recognizable and the opisthe rotated by about 180° shifting the oral apparatus on the dorsolateral margin of the cell (h). The new opisthe oral apparatus has on average more adoral organelles than that of morphostatic specimens (Table 192), and its paroral appears to be composed of quadruplets of basal bodies (g). The proter oral apparatus still lacks the pharyngeal basket (f). The duplicated somatic kinetids move apart and macronucleus division is almost completed. Scale bar 20 µm.

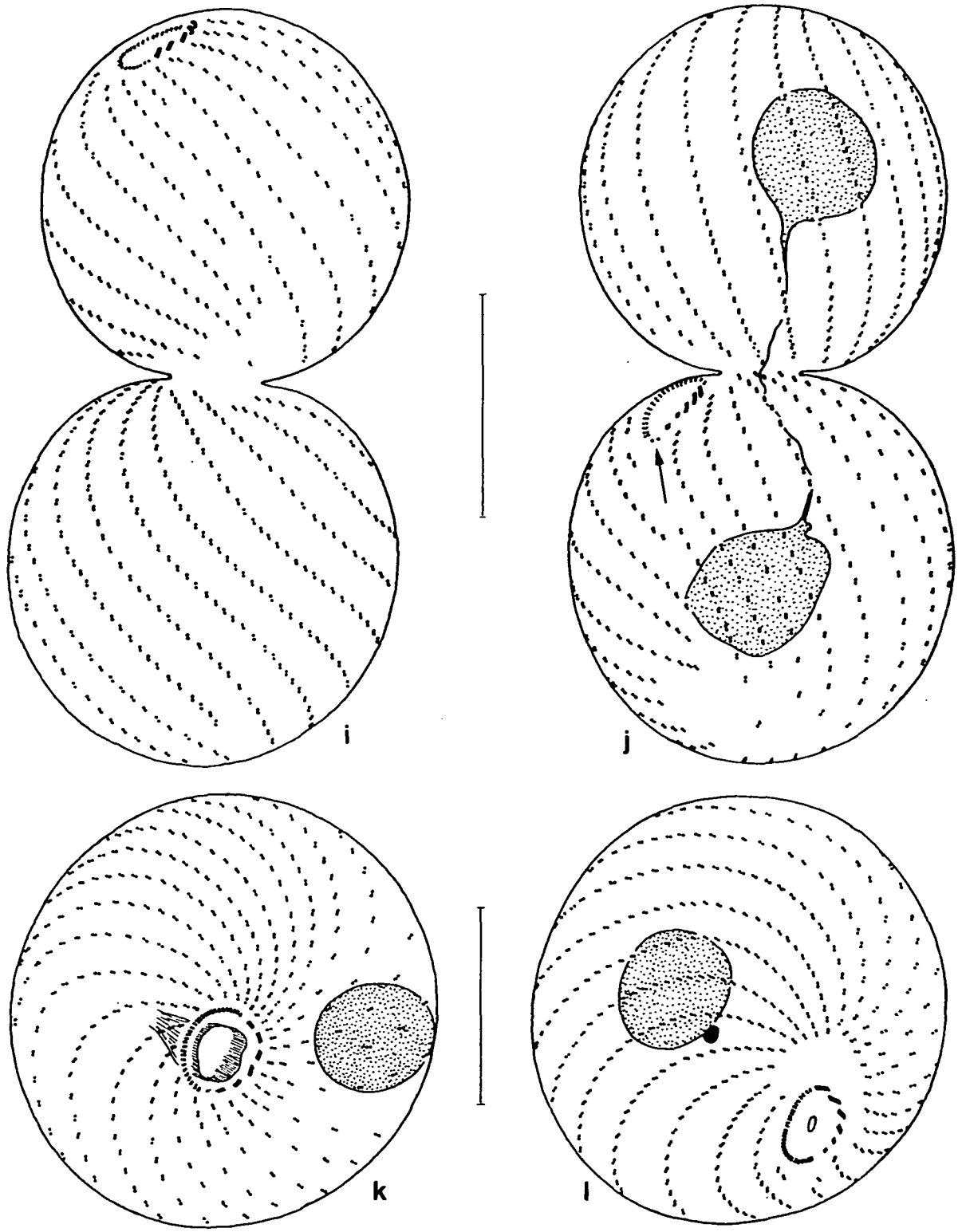


Fig. 211i–l. *Platyophryides latus* from Namibian site (71), ciliary pattern of a very late divider (i, j) and post-dividers (k, l) after protargol impregnation. **i, j:** Proter and opisthe are still rotated by about 180° and two supernumerary opisthe adoral organelles are resorbed (arrow). The proter still lacks the pharyngeal basket. **k, l:** Proter and opisthe post-divider; the proter is developing the pharyngeal basket. Scale bars 20 μm.

also on careful live observation by the orientation (parallel vs. distinctly oblique to main mouth axis) and number (about six in *P. latus* vs. ≥ seven in the *Platyophrya* species mentioned above) of adoral organelles. Likewise, the extreme shape variants of *P. latus* and *O. dragescoi* are difficult to distinguish (Fig. 210o–q); the different silverline pattern is the only reliable feature. Usually, however, both are rather easily distinguished, even in vivo, by the stouter shape and the much broader oral area: the ratio body width:length of paroral membrane is 3–3.3:1 in *P. latus* and 2.3:1 in *O. dragescoi* (Fig. 210o–q; Table 192).

Ontogenesis: *Platyophryides latus* was very abundant in the non-flooded Petri dish culture set up with the Namibian site (71) soil. Many excellently impregnated dividers were found in the protargol slides, and thus a detailed description of the process can be provided.

Division is homothetogenic, pleurokinetal, and proceeds in freely motile (non-encysted) condition. It commences with an intense duplication of basal bodies in the posterior ventral half of about six right lateral kineties (Fig. 211c). Next, the cell begins to round up, the macronucleus swells, and kinetid duplication occurs in all kineties producing basal body triplets. The opisthe oral structures are assembling subequatorially on the ventral surface and both paroral membrane and adoral organelles become recognizable. The parental (proter) oral apparatus shows distinct signs of reorganization: the paroral dikinetids become scattered and the pharyngeal basket disorganizes (Fig. 211d). When the cell becomes globular, the macronucleus is elongate ellipsoidal and many basal body quadruplets are recognizable in the ciliary rows. The opisthe oral structures are almost complete and in the axis of the proter oral apparatus, whose paroral completed reorganization, while the pharyngeal basket was resorbed (Fig. 211e).

Table 192. Comparison of main morphometrics in morphostatic (upper line) and dividing (lower line) specimens of *Platyophryides latus* from Namibian site (71).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	82.0	78.0	14.6	3.2	17.8	63.0	132.0	21
	41.3 [b]	43.0	3.3	1.0	8.0	35.0	45.0	11
Body, width	32.4	30.0	6.4	1.4	19.8	25.0	49.0	21
	40.0 [b]	40.0	3.2	1.0	7.9	34.0	44.0	11
Proter adoral organelles, number	5.0	5.0	0.4	0.1	8.9	4.0	6.0	21
	4.8 [c]	5.0	0.9	0.2	18.7	3.0	6.0	11
Opisthe adoral organelles, number	–	–	–	–	–	–	–	–
	6.2 [c]	6.0	0.7	0.2	11.9	5.0	8.0	23
Adoral organelles in post-dividers, number	–	–	–	–	–	–	–	–
	5.5	6.0	0.7	0.2	12.5	4.0	6.0	11

[a] Data based on mounted and protargol-impregnated (FOISSNER's method) specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] From post-dividers.

[c] From middle to late dividers.

Middle dividers show the onset of cell division, accompanied by an about 90° rotation of the opisthe relative to the proter. Thus, proter and opisthe oral apparatus are now on different sides of the cell and cannot be seen at the same focal plane. The opisthe paroral is composed of granule quadruplets, and macronucleus division is almost completed. The proter still lacks a pharyngeal basket, and there is possibly some internal reorganization of the adoral organelles (Fig. 211f–h). On average, the opisthe oral apparatus has one adoral organelle more than the interphase specimens (Table 192). Late and very late dividers are distinctly dumb-bell-shaped and the opisthe is still rotated by 180° relative to the proter, which still lacks a pharyngeal basket. The opisthe resorbs the supernumerary adoral organelles (Fig. 211i, j). Post-dividers are globular and about half the size of interphase specimens (Table 192). The pharyngeal basket commences to form (Fig. 211k, l). Cell shaping obviously occurs later. Micronuclear division could not followed because the micronucleus did not impregnate.

Ontogenetic comparison: Division of *P. latus* is highly similar to that of cyrtolophosidid colpodids (for a review, see FOISSNER 1993c). The sole difference noteworthy is the rather distinct proter reorganization, as yet observed only in *Cyrtolophosis* spp. and *Woodruffides metabolicus*.

Etoschophrya nov. gen.

Diagnosis: Small to medium-sized Woodruffiidae GELEI, 1954 with platyophryid silverline system on right side and kreyellid on left. Paroral membrane elliptical, almost closed to form a "circumoral kinety". Few adoral organelles extend beyond paroral membrane.

Type species: *Etoschophrya oscillatoriophaga* nov. spec.

Etymology: Composite of *Etoscha* (German spelling of Etosha = great white pan in the native language) and the Greek noun *ophrya* (eyebrow ~ cilia ~ ciliate s.l.), meaning a ciliate from the Etosha Pan. Feminine gender.

Comparison with related genera: See FOISSNER (1993c) for family diagnosis and a detailed review of all genera and species concerned. The general organization of *Etoschophrya* indicates a relationship with either → *Kuklikophrya* NJINE, 1979b (almost "closed" paroral membrane) or → *Rostrophryides* FOISSNER, 1987c (see below and Fig. 212n, o). *Etoschophrya* differs from both by the unique silverline system, and from *Kuklikophrya* also by the lack of curved postoral kineties. *Rostrophryides* has a postoral pseudomembrane lacking in *Etoschophrya*, as shown by a detailed analysis of several silver carbonate and silver nitrate-impregnated, properly orientated specimens (Fig. 429e). However, the occurrence of shortened postoral ciliary rows indicate a tendency to generate such an organelle relating *Etoschophrya* to *Rostrophryides*. Certainly, *Etoschophrya* also resembles *Reticulowoodruffia* FOISSNER, 1993c, especially in the silverline system. However, *Reticulowoodruffia* has the oral apparatus orientated in the main body axis, possesses an only slightly curved paroral membrane, and has a very different general appearance.

Etoschophrya oscillatoriophaga nov. spec. (Fig. 212a–m; 298, 431a–i, 442m; Table 193)

Diagnosis: Size about 40 × 25 µm in vivo; obovoidal with inconspicuous beak at anterior left end. On average, 18 somatic ciliary rows, 4 adoral organelles, and 24 paroral dikinetids.

Type location: Highly saline soil from margin of Etosha Pan, Namibia, 18°50'S 16°30'E (site 67 in figures 2, 3 and chapter 2.1.2).

Etymology: Named after the preferred food (*Oscillatoria* sp.).

Description: Size 30–50 × 20–35 µm in vivo, usually about 40 × 25 µm, obviously shrinks rather strongly in preparations due to the fragile cortex (Table 193). Shape highly depending on nutrition state, basically laterally slightly flattened and obovoidal with dorsal margin more distinctly convex than ventral; anterior left end, where the adoral organelle band is located, usually slightly projecting providing some specimens with a *Chilodonella uncinata*-like outline (Fig. 212b). Starving cells conspicuously narrowing posteriorly, overfed specimens almost globular. Nuclear apparatus in or near body centre. Macronucleus globular and with large nucleoli. Micronucleus about 2.5 × 1.5 µm, in perinuclear space of macronucleus, which becomes evident in stained specimens, where the macronuclear content shrinks leaving the micronucleus attached to the inner macronuclear membrane (Fig. 212e). Contractile vacuole subterminal with single excretory pore near left (ventral) margin of cell (Fig. 212a, c, i, j). Cortex thin, fragile, often does not withstand formalin fixation as used for silver carbonate impregnation, studded with rows of pale granules about 0.8 µm across; when methyl green-pyronin is added, granules stain red and become extruded forming a voluminous fibrous coat (Fig. 212f, g; 431f). Well-fed specimens green due to ingested cyanobacteria; cytoplasm, however, colourless and opaque containing some 1–2 µm-sized lipid droplets and often many food vacuoles up to 20 µm across. Possibly feeds exclusively on filamentous cyanobacteria (*Oscillatoria* sp.) ingested as short pieces breaking to globular subunits in the food vacuoles (Fig. 212a). Vacuoles not spotted during digestion, as in many nassulids, but turning to an inconspicuous yellowgreen. Some specimens contain many argyrophilic rods, possibly bacteria (Fig. 431g). Swims fast to very fast in wide spirals; never rests.

Somatic cilia about 7 µm long in vivo, paired except in posterior thirds of ventral and left side, where only the posterior basal body of the dikinetids is ciliated (Fig. 431b). Cilia form slightly spiral rows all commencing around oral apparatus, right side more densely ciliated than left, where two to three shortened kineties composed of only 2–4 kinetids occur; usually, one shortened kinety is on ventral side in the transition zone of right and left side kineties (Fig. 212a, h–m; 431a, b, e). Distances of kinetids within kineties gradually increase from anterior to posterior, first pair rather closely spaced and thus easily mistaken as postoral pseudomembrane, as defined by FOISSNER (1993c).

Oral apparatus in left anterior quadrant of cell, overall appearance flat and elliptical (Fig. 212a, h, j, l; 298, 431a, c, d, h, i). Oral field elliptical and slightly concave, rather conspicuous because opaque and bright. Centre with small slit marking inconspicuous, proximally diverging oral basket hardly recognizable in live specimens. Paroral membrane at margin of oral field, forms elliptical "circumoral kinety" because open only at anterior left end, where

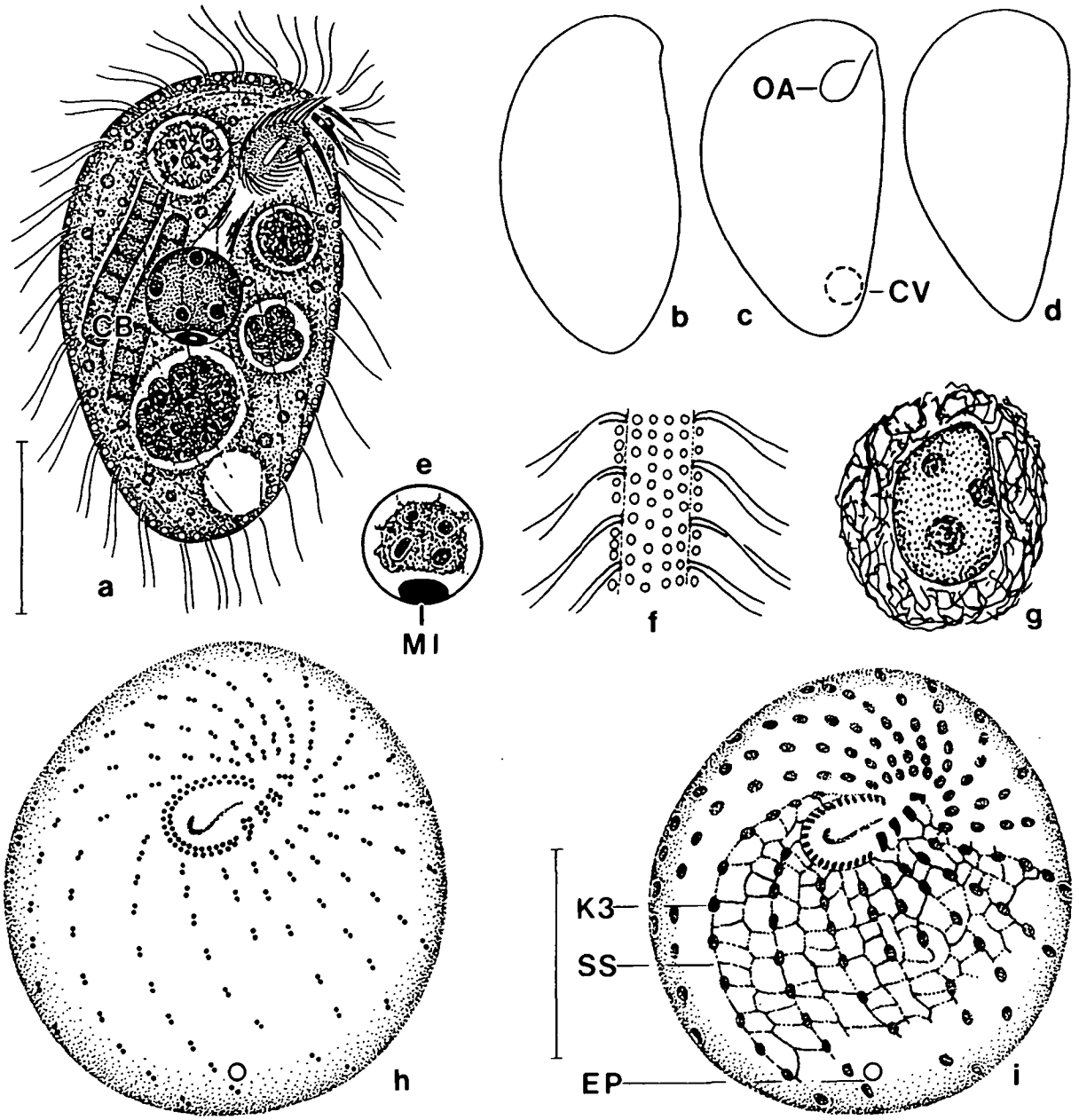


Fig. 212a–i. *Etoschophrya oscillatoriophaga* from life (a–d, f), after methyl green-pyronin staining (e, g), and after silver carbonate (h) and CHATTON-LWOFF silver nitrate (h, i) impregnation. **a:** Right lateral view of a representative specimen with many food vacuoles containing *Oscillatoria* remnants. **b:** Chilodonellid shape variant. **c, d:** Starved specimens look like a piece of cake. **e:** When the karyoplasm shrinks, the micronucleus remains attached to the inner side of the macronuclear membrane because it is in the perinuclear space. **f, g:** The cortex is studded with rows of pale granules, which become extruded and form a voluminous coat after addition of the stain. **h, i:** Same specimen, in (h) supplemented with observations from silver carbonate preparations. The somatic and oral infraciliature consists of dikinetids; however, the anterior cilium is lacking in certain regions (Fig. 212a). The elliptical paroral membrane forms some kind of circumoral kinety because it is open only at the left anterior corner, where four minute adoral organelles insert. The silverline system of *E. oscillatoriophaga* is the main genus character because it is platyophryid on the right side and irregular (kreyellid) on the left. CB – cyanobacterial filaments, CV – contractile vacuole, EP – excretory pore of contractile vacuole, K3 – somatic kinety 3, MI – micronucleus, OA – oral apparatus, SS – silverline system. Scale bars 15 μm.

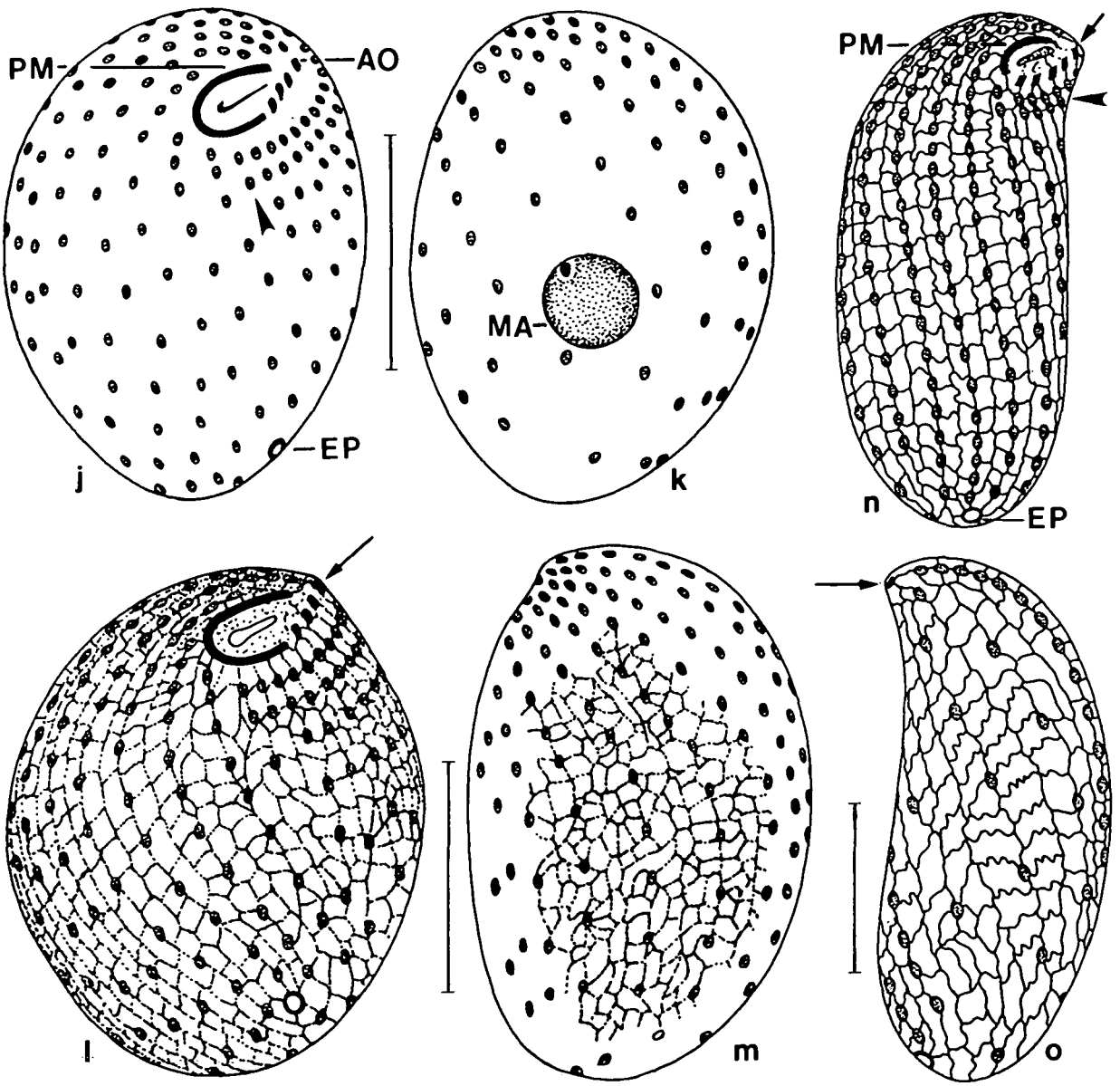


Fig. 212j–o. *Etoschophrya oscillatoriophaga* (j–m) and *Rostrophryides africana* (n, o; from FOISSNER 1993c), ciliary pattern and silverline system after CHATTON-LWOFF silver nitrate impregnation. **j, k:** Somatic and oral ciliary pattern of right and left side of a representative specimen. Arrowhead marks a strongly shortened postoral ciliary row. Note that most postoral ciliary rows are slightly shortened (k), making the posterior left surface loosely ciliated. **l, m:** Somatic and oral ciliary pattern and silverline system of right and left side. Arrow marks adoral organelle band. The silverline system is platyophryid (a median silverline between two ciliary rows each divides the meshes forming a regular pattern) on the right side and irregular (kreyellid) on the left. **n, o:** Somatic and oral ciliary pattern and silverline system of right and left side. Arrows mark adoral organelle band; arrowhead denotes postoral pseudomembrane. *Rostrophryides* differs from *Etoschophrya* by three main features: the silverline system is platyophryid throughout (cp. figures 212m, o); the paroral membrane is short and thus does not extend onto the left oral area (cp. figures 212j, n); and it has a postoral pseudomembrane (Fig. 212n, arrowhead; for detailed explanation, see Fig. 216g). Seemingly, such a structure is present also in *Etoschophrya* (Fig. 212j, l). However, a detailed analysis shows that most postoral dikinetids are attached to a left side somatic kinety (Fig. 431e). AO – adoral organelle band, EP – excretory pore, MA – macronucleus, PM – paroral membrane. Scale bars 15 µm.

the adoral organelle band commences; composed of zigzagging dikinetids of which possibly only one basal body bears an about 4 µm long cilium. Almost invariably four minute adoral organelles: two at anterior left margin of oral field in continuation of paroral membrane and two in a minute preoral suture; individual organelles with 5 µm long cilia and composed of two ciliary rows with three basal bodies each; some basal bodies possibly barren or lacking, especially in distalmost organelle; each organelle surrounded by fibrous material forming short bundle obliquely extending posteriorly from left posterior corner of organelle.

Silverline system platyophryid on right side and kreyellid on left, with transition zone where patterns abut. Platyophryid portion without peculiarities, kreyellid part very irregular and most distinct in central area of left side (Fig. 212i, l, m; 442m)[33].

Occurrence and ecology: To date found only in the highly saline soil sample from type location, *where it was abundant. Possibly, E. oscillatoriophaga* is not a soil ciliate sensu

Table 193. Morphometric data on *Etoschophrya oscillatoriophaga*.

Characteristics [a]	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length [b]	CHL	31.3	32.0	2.5	0.5	7.9	25.0	36.0	21
Body, width [b]	CHL	24.8	25.0	3.6	0.8	14.4	19.0	32.0	21
Anterior end to vertex of paroral, distance [b]	CHL	7.9	8.0	1.3	0.3	16.9	5.0	10.0	21
Anterior end to macronucleus, distance [b]	CHL	14.5	15.0	1.4	0.3	9.7	11.0	17.0	21
Macronucleus, length	CHL	6.8	7.0	0.7	0.1	10.0	5.0	8.0	21
Macronucleus, width	CHL	6.7	7.0	0.6	0.1	9.6	5.0	8.0	21
Macronuclei, number	SC	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Micronuclei, number	SC	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Somatic kineties, number [c]	CHL, SC	17.8	18.0	1.2	0.2	6.7	15.0	21.0	30
Kinetids in kinety 3, number [d]	CHL	15.9	16.0	1.7	0.4	11.0	13.0	19.0	21
Paroral, long axis [e]	CHL	6.6	6.0	0.7	0.1	10.3	6.0	8.0	21
Paroral, short axis [e]	SC	4.8	5.0	0.5	0.1	11.3	4.0	6.0	21
Paroral dikinetids, number	SC	23.8	24.0	1.7	0.4	7.0	21.0	28.0	21
Adoral organelles, number [f]	SC	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21

[a] Data based on randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SC – wet, squashed silver carbonate preparations, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] From properly orientated specimens.

[c] Anterior polar views.

[d] As designated in figure 212i.

[e] Roughly corresponds to size of oral field.

[f] Of 25 specimens analyzed, one had five organelles.

[33] Unfortunately, the slides bleached rather strongly. Thus, the silverlines are very faint. However, all details described and figured are recognizable in the specimens marked on the type slides.

stricto, but mainly an inhabitant of ephemeral puddles with cyanobacterial mats. In any case, the distribution must be very patchy because it was not found in other samples from this region.

Comparison with related species: A similar species has not been described (FOISSNER 1993c). However, *E. oscillatoriophaga* is easily confused with → *Rostrophryides africana* FOISSNER, 1987c, which has a similar size, shape, and ciliary pattern (Fig. 212n, o); in vivo, these species are best distinguished by the paroral membrane, which is easily recognizable and C-shaped in *R. africana*. Inexperienced workers may even confuse *E. oscillatoriophaga* with *Chilodonella uncinata*, which, however, never feeds on filamentous cyanobacteria (FOISSNER et al. 1991).

Rostrophrya namibiensis **nov. spec.** (Fig. 213a–f, 214a–i; 432a–j, 433a–h, 434a; Table 194)

Diagnosis: Size about 130 × 40 µm in vivo, length:width ratio 3–3.7:1. Elongate ellipsoidal with pointed or truncate rostrum; posterior portion narrowed or inflated. On average 32–42 somatic ciliary rows. Oral aperture elongate elliptical with about 18 adoral organelles, of which approximately 10 are on left vestibular slope.

Remarks: This species is split into two subspecies differing mainly in body shape and number of ciliary rows. At first glance, → *R. fenestrata*, described below, looks like a third subspecies. However, including → *R. fenestrata* in *R. namibiensis* would result in a very broad, unnatural variability of this species, far outside that usually encountered in colpodids (see table 1 in FOISSNER 1993c). Variability of kinety number, for instance, would increase from the usual 6% to 26.4%, if the individual kinety numbers of *R. namibiensis namibiensis*, *R. namibiensis maldivensis*, and → *R. fenestrata* are pooled ($\bar{x}$ = 32.5, SD = 8.6, CV = 26.4%, n = 35).

The silverline system of *Rostrophrya* was unknown (FOISSNER 1993c). Our results show that it is platyophryid, that is, has meshes divided by a longitudinal ("median") silverline between each two kineties. Thus, all genera of the Woodruffiidae have a platyophryid silverline system, except for → *Woodruffia*, where it is colpodid (FOISSNER 1993c), indicating that the group is biphyletic.

Comparison with related species (genus review, FOISSNER 1993c): *Rostrophrya namibiensis* is easily distinguished from *R. camerounensis* and *R. regis*, discovered in temporary pools of tropical Africa, by the smaller size (≤ 160 µm vs. ≥ 160 µm) as well as the much smaller number of ciliary rows (≤ 50 vs. ≥ 80) and adoral organelles (≤ 20 vs. ≥ 30). *Rostrophrya terricola* FOISSNER, 1993c differs from *R. namibiensis* by the broader shape (length:width ratio 2.5:1 vs. 3:1) and, especially, the much smaller and rounder oral opening (8 × 6 µm vs. 15 × 5 µm). → *Rostrophrya fenestrata* lacks a distinct rostrum, is usually thinner (4:1 vs. 3–3.7:1), and has only half the number of ciliary rows and adoral organelles.

Rostrophrya namibiensis namibiensis nov. sspec. (Fig. 213a–f; 296, 297, 432a–j; Table 194)

Diagnosis: Body shape regular, slightly sigmoidal and/or lanceolate, rostrum pointed, narrowed posterior end rounded; length:width ratio about 3.7:1. On average 32 somatic ciliary rows.

Type location: Highly saline soil from margin of Etosha Pan, Namibia, 19°S 15°50'E (site 54 in figures 2, 3 and chapter 2.1.2).

Etymology: Named after the country discovered.

Description: Size 100–150 × 30–45 µm, usually about 125 × 32 µm in vivo, length:width ratio 3–4:1, on average 3.7:1. Shape regular as in *R. terricola* FOISSNER, 1993c, that is, margins usually without indentations and convexities, often very slender and up to 2:1 dorsoventrally flattened; elongate ellipsoidal to fusiform, occasionally slightly sigmoidal, rostrum pointed or narrowly rounded, posterior end usually slightly broader than anterior, rarely bluntly pointed (Fig. 213a, d). Macronucleus near body centre, with thick membrane, conspicuously small (about 15 × 10 µm in vivo) compared to size of cell, as in most other members of order (FOISSNER 1993c). Micronucleus recognizable neither in vivo nor in silver carbonate preparations. Contractile vacuole subterminal at left margin of cell, with single, conspicuous collecting canal extending to mid-body at left margin. Cortex very flexible, contains numerous colourless mucocysts about 0.8 µm across; mucocysts irregularly and closely spaced on left side, while in distinct clusters on right forming peculiar pattern with mitochondria at left side of ciliary rows (Fig. 213e, f). Cytoplasm colourless, contains numerous lipid droplets about 1 µm across and many food vacuoles, mainly in posterior half of cell. Feeds on bacteria, fungal conidia, and cyanobacterial filaments ingested as long pieces later split into small portions forming about 10 µm-sized, green food vacuoles turning orange during digestion (Fig. 213a; 432a, h, i). Movement without peculiarities, glides rather rapidly on microscope slide and soil particles showing great flexibility.

Cilia only about 7 µm long in vivo, mostly paired, some singles occur on less densely ciliated dorsal side (Fig. 432j), form about 32 rows arranged as in other members of genus (FOISSNER 1993c), that is, slightly spiral producing distinct preoral suture containing adoral organelles; some shortened ciliary rows commence along posterior left half of oral opening and generate an indistinct postoral suture, where left and right side kineties abut. Anteriormost two or three kinetids of each kinety more closely and very regularly spaced along left slope of oral opening and preoral suture, producing membranoid ciliary condensation, but not a postoral pseudomembrane, as in most Platyophryidae (FOISSNER 1993c), because most ciliary rows extend to at least mid-body (Fig. 213b; 296, 297, 432a, b, e, h–i). Silverline system platyophryid as in → *R. namibiensis maldivensis*.

Oral opening slightly obliquely orientated to main body axis at base of rostrum, that is, distinctly subapical; elongate elliptical, viz., about 10–15 × 4–6 µm in vivo (Fig. 213a–c; 296, 297, 432a–h). Paroral and adoral cilia only 3–4 µm long. Paroral membrane on right slope of vestibulum, uncinate, that is, surrounds posterior end of oral opening; composed of about 42 dikinetids having only the proximal basal body ciliated in the uncinate portion because the distal basal body is impregnated very faintly or not at all (Fig. 213c; 432c, e, f). On average

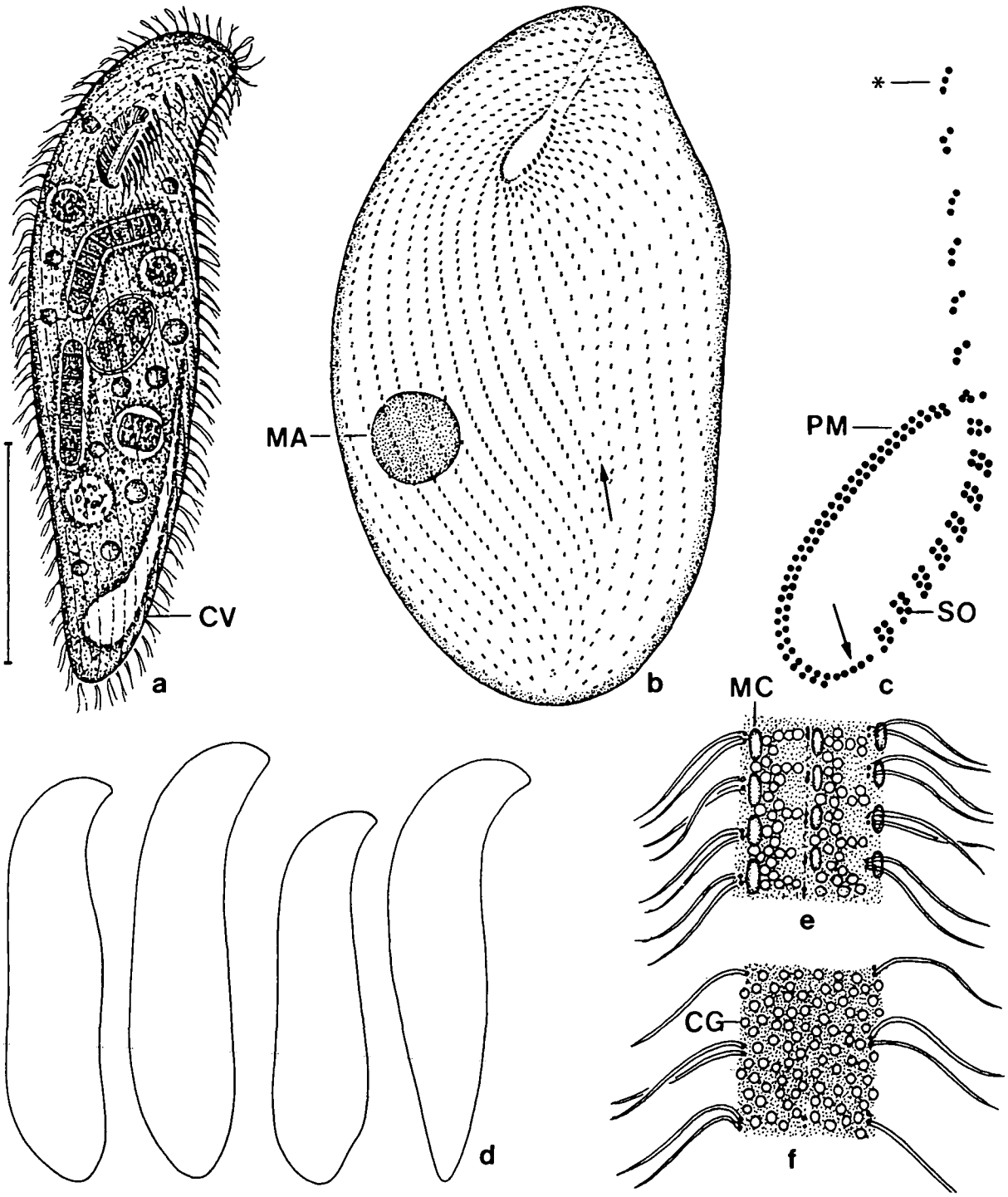


Fig. 213a–f. *Rostrophrya namibiensis namibiensis* from life (a, d–f) and after silver carbonate impregnation (b, c). **a:** Ventral view of a representative specimen with ingested cyanobacteria filaments. **b:** Somatic and oral ciliary pattern (redrawn from squashed specimen). Arrow marks shortened ciliary rows producing inconspicuous postoral suture. **c:** Fine structure of the oral ciliary pattern. Asterisk marks adoral organelles in preoral suture, each composed of three basal bodies. The uncinate portion of the paroral has only the proximal basal bodies ciliated (arrow). The same pattern occurs in → *R. namibiensis maldivensis*, only the number of adoral organelles is slightly different. **d:** Shape variability. **e, f:** Surface views showing cortical granulation on ventral and dorsal side. CV – contractile vacuole, CG – cortical granules, MA – macronucleus, MC – mitochondria, PM – paroral membrane, SO – slope adoral organelles. Scale bar 40 µm.

15 adoral organelles, of which about nine insert on left slope of vestibulum and six in preoral suture, which is thus only about half as long as in → *R. namibiensis maldivensis*. Slope organelles each composed of six basal bodies forming minute rectangles; distal basal body pair slightly dislocated posteriad. Rostrum organelles minute, each consisting of only three basal bodies forming small, oblique rows surrounded by faintly impregnated material producing small process at left anterior corner of organelles (Fig. 213c; 432e). Oral basket recognizable neither in vivo nor in silver carbonate preparations.

Occurrence and ecology: To date found only at three sites (53, 54, 70) in Namibia, all highly saline, indicating that it prefers saline soils.

Rostrophrya namibiensis maldivensis nov. sspec. (Fig. 214a–i; 433a–i, 434a; Table 194)

Diagnosis: Body with indentations and convexities, rostrum angular, posterior end usually inflated and widely rounded; length:width ratio about 3:1. On average 42 somatic ciliary rows.

Type location: Coastal soil near the village of Hembadoo, North Male Atoll, Maldives, 04°N 74°E.

Etymology: Named after the country discovered.

Description: Size 100–160 × 35–60 µm in vivo, usually about 130 × 42 µm, length:width ratio 2.3–3.7:1, on average 3:1. Shape elongate ellipsoidal, dorsoventrally slightly flattened, often rather irregular, that is, with some small indentations and convexities; usually gradually broadening from anterior to posterior, rear end thus widely rounded, preoral portion narrows to obliquely truncate rostrum, making the organism easily recognizable (Fig. 214a, h, i); rostrum, however, rounded in silver preparations, obviously due to insufficient preservation (Fig. 214b, e). Very flexible, slightly decreasing in length and becoming broader when touching an obstacle during forward gliding (Fig. 214h, i), and up to 50% contractile under slight cover glass pressure. Macronucleus subequatorial, broadly ellipsoidal (22 × 14 µm; Table 194), with an about 0.7 µm thick membrane containing micronucleus 3–4 µm across; nucleolus reticular (Fig. 433d). Contractile vacuole subterminal at left margin of cell, occupies posterior end when filled completely and bulges cell margin just before emptying; with single, conspicuous collecting canal extending to level of oral apparatus at left body margin. Cytopyge in posterior end slightly left of midline; faecal mass slimy containing some crystals (Fig. 214a, h). Cortex very flexible, contains numerous colourless mucocysts about 0.5 µm across; on ventral side, mucocysts form necklet-like strand between each two kineties and clusters around individual kinetids; on dorsal side, they are rather irregularly arranged (Fig. 214f, g; 433a). Cytoplasm colourless and finely granulated, cells usually very transparent; contains some lipid droplets 3–8 µm across mainly in posterior half of cell; not vacuolized as in *R. terricola* FOISSNER, 1993c. Food vacuoles bright and with indeterminable content. Glides rather rapidly on microscope slide and soil particles, showing a great flexibility; swims slowly by rotation about main body axis.

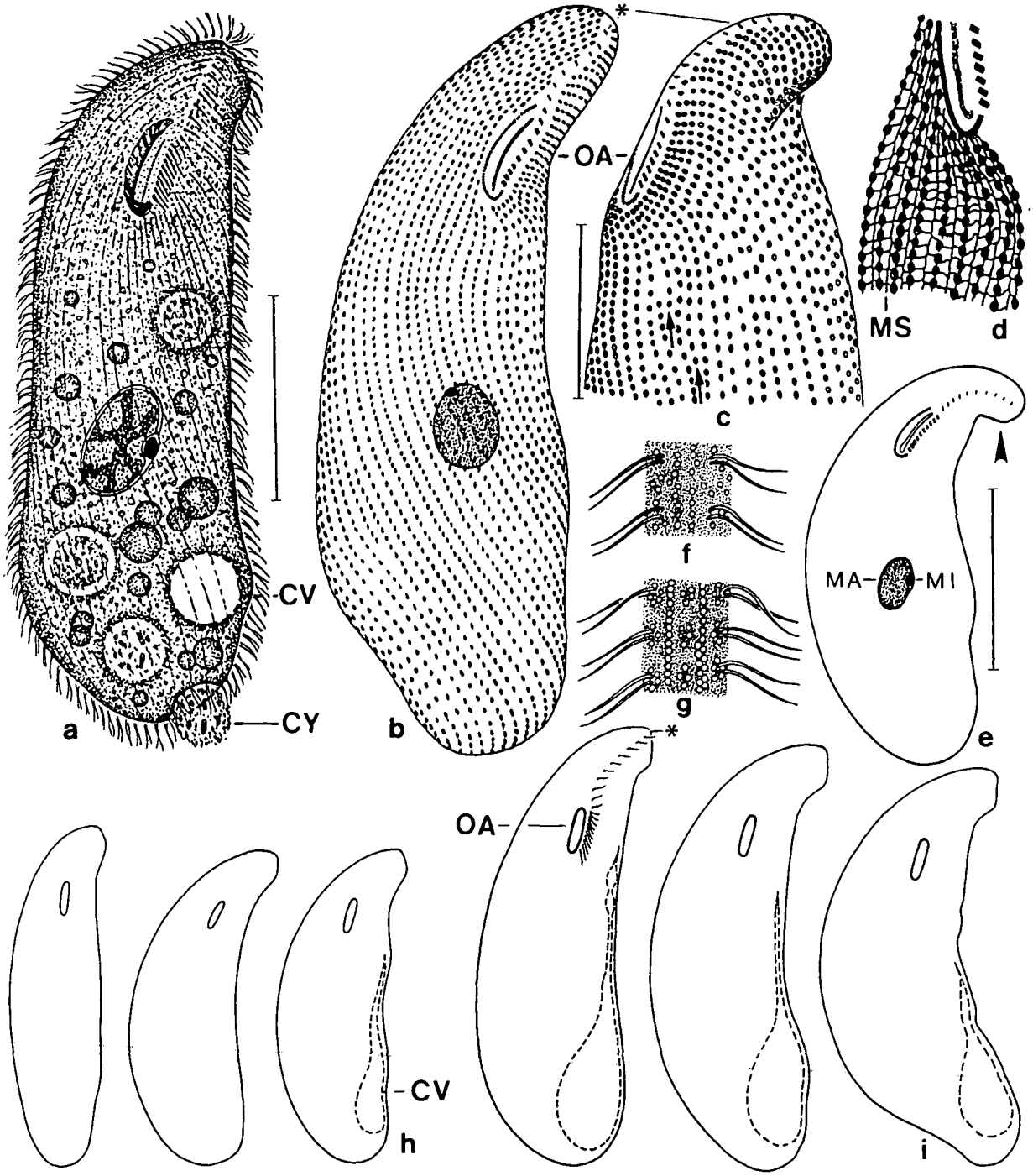


Fig. 214a–i. *Rostrophrya namibiensis maldivensis*, type population from live (a, f–i) and after CHATTON-LWOFF silver nitrate impregnation (b–e). For details on oral structures, see figure 213c under → *R. namibiensis namibiensis* and figures 433f, h. Asterisks mark minute adoral organelles in preoral suture. **a:** Ventral view of a representative specimen. **b:** Ciliary pattern of ventral side. **c:** Anterior left lateral portion of cell. Note shortened ciliary rows (arrows) producing inconspicuous postoral suture. **d:** Silverline system. **e:** A representative specimen with distinct, angular rostrum (arrowhead). **f, g:** Cortical granulation on dorsal and ventral side. **h, i:** Two specimens redrawn from video records. The left figure of each series shows the fully extended, gliding cell; the middle and right figures demonstrate the changes in body shape and length when the specimens touch an obstacle. CV–contractile vacuole, CY – faecal mass leaving cytopyge, MA – macronucleus, MI – micronucleus, MS – median silverline, OA – oral apparatus. Scale bars 40 µm (a, b), 30 µm (c), 60 µm (e).

Cilia only about 7 µm long in vivo, paired throughout, even on less densely ciliated dorsal side, form about 42 rows arranged as in other members of genus (FOISSNER 1993c), that is, slightly spiral producing distinct preoral suture containing adoral organelles; kineties in rather deep furrows on right side and often somewhat irregular at various sites of cell, possibly due to small injuries. Some shortened ciliary rows commence along posterior left half of oral opening and generate rather indistinct postoral suture, where left and right side kineties abut. Postoral kinetids along left margin of oral opening and preoral suture very regularly arranged forming crossed pattern (Fig. 214a–c; 433e–i). Silverline system platyophryid, as described in remarks on species diagnosis (Fig. 214d; 433b, c).

Table 194. Morphometric data on *Rostrophrya fenestrata* (RF), *Rostrophrya namibiensis namibiensis* (RN), and *Rostrophrya namibiensis maldivensis* (RM).

Characteristics [a]	Species	Method [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	RM	CHL	128.1	129.0	14.9	4.3	11.6	106.0	155.0	12
Body, width	RM	CHL	45.8	43.0	7.3	2.1	15.9	35.0	62.0	12
Anterior body end to paroral, distance	RM	CHL	26.3	26.0	5.2	1.5	20.0	20.0	36.0	12
Anterior end to macronucleus, distance	RM	CHL	73.2	72.0	6.7	2.0	9.1	65.0	85.0	11
Oral opening, length	RM	CHL	17.4	17.5	2.7	0.8	15.8	14.0	22.0	12
Oral opening, width	RM	CHL	5.1	5.0	0.8	0.2	15.5	4.0	7.0	12
Macronucleus, length	RM	CHL	17.3	16.0	2.5	0.7	14.6	15.0	22.0	12
Macronucleus, width	RM	CHL	9.5	10.0	3.0	0.9	31.5	10.0	14.0	12
Micronucleus, diameter	RM	CHL	2.8	3.0	–	–	–	2.0	3.0	8
Somatic kineties, number	RF	SC	18.9	19.0	–	–	–	18.0	19.0	7
	RN	SC	31.8	31.5	1.4	0.3	4.5	30.0	35.0	18
	RM	CHL, SC	42.3	42.0	3.3	1.0	7.7	37.0	46.0	11
Kinetids in a dorsolateral kinety, number	RF	SC	38.4	40.0	3.9	1.7	10.2	33.0	43.0	5
	RN	SC	61.7	60.0	7.5	2.8	12.1	50.0	75.0	7
	RM	SC	92.0	95.0	12.5	3.8	13.6	70.0	110.0	11
Adoral organelles, total number	RF	SC	9.1	9.0	–	–	–	9.0	10.0	8
	RN	SC	15.2	15.0	1.0	0.2	6.5	14.0	17.0	18
	RM	CHL, SC	21.0	22.0	2.6	1.2	12.6	17.0	24.0	5
Slope adoral organelles, number	RF	SC	4.2	4.0	–	–	–	4.0	5.0	10
	RN	SC	8.9	9.0	0.8	0.2	9.0	8.0	10.0	18
	RM	CHL, SC	10.8	12.0	1.6	0.5	15.2	8.0	13.0	13
Rostrum adoral organelles, number	RF	SC	5.0	5.0	0.0	0.0	0.0	5.0	5.0	8
	RN	SC	6.2	6.0	0.5	0.1	8.8	5.0	7.0	18
	RM	CHL, SC	10.2	10.0	1.1	0.5	10.7	9.0	12.0	5
Paroral dikinetids, number (monokinetids at left end counted as dikinetids)	RF	SC	21.2	20.0	2.4	0.8	11.3	18.0	25.0	9
	RN	SC	42.3	42.0	2.7	0.9	6.4	40.0	47.0	9
	RM	SC	56.7	57.5	6.3	2.6	11.0	46.0	64.0	6

[a] Data based on silver-impregnated and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CHL – CHATTON-LWOFF silver nitrate impregnation, CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SC – silver carbonate impregnation, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Oral opening in main body axis at base of rostrum, commences about 17 µm back from anterior end; elongate elliptical, that is, 17 × 5 µm in silver nitrate preparations. Details of ciliary pattern as shown in figure 213c of → *R. namibiensis namibiensis*. Paroral membrane on right vestibular slope, uncinate, that is, surrounds posterior end of oral opening, composed of about 57 dikinetids bearing 4–5 µm long cilia; uncinate portion either composed of monokinetids or of dikinetids having only the proximal basal body ciliated. About same number (10–11) of adoral organelles each on left slope of vestibulum and in preoral suture. Slope organelles each composed of six basal bodies forming minute rectangles having small, fibrillar process at left posterior corner; cilia within individual organelles of different length, that is, 2–5 µm. Rostrum organelles minute, each consisting of only three basal bodies forming small, oblique rows surrounded by faintly impregnated material producing small process at anterior left corner of organelles (Fig. 214a–c, e, i; 433e–i, 434a).

Occurrence and ecology: The sample from type location was collected by Dr. Wolfgang PETZ (Salzburg University) about 15 m inshore in a coco forest. The dark grey, highly saline soil had pH 7.5 and was mixed with surface litter and roots from grasses and shrubs. *Rostrophrya namibiensis maldivensis* was found, inter alia, also at the highly saline Namibian sites (11) and (54), indicating that it prefers saline soils or is euryhaline.

Rostrophrya fenestrata nov. spec. (Fig. 215a–h; 434b–l, 442j–l; Table 194)

Diagnosis: Size about 85 × 15 µm in vivo, length:width ratio thus 6:1. Body elongate ellipsoidal and distinctly curved, both ends narrowly rounded. 19 somatic kineties on average. Oral aperture minute, that is, 5 × 3 µm; 9 adoral organelles on average, of which 4 are on left vestibular slope.

Type location: Highly saline crust soil on quartz pieces in the coastal National Park near Lüderitz, Namibia, 26°40'S 15°10'E (site 11 in figure 2 and chapter 2.1.2).

Etymology: The Latin noun *fenestrata* (window) does not refer to the species as such, but to its peculiar habitat, that is, the "window" fauna and flora developing under transparent quartz pieces (for details, see site description in chapter 2.1.2).

Description: Size 70–110 × 15–20 µm in vivo, usually about 85 × 15 µm, length:width ratio 5–6:1, usually near 6:1. Shape regular as in *R. terricola* FOISSNER, 1993c, that is, margins without indentations or convexities; highly variable but often more or less distinctly curved (maintained even in silver carbonate preparations; Fig. 434b–g) and invariably very slender, even in well-fed specimens; rostrum morphologically indistinguishable. The following shape variants were recorded: slightly to distinctly curved and narrowing posteriorly with both ends narrowly rounded (Fig. 215a, e, h); slightly to distinctly curved and linear with both ends narrowly rounded (Fig. 215d); slightly sigmoidal and linear with anterior end narrowly rounded and pointed (Fig. 215f); slightly curved and narrowed posteriorly with both ends posterior pointed (Fig. 215g). Flattened dorsoventrally up to 1.5:1, very flexible and even contractile by up to 25% when touching an obstacle, showing characteristic posterior knee (Fig. 215d, e, g, h). Macronucleus in body centre, ellipsoidal, with thick membrane and reticular nucleolus. Micronucleus difficult to recognize in vivo, attached to macronucleus in silver carbonate preparations. Contractile vacuole subterminal at left margin of cell, with single

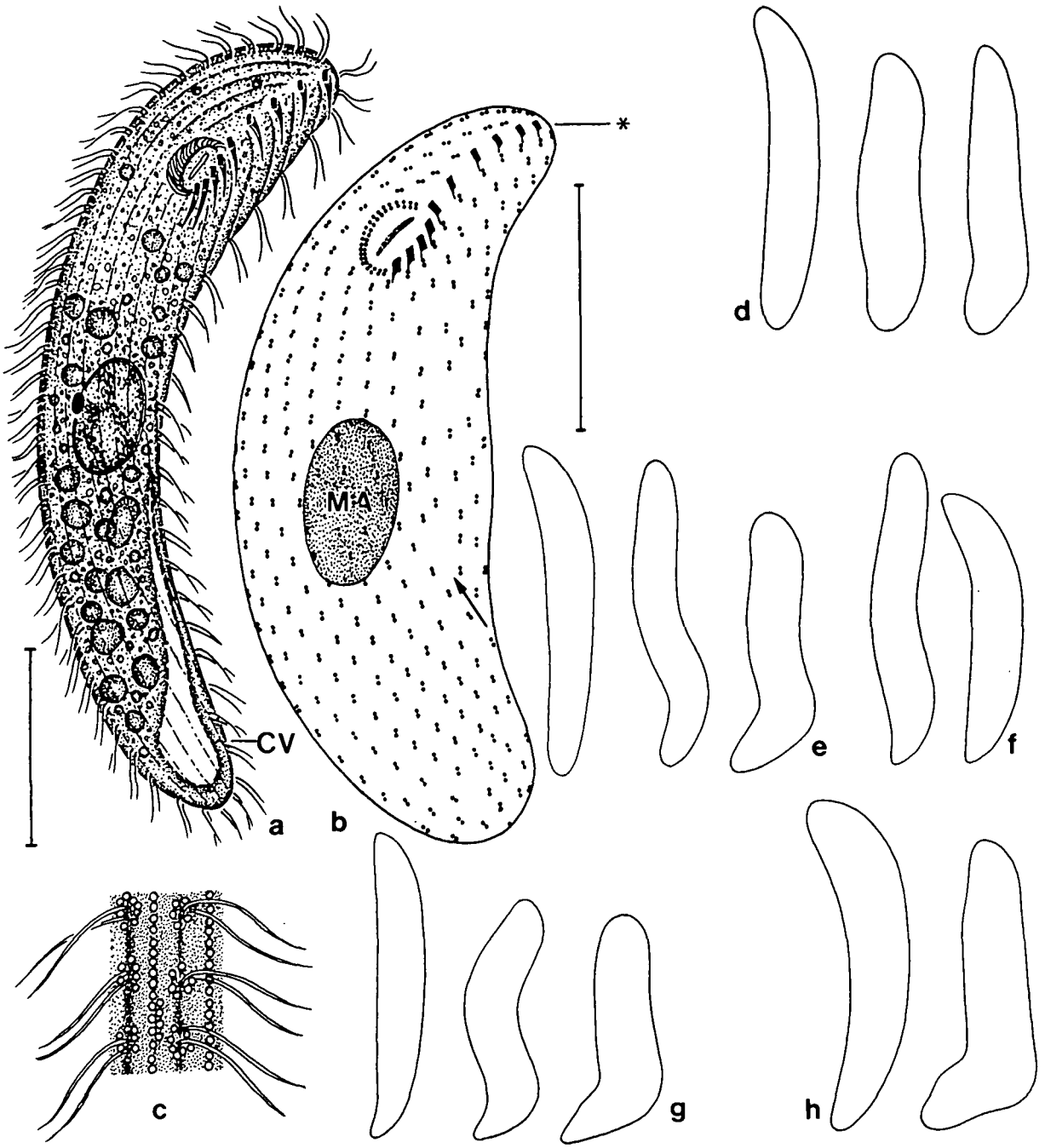


Fig. 215a–h. *Rostrophrya fenestrata* from life (a, c, d–h) and after silver carbonate impregnation (b). **a, b:** Ventral view of representative specimens. Shape of cell shown in figure (a) redrawn from a video record. Note shrinkage of prepared specimen (b), redrawn from Fig. 434d. Arrow marks postoral suture. Asterisk denotes preoral (suture) adoral organelles. **c:** Surface view showing mucocyst pattern of ventral side. **d–h:** Shape variability of extended (first illustration in each series), partially contracted (second illustration in each series), and fully contracted (third illustration in each series) specimens. Redrawn from video records. Note knee-shaped posterior body portion in fully contracted cells, a very characteristic feature of this species. CV – contractile vacuole, MA – macronucleus. Scale bars (a, b) 20 µm.

collecting canal extending to mid-body. Cortex very flexible, contains numerous colourless mucocysts about 0.5 µm across; mucocyst pattern as in → *R. namibiensis maldivensis*, that is, a necklet-like strand between each two kineties on right side, while rather irregular on left (Fig. 215c; 442j–l). Cytoplasm colourless, contains numerous minute lipid droplets about 1 µm across and, in posterior half, many slightly irregular fat inclusions 3–4 µm across; not vacuolized as in *R. terricola* FOISSNER, 1993c. Slowly gliding on water surface, microscope slide and soil particles showing great flexibility.

Cilia paired throughout, even on less densely ciliated dorsal side, form 18–19 rows arranged as in other members of genus (FOISSNER 1993c), that is, slightly spiral forming distinct preoral suture containing adoral organelles; some shortened ciliary rows commence along left posterior margin of oral opening and produce rather distinct postoral suture, where left and right side kineties abut. Ciliature not polymerized underneath left vestibular slope (Fig. 215a, b; 434b–i). Silverline system not studied.

Oral opening in main body axis and distinctly subterminal, that is, at border of first and second sixth of body, conspicuously small, viz. about 5 × 3 µm in vivo (Fig. 215a, b; 434b, d–i). Paroral membrane on right slope of vestibulum, uncinate, that is, surrounds posterior end of oral opening, composed of dikinetids throughout bearing 4 µm long cilia. 9–10 minute, rectangular adoral organelles, of which 4–5 insert along left slope of vestibulum and 5–6 in preoral suture; slope and preoral adoral organelles of same size and thus possibly also of same structure, have minute process (fibre?) at left posterior corner. Oral basket recognizable neither in vivo nor in silver carbonate preparations.

Occurrence and ecology: Occurs at several moderately to highly saline sites of Namibia, including the Dune Sea Namib and the Etosha Pan margin (Table 4). Furthermore, we found *R. fenestrata* in Saudi Arabia, where it occurred also in a highly saline (21‰, pH 6.7) soil sample from near the village of Alqasab, about 130 km northeast of Riyadh. However, the Saudi Arabian specimens are larger, that is, have about 25 ciliary rows, 12 adoral organelles and 30 paroral dikinetids; thus, they might represent a distinct subspecies. Likely, *R. fenestrata* prefers saline, extreme soils.

Comparison with related species: *Rostrophrya fenestrata* is much more slender (5–6:1 vs. ≤ 4:1) and has distinctly fewer ciliary rows (20 vs. > 30) and adoral organelles (10 vs. ≥ 15) than any other described species of the genus (FOISSNER 1993c). Furthermore, it lacks a morphological rostrum, the postoral polymerization of the ciliature, "monokinetids" in the uncinate portion of the paroral, and (possibly) a structural differentiation of the slope and preoral adoral organelles. Certainly, the morphological differences look inconspicuous but might be of greater importance than presently assumed, especially the lack of the postoral polymerization of the ciliature and of "monokinetids" in the uncinate portion of the paroral (cp. → *R. namibiensis maldivensis*).

Rostrophryides africana FOISSNER, 1987

We split this species into two subspecies according to distinct morphometric differences of the Kenyan and the Namibian populations.

Improved diagnosis: Size 40–70 × 20–30 µm in vivo. About 15–26 somatic ciliary rows, which form a typical or modified postoral pseudomembrane. 5–9 adoral organelles.

Rostrophryides africana africana FOISSNER, 1987c **nov. stat.**

Diagnosis (from FOISSNER 1987c): Size about 40–60 × 20–30 µm in vivo. About 10–15 somatic ciliary rows, which form a typical postoral pseudomembrane. 5–7 adoral organelles.

Locus classicus: Highly saline soil from margin of Lake Nakuru in Kenya (East Africa).

Remarks: The features of the type population were confirmed on reinvestigation of specimens from a saline, sandy soil from the coast of Florida, USA (FOISSNER 1993c).

Rostrophryides africana etoschensis **nov. sspec.** (Fig. 216a–f; Table 195)

Diagnosis: Size about 60 × 25 µm in vivo. On average 23 somatic ciliary rows, which form a modified postoral pseudomembrane composed of postoral kinety fragments with more than two dikinetids. Usually 8 adoral organelles.

Type location: Highly saline soil from margin of Etosha Pan, Namibia, 18°50'S 16°30'E (site 67 in figure 2 and chapter 2.1.2).

Etymology: Named after the region discovered.

Description: Size 50–70 × 20–30 µm in vivo, usually about 60 × 25 µm. Ellipsoidal with anterior left end bluntly pointed and posterior broadly rounded (Fig. 216a, d); slightly to distinctly flattened laterally depending on nutrition state. Nuclear apparatus in middle third of cell, slightly subequatorial on average (Table 195). Micronucleus tightly attached to macronucleus and thus very likely in its perinuclear space, as in other members of order (FOISSNER 1993c). Contractile vacuole and excretory pore subterminal on ventral side (Fig. 216a, b, d). Cortex colourless and very flexible; cortical granules (mucocysts) likely present but not studied. Cytoplasm with some lipid droplets and food vacuoles containing cyanobacterial and ciliate (?) remnants. Glides rather rapidly on microscope slide.

Somatic and oral ciliary pattern similar as in *R. africana africana*, mainly differing in morphometric details (Table 195). Thus, we concentrate on the postoral pseudomembrane, which is prominent but rarely consists of pairs of dikinetids, as is usual (Fig. 216g), but of three or more dikinetids producing many irregularly shortened postoral ciliary rows (Fig. 216b–f). Adoral organelle band rather conspicuous, two organelles in minute preoral suture.

Occurrence and ecology: To date found only at type location, a highly saline soil. All records of *R. africana africana* are from saline soil habitats too, indicating that *R. africana* is possibly restricted, or at least prefers saline, terrestrial habitats. Distribution is likely cosmopolitan (FOISSNER 1998a).

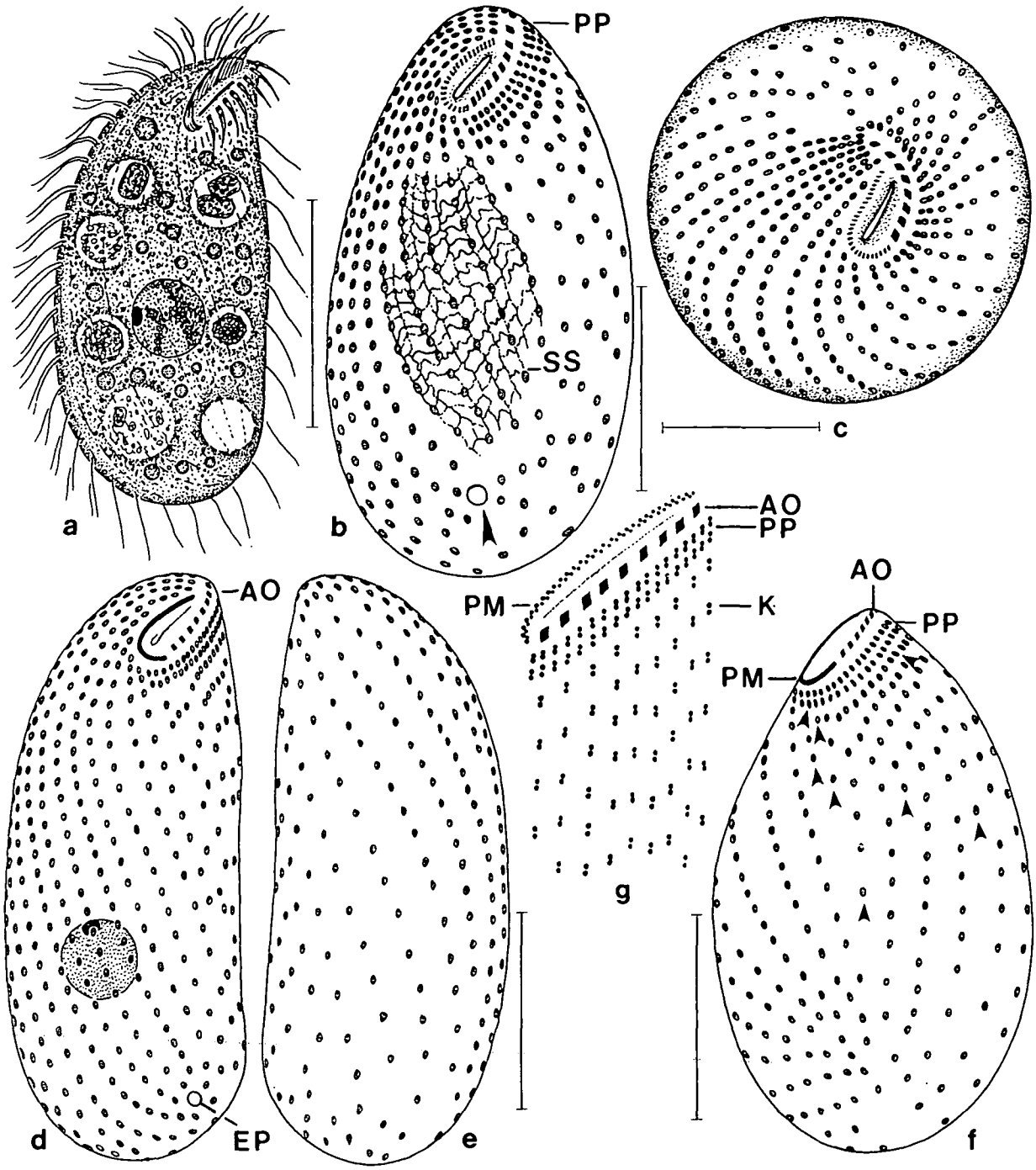


Fig. 216a–q. *Rostrophryides africana etoschensis* from life (a) and after CHATTON-LWOFF silver nitrate impregnation (b–f). **a:** Right lateral view of a representative specimen. **b:** Ciliary pattern and silverline system (only partially shown) of ventral side. Arrowhead marks excretory pore. **c:** Anterior polar view of an encysting specimen. **d, e:** Ciliary pattern of right and left side of same specimen. **f:** Ciliary pattern of left side, where many ciliary rows are shortened (arrowheads). **g:** Scheme of a postoral pseudomembrane. Between each two unshortened ciliary rows a short row, consisting of only two dikinetids, is implanted, causing a densely ciliated postoral band, the "postoral pseudomembrane". A densely ciliated postoral band is present also in *R. africana etoschensis*, but usually composed of three or more dikinetids. AO – adoral organelle band, EP – excretory pore of contractile vacuole, K – left side somatic kinety, PM – paroral membrane, PP – postoral pseudomembrane, SS – silverline system. Scale bars 30 µm (a), 20 µm (b, d, e, f), 10 µm (c).

Table 195. Morphometric data on *Rostrophryides africana etoschensis* (upper line) and *R. africana africana* (lower line; USA population from FOISSNER 1993c).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	53.6	54.0	5.4	1.3	10.0	45.0	64.0	16
	46.3	46.0	3.8	1.3	8.3	40.0	52.0	9
Body, width	26.9	27.0	3.4	0.8	12.5	21.0	32.0	16
	20.8	20.0	1.6	0.5	7.9	18.0	23.0	9
Anterior body end to paroral vertex, distance	8.9	9.0	1.2	0.3	12.9	7.0	11.0	16
	–	–	–	–	–	–	–	–
Anterior body end to macronucleus, distance	28.7	27.0	5.8	1.5	20.3	22.0	40.0	16
	–	–	–	–	–	–	–	–
Macronucleus, length	8.2	8.0	1.2	0.3	14.3	6.0	10.0	16
	6.3	6.0	0.5	0.2	8.2	6.0	7.0	6
Macronucleus, width	7.8	8.0	1.1	0.3	14.5	5.0	10.0	16
	6.3	6.0	0.5	0.2	8.2	6.0	7.0	6
Oral field, length [b]	8.8	9.0	1.0	0.3	11.1	8.0	11.0	16
	6.3	6.0	0.8	0.3	13.0	6.0	8.0	6
Oral field, width [b]	4.4	4.0	–	–	–	4.0	5.0	16
	3.5	3.5	–	–	–	3.0	4.0	6
Adoral organelles, number	8.2	8.0	0.5	0.1	6.6	7.0	9.0	16
	5.4	5.0	–	–	–	5.0	6.0	7
Paroral dikinetids, number	26.6	26.0	2.7	0.9	10.3	22.0	31.0	9
	–	–	–	–	–	–	–	–
Somatic kineties, number	23.5	23.0	1.3	0.3	5.8	21.0	26.0	16
	10.3	10.0	–	–	–	10.0	11.0	6
Kinetids in kinety 4, number	29.4	30.0	3.4	0.9	11.7	24.0	37.0	16
	–	–	–	–	–	–	–	–
Kinetids in a left-side kinety, number	17.4	17.0	3.0	0.8	17.1	13.0	25.0	16
	–	–	–	–	–	–	–	–

[a] Data based on CHATTON-LWOFF silver nitrate-impregnated and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Measured as distance from anterior body end to proximal vertex of paroral membrane, respectively, from outer margin of paroral to outer margin of adoral organelle band.

Generic assignment: We classify the Namibian population in *Rostrophryides* because its overall organization is most similar to *R. africana*, type of genus (FOISSNER 1993c). However, the postoral pseudomembrane, although very distinct, lacks the usual structure shown in figure 216g. In this feature, the Namibian population is similar to *Woodruffides* and *Woodruffia* because most of the postoral kineties consist of more than two kinetids. It seems that the postoral pseudomembrane is a difficult (weak) genus character. On the other hand, we would dislike to synonymize these genera because then, for instance, the small *Rostrophryides africana* would fall into the same genus as the large *Woodruffides metabolicus*. Or species with platyophryid (*Rostrophryides*, *Woodruffides*) and colpodid (*Woodruffia*)

silverline system would be in the same genus, if all genera are put together. Further studies are necessary.

Comparison with related species: The population from the Etosha Pan highly resembles *Rostrophryides africana*, differing from that species mainly by the higher number of ciliary rows (23 vs. 10–15) and the lack of a typical postoral pseudomembrane (see above). On the other hand, the dense postoral ciliature is a distinct difference to the few (~8) kinetid quadruplets present in *R. africana*, as described in FOISSNER (1993c). Certainly, these differences are partially related to the larger size of the Pan specimens (54 × 27 µm vs. 46 × 20 µm in silver-prepared specimens). Thus, we classify the Namibian population as a subspecies only.

Kuklikophrya ougandae (DRAGESCO, 1972) FOISSNER, 1993c (Fig. 217a–p; 435a–u, 436a–g; Table 196)

Nomenclature and synonymy: See FOISSNER (1993c). The main genus features are the curved postoral kineties and the paroral membrane, which is open only at left anterior corner, where the adoral organelle band commences. We do not neotypify *K. ougandae*, although type material has not been mentioned previously (FOISSNER 1993c), because it has a firm identity and our observations largely agree with the literature data. Voucher slides from our material have been deposited (Table 1).

Description of Namibian population: Most in vivo observations are from specimens of a non-flooded Petri dish culture from site (67). We could cultivate *K. ougandae* for some months with *Oscillatoria* sp., but growth was slow and did not produce high densities.

Size 100–170 × 50–90 µm in vivo, usually about 140 × 70 µm. Shape also highly variable, as already mentioned by DRAGESCO (1972), usually, however, *Chilodonella*-like, that is, with rather conspicuous rostrum anteriorly left of oral opening and posteriorly, producing a more or less distinct sigmoidal outline (Fig. 217a, l, m); both, rostrum and posterior pointing rather fragile and thus only partially preserved in preparations (Fig. 217b, k). Highly flexible and 2–3:1 dorsoventrally flattened, depending on nutrition conditions; strongly flattened specimens look like swimming leaves. Nuclear apparatus in middle third of cell, on average subequatorial, anchored to the cortex by a fibrous basket with long extensions, a unique property within the class (Fig. 217 l; 435 l). Macronucleus slightly ellipsoidal, about 20 µm across in vivo, with reticular nucleolus. Micronucleus lenticular, about 4 µm across in vivo, tightly attached to and thus very likely within perinuclear space of macronucleus (Fig. 217a, k; 435c, 436a). Contractile vacuole not registered, near posterior body end in Austrian specimens; excretory pore not impregnated. Cortex flexible and bright due to many scattered mucocysts (Fig. 217i). Mucocysts difficult to recognize in vivo because of similar shape (globular) and size (1 µm) as mitochondria and easily extruded, for instance, when cells are slightly squeezed by the cover glass or fixed for scanning electron microscopy; stain red and become extruded when methyl green-pyronin is added, forming voluminous reticulum around cell (Fig. 217i, j; 435f–j, r). Cytoplasm colourless, cells, however, greenish due to many food vacuoles with filamentous cyanobacteria ingested as rather long pieces soon breaking into about 5 µm-sized

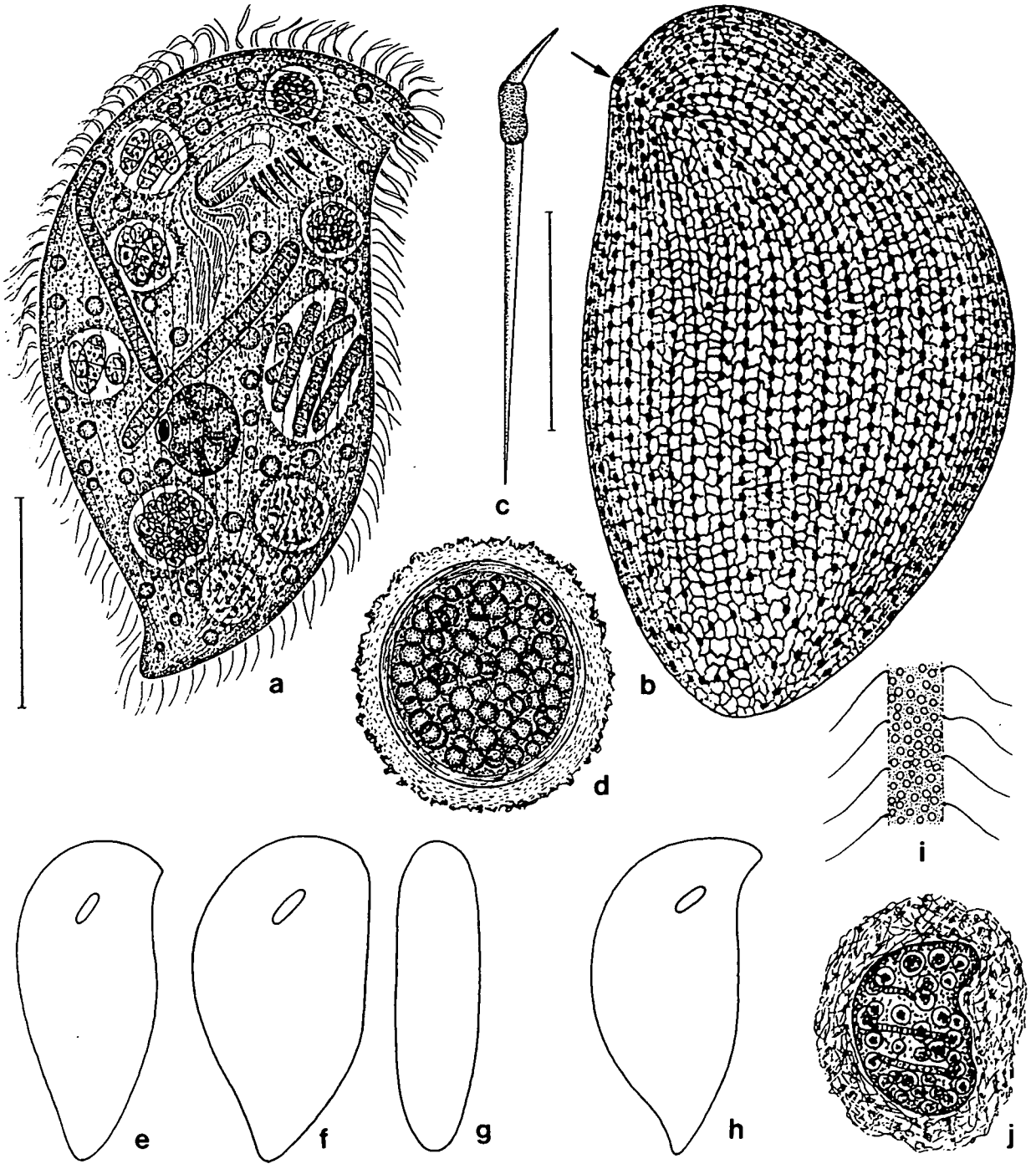


Fig. 217a–j. *Kuklikophrya ougandae*, Namibian (a, b, d, i, j), Kenyan (e–g), and Austrian (c, h) specimens from life (a, c–h), after CHATTON-LWOFF silver nitrate impregnation (b), and methyl green-pyronin staining (j). **a:** Ventral view of a representative specimen with many filamentous cyanobacteria in various stages of digestion. **b:** Dorsal view showing platyophryid silverline system and suture caused by the adoral organelle band (arrow). **c:** Pharyngeal rod, length 25 µm. This kind of rod was seen only in Austrian and, very recently, also Venezuelan specimens. **d:** Early division cyst with many greenish food vacuoles and a conspicuous mucous coat, diameter about 110 µm. **e–g:** Shapes of Kenyan specimens, length 90–100 µm; figure (g) is the lateral view of the specimen shown in figure (f). **h:** Austrian specimen. **i:** Surface view showing many faint, globular mucocysts. **j:** When methyl green-pyronin is added, *K. ougandae* secretes a fibrous, mucous coat. Scale bars 50 µm (a) and 30 µm (b).

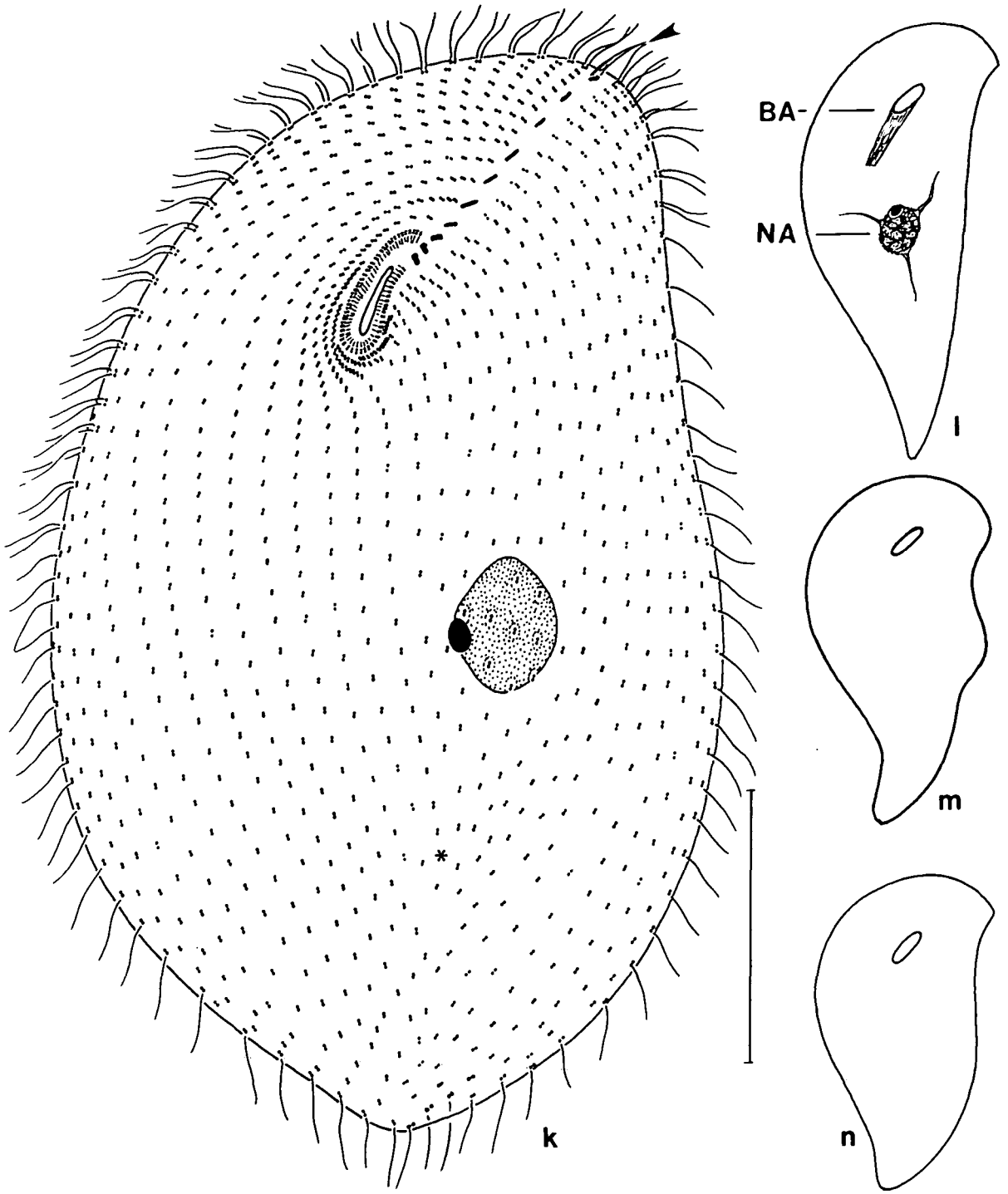


Fig. 217k–n. *Kuklikophrya ougandae*, Namibian (k–m) and Austrian (n) specimens from life (l–n) and after protargol (k) and silver carbonate (l, nuclear apparatus) impregnation. **k:** Somatic and oral ciliary pattern. The ciliary rows commence along the oral opening and the adoral organelle band. They consist of dikinetids, which have both basal bodies ciliated only in the anterior half of the cell; postorally, they form a rather distinct suture (asterisk). The adoral organelle band commences in the left anterior corner of the oral field and extends onto the dorsal side (arrowhead). Further details, see next plate. **l, m:** Rare shape variants. A fibrous coat with long branches encloses and anchors the nuclear apparatus in the cell (l). This is a unique property within the class (FOISSNER 1993c). **n:** The Austrian specimens have very similar shapes as the Namibian ones. BA – oral basket, NA – nuclear apparatus. Scale bar 30 µm.

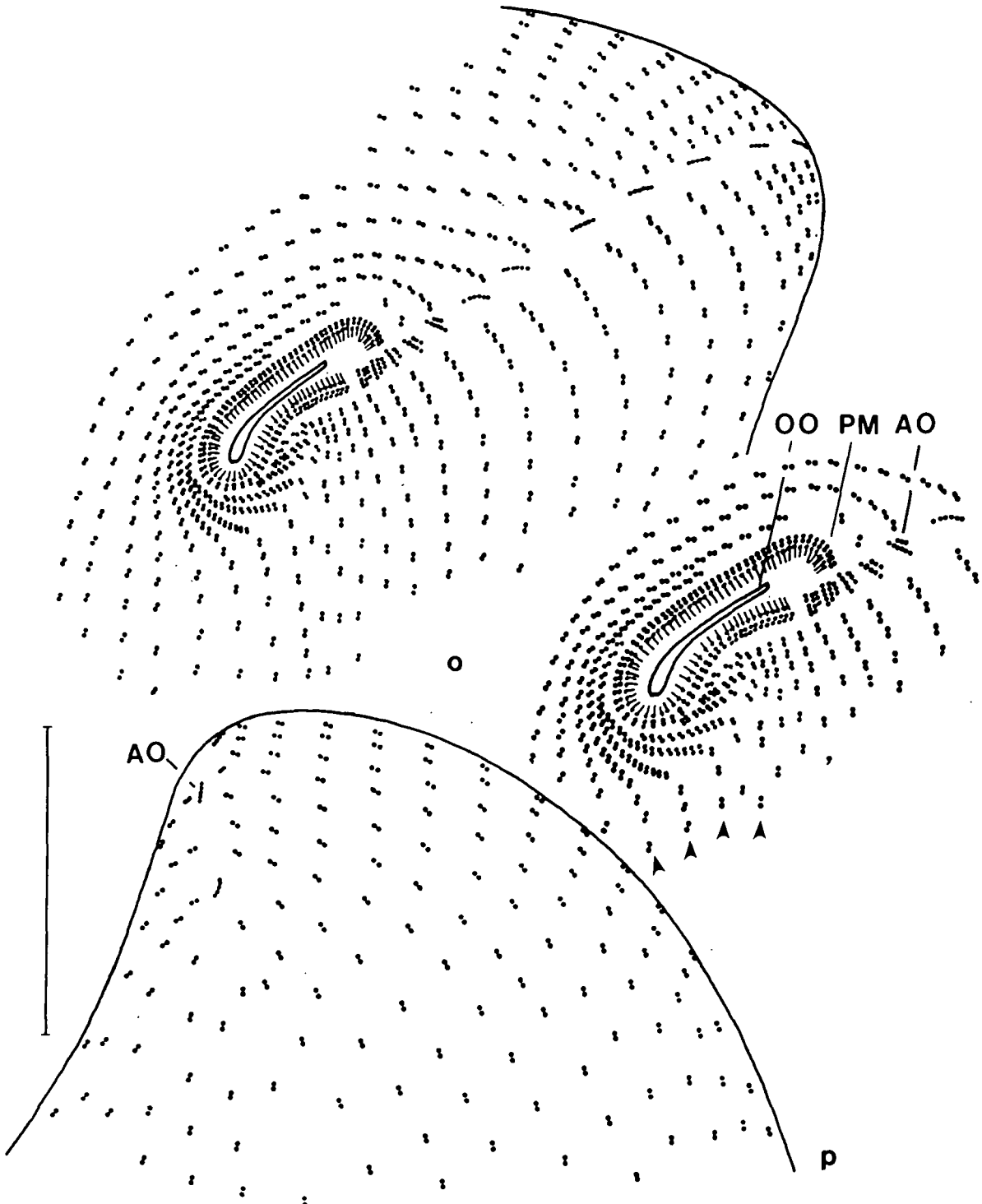


Fig. 217o, p. *Kuklikophrya ougandae*, ventral and dorsal oral ciliary pattern of a Namibian specimen after protargol impregnation. The genus is defined by two oral features: (i) the paroral membrane is open only at the anterior left corner, where the adoral band commences; (ii) some postoral ciliary rows (arrowheads), whose anterior portion is strongly bent and bears very closely spaced cilia, curve around the proximal oral vertex, producing a membranoid structure. Note that the proximal adoral organelles are composed of two to three rows of basal bodies, while the distal ones consist of a single row of cilia. AO – adoral organelles, OO – oral opening, PM – paroral membrane. Scale bar 20 μm.

fragments, several of which form food vacuoles 15–20 µm across; further the cytoplasm contains numerous 1–3 µm-sized lipid droplets and countless mucocysts revealed by methyl green-pyronin. Usually glides slowly between filamentous cyanobacteria showing great flexibility.

Somatic ciliature dikinetidal, cilia about 10 µm long in vivo, paired in oral region and right anterior half of cell, anterior basal body of dikinetids bare in other body regions (Fig. 217a, k). Ciliary rows commence along adoral band and oral opening, follow body curvature, and terminate in loosely ciliated posterior pole area (Fig. 217k; 435a, b, n, o). The following specializations occur in structure and pattern of rows: (i) the very densely ciliated anterior portion of some postoral rows sharply curves rightwards, forming membranoid structures around posterior oral vertex (Fig. 217k, o; 435e, l, p, q, s); (ii) the kinetids are very regularly arranged and form a special field between right dorsal body margin, adoral band, and oral opening (Fig. 217k; 435a, b, e, q, 436a, c); (iii) some rows are shortened postorally right of midline, producing a rather distinct postoral suture (Fig. 217k; 435a); (iv) the preoral suture, which contains the adoral band, traverses the rostrum and extends onto dorsal side, forming a minute but distinct dorsal suture (Fig. 217b, o, p; 435 l, m, o, 436d, e).

Oral field (area surrounded by paroral membrane) on average 34% back from peak of rostrum in midline of cell and obliquely orientated to main body axis, slightly depressed and elongate dumb-bell-shaped (3:1) due to concave left margin. Oral slit in centre of oral field, membranous, can open widely during ingestion of filamentous cyanobacteria. Oral basket rather inconspicuous, composed of fine rods originating from paroral dikinetids and forming stout, about 30 µm long funnel directed dorsally and posteriorly; impregnates faintly with protargol, but not with silver carbonate; individual rods with distinct apical inflation and tooth, both obviously overlooked previously (Fig. 217a, c, k, l; 435a, p, q, 436a). Oral ciliature composed of a paroral membrane and a long band of adoral organelles extending onto dorsal side of rostrum; additionally, the densely ciliated anterior region of some postoral ciliary rows forms some kind of circumoral ciliature, as described above (Fig. 217a, k, o, p; 435a, p, q–t, 436b, c, f, g). Paroral membrane slightly dumb-bell-shaped due to concave left side, surrounds almost entire oral field, except for break in left anterior corner, where the adoral band commences; composed of more or less distinctly zigzagging dikinetids associated with oral basket rods, as described above, and about 5 µm long cilia very closely spaced in left posterior portion of membrane. Adoral band composed of 13 organelles on average (Table 196), extends across rostrum onto dorsal side producing small suture, as described above; individual organelles proximally more narrowly spaced than distally and of different structure in various regions of band, details however difficult to recognize due to their small size: first two or three organelles in left anterior corner of oral field, that is, between ends of paroral, each very likely composed of three minute basal body rows, of which one is possibly unciliated; then follow three or four organelles, each composed of two basal body rows, of which the distal row is shorter and possibly unciliated; the distal organelles each consists of five to seven, about 7 µm long cilia in a single row.

Silverline system platyophryid throughout, as already described by DRAGESCO (1972); rather finely and irregularly meshed in loosely ciliated posterior pole area (Fig. 217b; 435o, u).

Reproduction: *Kuklikophrya ougandae* reproduces in globular to slightly ellipsoidal, green (due to the food vacuoles) division cysts producing four offspring. Interestingly, the cysts have a 1–3 µm thick, firm membrane covered by an about 10 µm wide mucous layer to

which bacteria and debris adhere (Fig. 217d; 435d, k; Table 196); furthermore, dividers excrete brownish food remnants remaining in the mucous layer.

Observations on a Kenyan population: In Kenya, *K. ougandae* occurred in dark grey, highly saline soil from the margin of the Nakuru Lake. The specimens were smaller (about 100 × 50 µm) than those from Namibia and the rostrum was occasionally lacking (Fig. 217e–g). The ciliary pattern was not studied in detail, but appeared very similar to that of the Namibian specimens.

Observations on an Austrian population: In autumn 1994, we were highly surprised to find *K. ougandae* in a saline, alkaline soil sample from the surroundings of Illmitz, Burgenland, eastern Austria (47°45'N 16°48'E). Although we looked for differences to the African populations, we could not find any! Even the number of adoral organelles (11–12, mostly 12, n = 9) and the complex oral and circumoral ciliature were highly similar, including the field of ordered kinetids in the right anterior body region (Fig. 217h, n; 436a–g).

Occurrence and ecology: To date found in Rwanda, Cameroun, Austria, Venezuela, and possibly also in Azerbaijan (FOISSNER 1993c). In Namibia, *K. ougandae* occurred, like in Kenya and Austria, only at the highly saline sites 57, 65, 67 (Table 4), indicating that it prefers such habitats. As an *Oscillatoria* feeder, *K. ougandae* is not a strictly terricolous species but an inhabitant of flooded soils and ephemeral pools.

Comparison with literature data: Our observations significantly supplement, but

Table 196. Morphometric data on Namibian specimens of *Kuklikophrya ougandae*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	128.2	123.0	19.5	5.9	15.2	105.0	155.0	11
Body, width	72.3	71.0	10.7	3.2	14.9	55.0	91.0	11
Anterior body end to macronucleus, distance	64.5	69.0	15.8	4.8	24.5	37.0	93.0	11
Peak of rostrum to proximal oral vertex, distance	43.6	42.0	6.9	2.0	15.9	33.0	55.0	11
Macronucleus, length	15.0	15.0	2.2	0.7	14.9	12.0	18.0	11
Macronucleus, width	12.0	12.0	1.8	0.6	15.4	9.0	15.0	11
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
Oral apparatus, length [b]	15.9	16.0	1.5	0.4	9.1	14.0	18.0	11
Oral apparatus, width [b]	4.8	5.0	0.6	0.2	12.5	4.0	6.0	11
Adoral organelles, number [c]	13.0	13.0	1.6	0.3	12.2	10.0	18.0	25
Somatic kineties, total number	53.4	53.0	4.9	1.7	9.2	47.0	60.0	8
Somatic kineties curving around proximal oral vertex, number	4.9	5.0	1.3	0.5	27.5	2.0	6.0	7
Division cysts, diameter (with mucous coat)	110.9	110.0	10.9	3.6	9.8	100.0	130.0	9
Division cysts, diameter (without mucous coat)	92.8	90.0	10.0	3.3	10.8	80.0	110.0	9

[a] Data based on mounted, protargol-impregnated (DRAGESCO's method), and randomly selected specimens from a pure culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Measured as outer margins of paroral membrane.

[c] Most values from silver carbonate-impregnated specimens.

basically agree with previous descriptions reviewed in FOISSNER (1993c); even the main morphometrics are very similar. Thus, conspecificity is beyond reasonable doubts. Of course, there are some differences, but all are inconspicuous or can be related to methodological peculiarities. DRAGESCO (1972), for instance, did not recognize the break in the paroral membrane because such details are difficult to see in silver nitrate preparations, and NJINE (1979c) illustrated all adoral organelles composed of two rows of basal bodies.

Woodruffides terricola FOISSNER, 1987c (Fig. 218a–p; 299, 300, 437a–n; Tables 197, 198)

Neotype material: Neotypified from cultivated specimens of Namibian site (55) according to reasons 1, 4, 6 given in chapter 2.4.2. The original description of *W. terricola* is based on live observations and transient silver carbonate impregnations; thus, no type material is available. As the species is rather similar to *W. metabolicus*, which also lacks type material, neotype slides with CHATTON-LWOFF silver nitrate-impregnated specimens have been deposited (Table 1).

Improved diagnosis (contains all new data described below): Size 110–200 × 40–100 µm in vivo, usually about 160 × 70 µm. 40–65, usually about 50 somatic ciliary rows. 13–28, usually about 21 adoral organelles. Paroral membrane curved, ends at proximal oral vertex.

Description of Namibian neotype population (Fig. 218a–d, g; 299, 300, 437a–c, f, g): The description is based on specimens from a multispecies culture set up in Eau de Volvic containing some crushed wheat grains to stimulate growth of indigenous food organisms, mainly *Colpoda cavicola* and *C. maupasi*.

Size 120–200 × 60–90 µm in vivo, usually about 160 × 70 µm, length:width ratio 1.8–3.5:1, on average 2.3:1 (Table 197). Shape highly variable, many intermediate forms occur between that of the type specimen (FOISSNER 1987c, Fig. 17a) and a "typical" *W. metabolicus* cell (FOISSNER 1987c, Fig. 22a) as in the population from the Galàpagos Islands (Fig. 218h–l). Usually, however, broadly rounded posteriorly and slightly narrowed and rostrate anteriorly; up to 2:1 flattened laterally, depending on nutrition state; anterior body half frequently rather distinctly twisted about main body axis, oral field thus turned upright when cell glides on left side (Fig. 218a). Nuclear apparatus in middle third of body, small compared to size of cell (Fig. 218a; 437a). Macronucleus about 25 × 15 µm in vivo, with distinct membrane and reticular nucleolus. Micronucleus minute and closely attached to macronucleus, very likely in perinuclear space, as in other members of order (FOISSNER 1993c). Contractile vacuole subterminal in ventral side, with several small and large excretory pores along ventral canal, strongly bulges cell surface (Fig. 218a, k) or occupies posterior body portion (Fig. 218b) when filled completely. Cortex very flexible, yellowish due to 0.7 µm-sized granules forming a stripe each between two ciliary rows (Fig. 218g). An opaque fibre, very likely a transverse microtubule ribbon (FOISSNER 1993c), left of ciliary rows (Fig. 218g; 437k). Cytoplasm of specimens from flourishing cultures packed with fat globules 1–7 µm across and large food vacuoles containing decaying *Colpoda cavicola*; smaller ciliates (e.g. → *Vorticella echini*) and other protists, such as flagellates and cysts of naked amoebae, are also ingested. Glides rather rapidly on microscope slide and organic debris showing great flexibility.

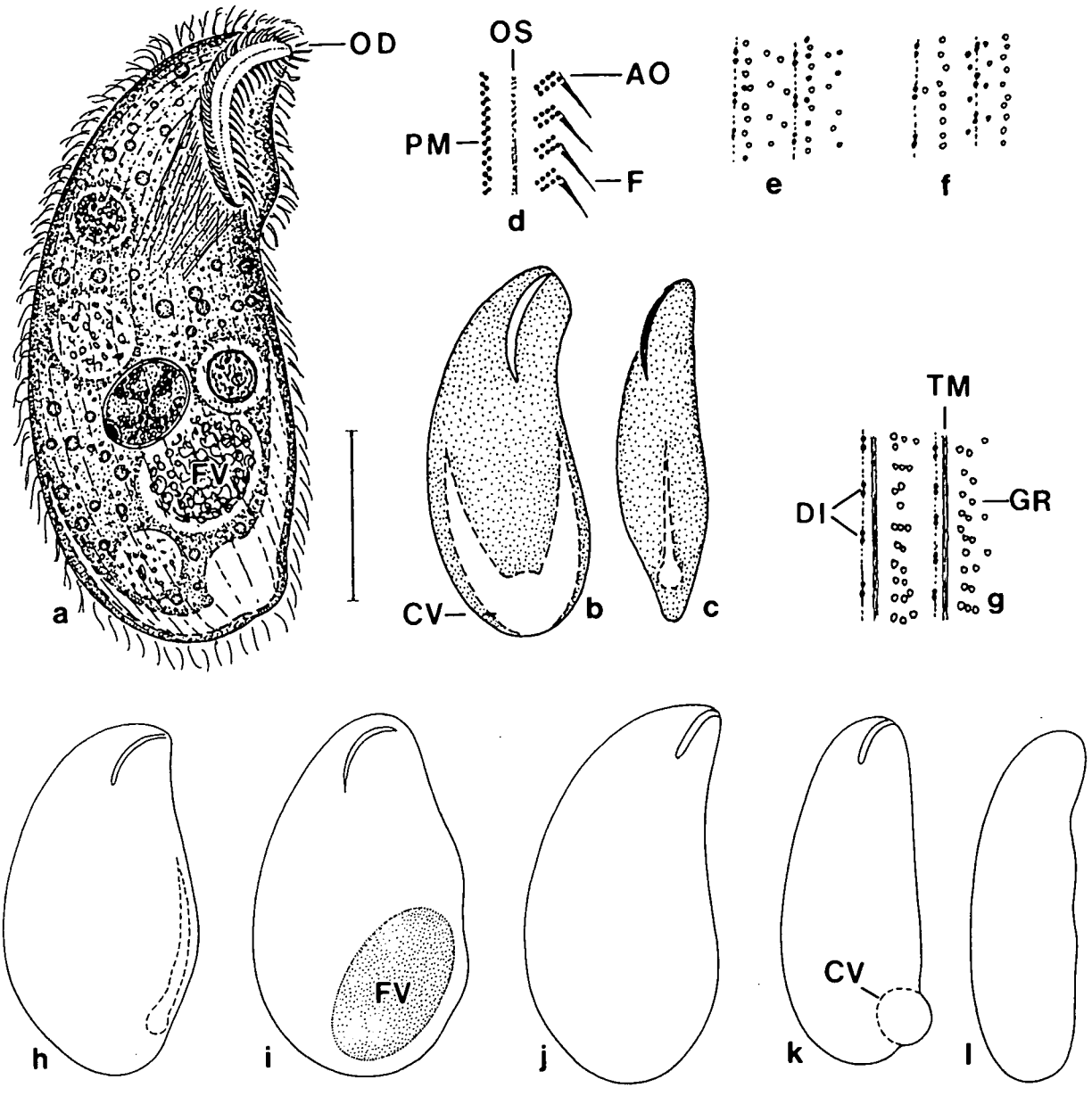


Fig. 218a–l. *Woodruffides terricola*, Namibian site 55 (a–d, g), Maldivean (f), and Galàpagos (e, h–l) specimens from life (a–c, e–l) and after silver carbonate impregnation (d). All populations, although differing in minor details (Table 198), are morphologically very similar. **a:** Right side view of a representative specimen, which is slightly twisted and thus shows the crescent-shaped, bright oral field in frontal view. Most dikinetids have only one basal body ciliated postorally. **b, c:** Lateral and dorsal view of same specimen showing flattening and large contractile vacuole. **d:** Oral structures. **e–g:** The cortical granulation is similar in all populations, that is, the yellowish, about 0.7 µm-sized granules (very likely mucocysts) are rather loosely arranged forming an inconspicuous stripe left or between each two ciliary rows. **h–l:** Shape variability of Galàpagos specimens (redrawn from video records). Figure (h) shows a specimen very similar to the Austrian type; figure (i) shows a specimen with a large vacuole containing remnants of a rotifer; figure (j) shows the same specimen as figure (i), but after defecation of the rotifer remnants; figures (k, l) show the same specimen ventrolaterally and dorsally. AO – adoral organelles, CV – contractile vacuole, DI – ciliary rows composed of dikinetids, F – fibre, FV – food vacuoles, GR – cortical granules, OD – oral field, OS – oral slit, PM – paroral membrane, TM – transverse microtubule ribbons. Scale bar (a) 50 µm.

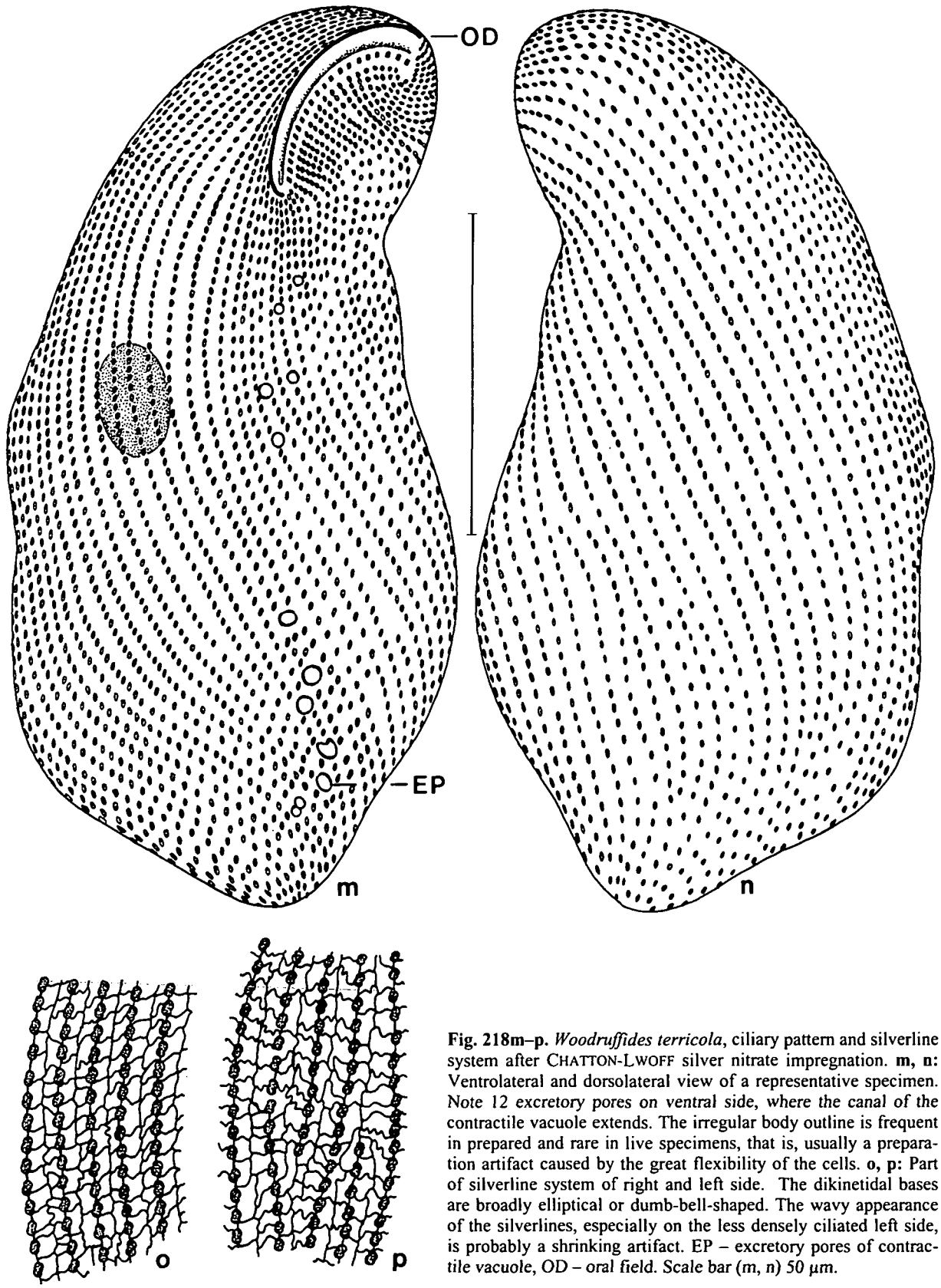


Fig. 218m–p. *Woodruffides terricola*, ciliary pattern and silverline system after CHATTON-LWOFF silver nitrate impregnation. **m, n:** Ventrolateral and dorsolateral view of a representative specimen. Note 12 excretory pores on ventral side, where the canal of the contractile vacuole extends. The irregular body outline is frequent in prepared and rare in live specimens, that is, usually a preparation artifact caused by the great flexibility of the cells. **o, p:** Part of silverline system of right and left side. The dikinetidal bases are broadly elliptical or dumb-bell-shaped. The wavy appearance of the silverlines, especially on the less densely ciliated left side, is probably a shrinking artifact. EP – excretory pores of contractile vacuole, OD – oral field. Scale bar (*m, n*) 50 μm.

Table 197. Morphometric data on *Woodruffides terricola*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	153.0	153.0	21.8	4.8	14.3	118.0	195.0	21
Body, width	67.0	67.0	11.2	2.4	16.7	46.0	85.0	21
Anterior body end to proximal end of paroral, distance	31.5	32.0	5.5	1.2	17.4	22.0	45.0	21
Anterior body end to macronucleus, distance	83.0	80.0	14.2	3.1	17.2	62.0	107.0	21
Anterior body end to 1st excretory pore, distance	52.1	52.0	7.2	1.8	13.8	43.0	67.0	17
Posterior body end to posteriormost excretory pore, distance	14.4	14.0	6.7	1.8	46.5	3.0	25.0	13
Macronucleus, length	19.9	20.0	3.9	0.8	19.4	13.0	27.0	21
Macronucleus, width	12.0	12.0	1.6	0.3	12.9	10.0	15.0	21
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Micronucleus, number [b]	1.0	1.0	0.0	0.0	0.0	1.0	1.0	14
Oral field, length [c]	28.7	29.0	5.0	1.1	17.4	21.0	40.0	21
Oral field, width [c]	5.9	6.0	1.1	0.2	18.9	4.0	9.0	21
Excretory pores, diameter	3.1	3.0	0.6	0.1	18.6	2.0	4.0	21
Excretory pores, number	9.7	8.0	2.2	0.6	22.8	7.0	13.0	13
Somatic ciliary rows, number	50.1	50.0	4.2	0.9	8.3	43.0	56.0	21
Adoral organelles, number	22.4	22.0	2.4	0.5	10.8	17.0	26.0	21

[a] Data based on mounted, CHATTON-LWOFF silver nitrate-impregnated, and randomly selected specimens from a multispecies culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Of 15 specimens analyzed, 1 had two micronuclei. In most specimens, no micronucleus could be found. Whether it was lacking or covered by the macronucleus could not be clarified.

[c] Measured as distance from anterior to posterior end of chord of paroral, respectively, from outer margin of paroral to outer margin of adoral organelle band.

Table 198. Number of ciliary rows and adoral organelles in various populations of *Woodruffides terricola*. Except for the Austrian type population, all data are original. A more detailed analysis of the population from Namibian site (55) is provided in table 197.

Characteristics [a]	Population	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Ciliary rows, number	AU	44.8	44	5.0	2.2	11.2	40	50	5
	NA	51.3	50	7.2	2.1	14.1	40	65	12
	MA	48.0	48	4.2	2.1	8.8	44	53	4
	GA	48.1	48	5.9	2.2	12.2	43	60	7
Adoral organelles, number	AU	17.8	17	4.5	1.8	25.5	13	25	6
	NA	22.3	22	3.4	0.8	15.3	16	28	18
	MA	23.3	23	2.6	1.3	11.3	21	27	4
	GA	21.4	22	3.3	1.2	15.4	18	28	8

[a] Data based on silver carbonate-impregnated specimens from non-flooded Petri dish cultures. AU – Austrian type population (from FOISSNER 1987c), CV – coefficient of variation in %, GA – Galàpagos Islands, M – median, MA – Maldives, Max – maximum, Min – minimum. n – number of individuals investigated, NA – Namibian site (55), SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Somatic cilia about 10 µm long, arranged in slightly spiral rows all commencing around oral opening; those of right side abut on paroral membrane at steep angles, while those of left side abut almost at right angles on left mouth margin. Kinetids very closely spaced in anterior portion of kineties, but do not form a postoral pseudomembrane (see → *Rostrophryides africana* for explanation) because most ciliary rows extend to or near to posterior body end; only few are more or less distinctly shortened, especially those commencing around buccal vertex (Fig. 218m, n; 299, 300, 437a, c, f, g). Silverline system platyophryid throughout. *Woodruffia*, in contrast, has a colpodid silverline pattern, that is, lacks a median silverline between each two ciliary rows (FOISSNER 1993c).

Oral apparatus in left upper quadrant of cell. Oral field a narrow, crescent-shaped area in anterior 11–26%, on average 19% of body length, recognizable even at low magnification (~ ×100) due to the thickened, bright right mouth margin, extends in main body axis or slightly obliquely to left anterior end (Fig. 218a; 299, 300, 437e, h; Table 197). Oral slit closed and thus inconspicuous, but can open widely when large prey is ingested, such as *Colpoda cavicola* and rotifers. Paroral restricted to right mouth margin, distinctly curved, composed of zigzagging basal bodies (dikinetids) with about 8 µm long cilia forming membranoid structure. Adoral organelles at left, concave mouth margin, one of them in minute preoral suture; composed of two kineties with four basal bodies each, cilia unite to minute, 8 µm long bundles; surrounded by faintly impregnated material forming conspicuous fibre extending obliquely backward from posterior left corner of organelles (Fig. 218a, d; 437a, e, f, g). Nematodesmata recognizable in vivo, one bundle each originates from paroral dikinetids and adoral organelles to contribute to the broad oral funnel obliquely extending to mid-body; adoral nematodesmal bundles thicker than paroral (Fig. 218a; 437d).

Observations on other populations: The specimens from the Galàpagos Islands and from a highly saline soil of the Maldives are very similar to those from Namibian site 55 (Fig. 437h–n; Table 198). However, both have two adoral organelles in the preoral suture, as the Austrian type specimens, which are slightly smaller in all main features, very likely because they are from a weak population (Table 198). See figure explanations for further details.

Occurrence and ecology: *Woodruffides terricola* obviously is a cosmopolitan, euryhaline ciliate, possibly restricted or at least preferring terrestrial habitats. In Namibia, it occurred in a variety of habitats (sites 3, 5, 40, 43, 48, 55, 73), showing its great ecological plasticity. In Hawaii, it was found in the mud of an ephemeral brook.

Comparison with → *Woodruffides metabolicus*: The genus *Woodruffides* comprises only two species, viz., *W. metabolicus* and *W. terricola* (for a review, see FOISSNER 1993c). Possibly, further species exist, although we do not have any in our notebook. *Woodruffides terricola* is usually smaller than *W. metabolicus* (about 160 × 70 µm vs. 200 × 100 µm), and thus has fewer ciliary rows (about 50 vs. > 50) and adoral organelles (about 21 vs. ≥ 30). Such differences, however, would justify only subspecies rank. Fortunately, there is now also a distinct **morphological** difference, not recognized by FOISSNER (1987c, 1993c): the paroral membrane of *W. terricola* is restricted to the right mouth margin, while that of → *W. metabolicus* extends onto the left mouth margin posteriorly (Fig. 438g, h). This difference occurs in each three populations and is thus a reliable species feature.

Woodruffides metabolicus (JOHNSON & LARSON, 1938) FOISSNER, 1987c (Fig. 438a–h; Table 199)

Woodruffides metabolicus was thoroughly reviewed by FOISSNER (1993c). Thus, we report only supplementary observations from a population of Namibian site 70 (Fig. 438a–h), emphasizing the paroral membrane, which sharply curves to the left at the proximal mouth margin to end some distance above. This is an important, constant *morphological* difference to → *W. terricola*.

Table 199 reviews some morphometric data, including new observations from populations of Namibian site (70) and the Cape Verde Islands. These data show, although not very detailed, that *W. metabolicus* is usually distinctly larger (about 200 × 100 µm vs. 160 × 70 µm) and has more adoral organelles (> 30 vs. < 30) than → *W. terricola*.

Table 199. Comparison of main morphometrics of *Woodruffides metabolicus* populations.

Characteristics [a]	Literature review (FOISSNER 1993c)	Kenya (FOISSNER 1987c) n = 8–12	Namibian site (70) n = 2	Cape Verde n = 2
Body size in vivo	85 × 46–400 × ? (200 × 100)	154–350 × 92–190 (238 × 132)	? ?	~ 200 × 75
Curved proximal paroral end	yes	yes	yes	?
Somatic kineties, number	80–180	45–60 (59)	100–110	~ 55
Adoral organelles, number	30–90	22–39 (31)	~ 50	32–39

[a] Measurements in µm. Values in brackets are arithmetic means.

Woodruffia australis FOISSNER, 1993c (Fig. 439a–d; Table 200)

This species occurred together with → *Rostrophrya fenestrata*, from which it was not easily separated because the location of the oral opening, a main distinguishing feature in vivo, is recognizable only at high magnification. It grew rather well for some time in Eau de Volvic with some crushed wheat grains and soil to stimulate growth of the natural bacteria and protist community.

The Namibian specimens, which occurred, like the type, in a highly saline soil sample, match the Australian type material very well in body shape and the somatic and oral ciliary pattern (Fig. 439a–d). They are, however, smaller and thus have fewer ciliary rows, adoral organelles, and paroral dikinetids (Table 200). The fine structure of the adoral organelles is also slightly different, indicating that the Namibian population could be a distinct subspecies.

Table 200. Main morphometrics of *Woodruffia australis* from Australia (upper line; from FOISSNER 1993c) and Namibia (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Somatic kineties, number	18.7	19.0	1.4	0.4	7.7	16.0	22.0	16
	12.7	13.0	1.1	0.3	8.7	12.0	15.0	11
Adoral organelles, number	6.6	7.0	0.7	0.2	10.9	5.0	8.0	16
	5.0	5.0	–	–	–	4.0	5.0	12
Paroral dikinetids, number	19.8	20.0	1.0	0.4	5.0	18.0	21.0	6
	13.4	13.5	1.8	0.6	13.3	12.0	17.0	10

[a] Data based on silver-impregnated and randomly selected specimens from a non-flooded Petri dish culture (Australian population) and a pure culture (Namibian population). CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Reticulowoodruffia terricola FOISSNER, 1993 (Fig. 219a–m; 440a–y, 441a–j; Table 201)

Improved diagnosis: Size 70–140 × 25–50 µm in vivo. On average 18–22 somatic kineties and a series of 8–9 adoral organelles with distances gradually increasing distally.

Description of Namibian populations and comparison with original description: FOISSNER (1993c) described *R. terricola* from CHATTON-LWOFF silver nitrate prepared specimens. Fortunately, we rediscovered the species in Namibia and could perform detailed in vivo and scanning electron microscopic observations, including some main ontogenetic stages. The oral and somatic ciliary and silverline pattern of the Namibian populations is highly similar to that of the USA type specimens. Thus, conspecificity is beyond reasonable doubt and emphasized by the very similar morphometrics (Table 201).

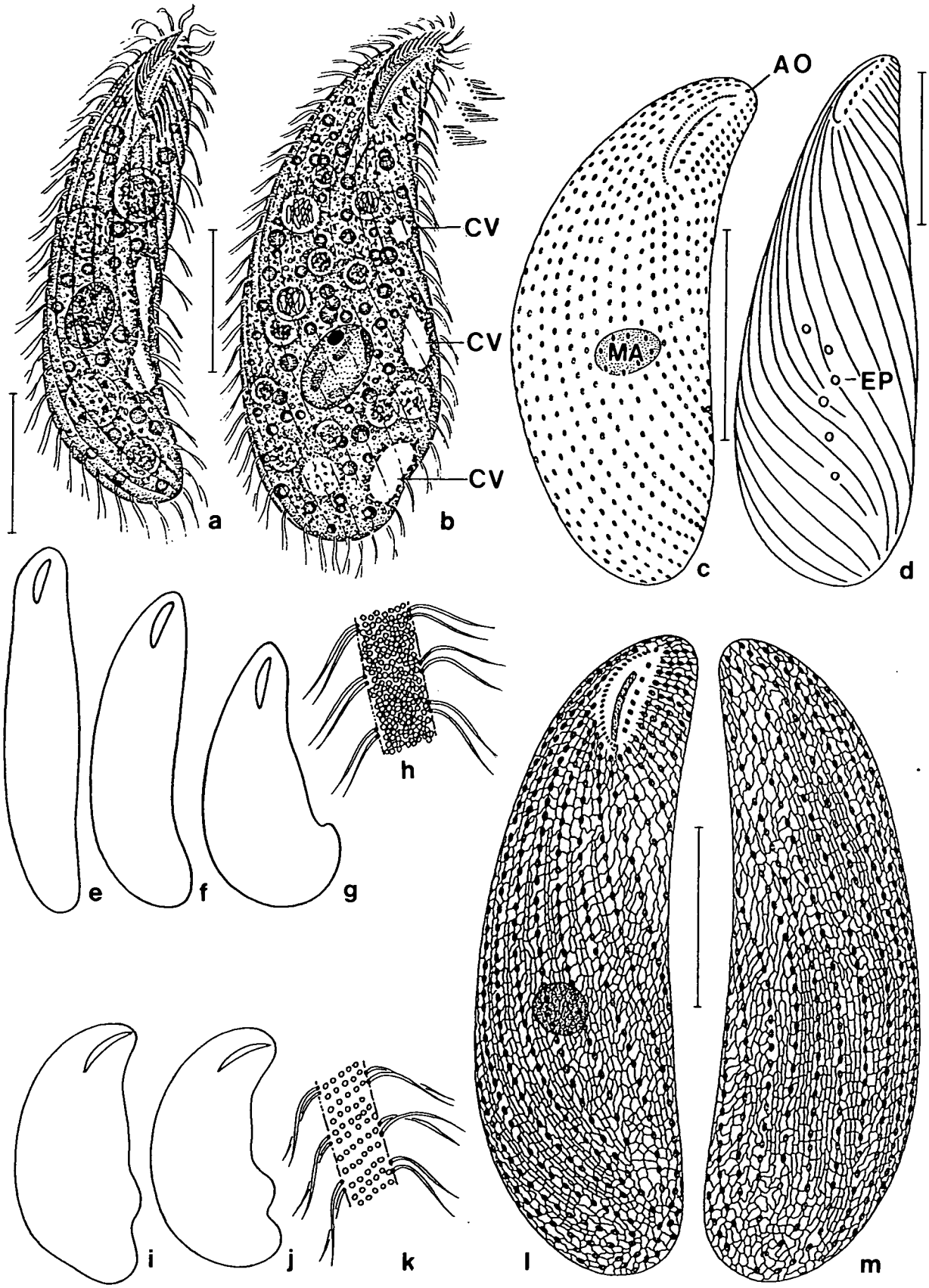
Cyrtolophosidid colpodids of this kind are difficult to identify in vivo because they closely resemble *Woodruffia rostrata* and → *W. australis*, and inexperienced workers may even confuse

Fig. 219a, c, d–g. *Reticulowoodruffia terricola* from Namibian site (36) in vivo (a, e–g) and after CHATTON-LWOFF silver nitrate impregnation (c, d). **a:** Ventral view of a representative specimen. **c:** Ventrolateral ciliary pattern (composite from several specimens). **d:** Ventral view showing excretory pores of the contractile vacuole. **e–g:** Same specimen extended and contracting.

Fig. 219b, h–k. *Reticulowoodruffia terricola* from Namibian site (39) in vivo. Ciliary pattern and details of oral structures, see Fig. 440a–y. **b:** Ventral view of a representative specimen. Right of oral apparatus three adoral organelles as seen with interference contrast optics. **h, k:** Surface views showing cortical granulation on left and right side. **i, j:** Same specimen extended and slightly contracted.

Fig. 219 l, m. *Reticulowoodruffia terricola*, ventral and dorsal view of USA type specimen after CHATTON-LWOFF silver nitrate impregnation (from FOISSNER 1993c). *Reticulowoodruffia* has a unique, narrowly meshed silverline pattern, except in the oral area, where an ordinary, platyophryid pattern occurs, that is, two silverline meshes between each two ciliary rows. The Namibian specimens match this pattern exactly (Fig. 440a–f).

AO – adoral organelles, CV – contractile vacuole, EP – excretory pores, MA – macronucleus. Scale bars 30 µm.


CV
CV
CV
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them with *Platyophrya spumacola* or → *Woodruffides terricola*. Thus, silver nitrate impregnation is indispensable for a reliable identification: only *Reticulowoodruffia* has a narrowly-meshed silverline pattern (Fig. 219 l; 440b, c, e, f).

Population from Namibian site 39 (Fig. 219b, h–k; 440a–y, 441a–j; Table 201): This population developed in the same culture as → *Exocolpoda augustini* and was fixed during exponential growth, as shown by several dividers. Size 90–130 × 30–50 µm in vivo, usually near 110 × 40 µm, length:width ratio also highly variable, viz., 1.7–4:1, on average 2.7:1 in silver nitrate preparations (Table 201). Shape basically oval and slightly reniform with anterior end pointed and posterior often broadly rounded, in detail, however, highly variable because cells are slightly contractile, flattened up to 2:1 dorsoventrally, and frequently slightly twisted about main body axis (Fig. 219b, i, j; 440a, d, g–o). Macronucleus subequatorial on average, broadly ellipsoidal, about 15–20 × 10–15 µm in vivo, while only 12 × 8 µm in the silver preparations, indicating considerable shrinkage, as in other members of the group (FOISSNER 1993c); nucleoli oblong. Micronucleus tightly attached to macronucleus and thus likely in its perinuclear space, about 3–4 × 2–3 µm in vivo. Contractile vacuole extends between oral vertex and body end, as shown by many scattered excretory pores (Fig. 219b, d; 440o, q). Cortex highly flexible and more or less distinctly striated by the ciliary rows, densely granulated, granules colourless and in short, oblique rows on right side, scattered on left (Fig. 219h, k). Cytoplasm colourless, often packed with fat globules 1–5 µm across and up to 10 µm-sized food vacuoles with bacterial remnants. Glides and swims moderately fast, showing great flexibility when touching obstacles or crawling among organic debris.

Somatic cilia 7–8 µm long in vivo, arranged on average in 19 distinctly spiralling rows all commencing around the oral apparatus, those on right side slightly more closely spaced than those on left; some rows shortened anteriorly and/or posteriorly, especially in excretory pore area. Kinetids slightly more closely spaced in anterior region of postoral kineties, but a postoral pseudomembrane is not formed; anterior cilium of dikinetids frequently lacking, appearing as a minute stub in SEM micrographs (Fig. 219b; 440b, c, e, g–s).

Silverline pattern as in specimens from USA type material, that is, closely and irregularly meshed, except in oral area, where an ordinary, platyophryid pattern occurs, that is, two silverline meshes between each two ciliary rows (Fig. 219 l, m; 440b, c, e, f).

Oral apparatus narrowly crescent-shaped, extends about 20 µm backwards along main body axis from beak-like anterior body end; oral funnel hardly recognizable in vivo, lined by fine fibres (Fig. 219b; 440a, d, e, g–j, o, p, s–v). Paroral membrane in flat furrow at right margin of oral opening, composed of very closely spaced, zigzagging dikinetids producing two distinctly different ciliary rows: outer (right) paroral row made of about 6 µm long, acicular, loose cilia beating distinctly in vivo; inner (left) paroral row composed of about 4 µm long, rod-shaped, likely almost or entirely immobile cilia so close together that a ribbon-like structure is formed that appears as a broad, bright wall in vivo. On average eight minute adoral organelles at left mouth margin; distances between individual organelles increase slightly from proximal to distal. Individual adoral organelles brick-shaped and likely made of two short ciliary rows in silver nitrate preparations, while composed of a single row of four rod-shaped cilia in vivo and scanning electron micrographs; cilia increase in length from approximately 2 µm proximally to about 4 µm distally, a remarkable pattern seen in several specimens both in vivo and scanning electron micrographs.

Population from Namibian site 36 (Fig. 219a, c, d–g; Table 201): This small population probably represents the lower limit of variability. It developed in a non-flooded Petri dish culture from the highly saline crust soil near site 39 (Fig. 2). Specimens were studied in vivo and in rather strongly bleached CHATTON-LWOFF silver nitrate preparations.

Size 70–120 x 20–40 µm in vivo, usually near 100 x 30 µm, stouter in preparations, viz., 85 x 38 µm, possibly due to some contraction and shrinkage; up to 30% contractile under cover glass, even if not touched, showing characteristic shape changes (Fig. 219e–g). Elongate ellipsoidal

Table 201. Morphometric data on *Reticulowoodruffia terricola* from USA type population (upper line), Namibian site 39 (middle line), and Namibian site 36 (lower line).

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	101.7	98.5	18.6	5.9	18.3	70.0	130.0	10
	102.6	103.0	11.6	2.7	11.3	82.0	122.0	19
	88.2	85.0	14.5	3.7	16.4	63.0	120.0	15
Body, width	34.0	34.0	3.9	1.2	11.6	29.0	40.0	10
	38.4	40.0	5.3	1.2	13.9	29.0	47.0	19
	31.5	31.0	4.6	1.2	14.6	23.0	38.0	15
Body length:width, ratio	3.0	3.0	0.6	0.2	20.9	2.1	4.3	10
	2.7	2.7	0.5	0.1	19.3	1.7	4.0	19
	2.9	2.8	0.8	0.2	27.3	1.8	5.2	15
Anterior body end to proximal mouth end, distance	17.8	17.0	2.5	0.8	14.2	15.0	22.0	10
	16.7	17.0	1.5	0.3	9.0	14.0	20.0	19
	16.4	17.0	2.1	0.6	13.0	12.0	19.0	15
Anterior body end to macronucleus, distance	53.9	57.5	8.4	2.7	15.6	40.0	62.0	10
	59.9	63.0	8.8	2.0	14.6	45.0	78.0	19
	45.0	49.0	9.2	2.4	20.5	28.0	60.0	15
Macronucleus, length	11.2	11.0	1.5	0.5	13.2	10.0	14.0	9
	11.6	12.0	1.4	0.3	11.6	9.0	15.0	19
	11.9	12.0	1.2	0.3	10.0	10.0	14.0	15
Macronucleus, width	9.2	9.0	1.4	0.5	15.2	8.0	12.0	9
	8.1	8.0	1.3	0.3	16.4	6.0	12.0	19
	7.1	7.0	1.2	0.3	16.6	5.0	10.0	15
Somatic kineties, number	18.4	18.5	0.7	0.2	3.8	17.0	19.0	10
	19.3	19.0	1.3	0.3	6.5	17.0	22.0	19
	21.9	22.0	1.7	0.6	7.7	20.0	24.0	7
Dikinetids in a right side kinety, number	42.6	45.5	8.2	2.6	19.2	25.0	50.0	9
	42.2	43.0	3.6	0.8	8.5	35.0	50.0	19
			not investigated					
Dikinetids in a left side kinety, number	37.9	40.0	7.2	2.4	19.1	25.0	50.0	9
	35.2	35.0	6.7	1.5	19.0	25.0	45.0	19
			not investigated					
Adoral organelles, number	7.7	8.0	0.9	0.3	11.2	6.0	9.0	9
	8.2	8.0	1.5	0.3	18.0	6.0	12.0	25
	8.8	9.0	1.1	0.4	12.5	7.0	11.0	9

[a] Data based on CHATTON-LWOFF silver nitrate-impregnated and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

to slightly reniform, anterior end bluntly pointed, posterior often curved leftward and narrowly to moderately broadly rounded; slightly flattened dorsoventrally (Fig. 219a). Macronucleus subequatorial on average, globular to ellipsoidal, on average broadly ellipsoidal; nucleolus reticular. Micronucleus not observed. Contractile vacuole extends between buccal vertex and body end, as shown by many scattered excretory pores (Fig. 219d). Cortex very flexible, cortical granules less conspicuous than in specimens from site (39). Cytoplasm colourless, contains some fat globules and food vacuoles with fluffy content. Glides moderately fast on microscope slide and soil particles, showing great flexibility.

Somatic and oral ciliary pattern as described for specimens from site (39), with inconspicuous morphometric differences (Table 201).

Ontogenesis: Morphogenesis basically proceeds as in other members of the group (→ *Platyophryides latus* and FOISSNER 1993c), as is obvious from some main stages found in the silver and scanning electron microscopic preparations. Division is homothetogenic, pleurokinetal, and proceeds in freely motile (non-encysted) condition. Early-middle dividers show that cells become ellipsoidal and fully reorganize the parental oral apparatus without, however, producing an anlagen field ("internal reorganization"; FOISSNER 1996c), while the new opisthe oral apparatus originates from a subequatorial anlagen field in line with the proter oral apparatus. Both the adoral organelles and the paroral membrane develop very early, that is, before cell furrowing commences. However, the four cilia of the adoral organelles are grouped in two minute rows each comprising two cilia, and the outer (right) paroral ciliary row develops much later than the inner one (Fig. 441a–c). Middle dividers show the onset of cell division, accompanied by an about 90° rotation of the opisthe relative to the proter. Thus, proter and opisthe oral apparatus are now on different sides of the cell and cannot be seen at the same focal plane. The adoral cilia arrange to a single row and the cilia of the outer paroral row grow out; accordingly, the oral ciliary pattern is complete at this stage (Fig. 441a–f). Early post-dividers are globular and of slightly different structure: proter post-dividers have a wide, flat, crescent-shaped oral opening, while opisthe post-dividers have a small, circular oral opening with a distinct collar (Fig. 441g–j).

Occurrence and ecology: *Reticulowoodruffia terricola* was discovered in highly saline dune sand from the Death Valley, Utah, USA (FOISSNER 1993c). In Namibia, it occurred in similar, but less saline and sandy habitats, viz., at sites (36) and (39). No other records are known (FOISSNER 1998a). *Reticulowoodruffia terricola* lacks specific morphological adaptations to the soil (sand) environment, except for the pronounced flexibility. Possibly, evolutionary constraints of the saline habitats the species obviously prefers caused the unique silverline pattern.

Semiplatyophrya acrostoma **nov. spec.** (Fig. 220a–m; 442a–i; Table 202)

Diagnosis: Size about 55 × 15 µm in vivo. Elongate ovoid to distinctly reniform, with 3–4 µm wide oral opening occupying narrowed anterior body end. On average 9 somatic ciliary rows, 9 paroral dikinetids, and 4 adoral organelles each consisting of four basal bodies.

Type location: Highly saline crust soil from the "Moon Landscape" in Namibia, 22°40'S 14°45'E (site 36 in figure 2 and chapter 2.1.2).

Etymology: Composite of the Greek words *ákron* (top of body) and *stoma* (mouth), referring to the main species feature, that is, the apical location of the oral opening. *Stoma* is used as a noun in apposition and thus does not adjust its neuter gender to the feminine generic name *Platyophrya*.

Description: Size 40–70 × 10–20 µm in vivo, rather distinctly contractile and thus smaller and stouter in preparations (Table 202); contracts and extends slowly, endpoints thus not exactly to determine. Shape highly variable, elongate ovoid to reniform when fully extended, more or less distinctly ovoidal or boomerang-shaped when fully or partially contracted; anterior end, bearing the oral opening, invariably bluntly pointed, posterior narrowly to broadly rounded (Fig. 220a–c, j–m); laterally flattened up to 2:1. Nuclear apparatus subequatorial on average. Macronucleus globular to slightly ellipsoidal, contains pale nucleoli. Micronucleus in vivo close to macronucleus, likely in its perinuclear space because not recognizable in silver carbonate preparations. Contractile vacuole in rear body end, excretory pore in or near posterior pole centre. Cortex very flexible, contains many about 0.5 µm-sized, colourless granules, very likely mucocysts, in same pattern as silverline system (Fig. 220e, f). Cytoplasm rather hyaline, contains up to 3 µm-sized fat globules and a few food vacuoles with fluffy content. Glides rather rapidly on microscope slide and soil particles showing great flexibility; moves like a fast, small amoebae under strong cover-glass pressure.

Somatic cilia only about 5 µm long in vivo, paired on right side, mostly single on left. On average nine curved to slightly spiralized, bipolar somatic kineties, those on right side slightly narrower spaced and about twice as densely ciliated than those on left (Fig. 220a, h–m; 422a, e, g–i; Table 202). In some specimens, a single dikinetid between anterior ends of left side kineties, forming some sort of postoral pseudomembrane (Fig. 220g; 422b). Silverlines in *Colpoda* pattern in right, dorsal and ventral cortex, while a *Platyophrya* pattern is formed between three to four left side ciliary rows, with the median silverline sometimes neighboured the left side of the kinety. Individual silverlines often strongly undulating and slightly narrower spaced than somatic kinetids (Fig. 220h–m; 422c, d, h, i).

Oral apparatus occupies narrowed anterior body end, minute, that is, merely 3–5 µm across and thus in vivo recognizable only in strongly squeezed and flattened cells (Fig. 220a–d, i–k; 442a, b, e–h). Paroral membrane distinctly curved, composed of an average of nine dikinetids, each having an about 3 µm long cilium associated likely with the distal basal body. Adoral organelles at left mouth margin, bear inconspicuous, almost immobile, about 3 µm long ciliary tufts curved posteriorly and to mouth centre; individual organelles composed of four basal bodies, of which one or two are likely unciliated, as indicated by the fineness of the tufts. Pharyngeal structures recognizable neither in vivo nor in silver carbonate preparations.

Occurrence and ecology: To date found only at type location, where it was rather abundant in the non-flooded Petri dish culture. The site is moderately saline and likely rather similar to that where *S. foissneri* was discovered, viz., in saline soil from the Sinai coast, Israel. Likely, *Semiplatyophrya* has a preference for saline soils.

Comparison with related species: See FOISSNER (1993c) for a detailed description of all taxa mentioned in the following discussion. Cyrtolophosidid colpodids like *S. acrostoma* are difficult to identify because they are small and have ordinary oral structures. The present species came to our attention by the minute and apically located oral apparatus and the terminally situated contractile vacuole. While the oral apparatus is minute and near the apical

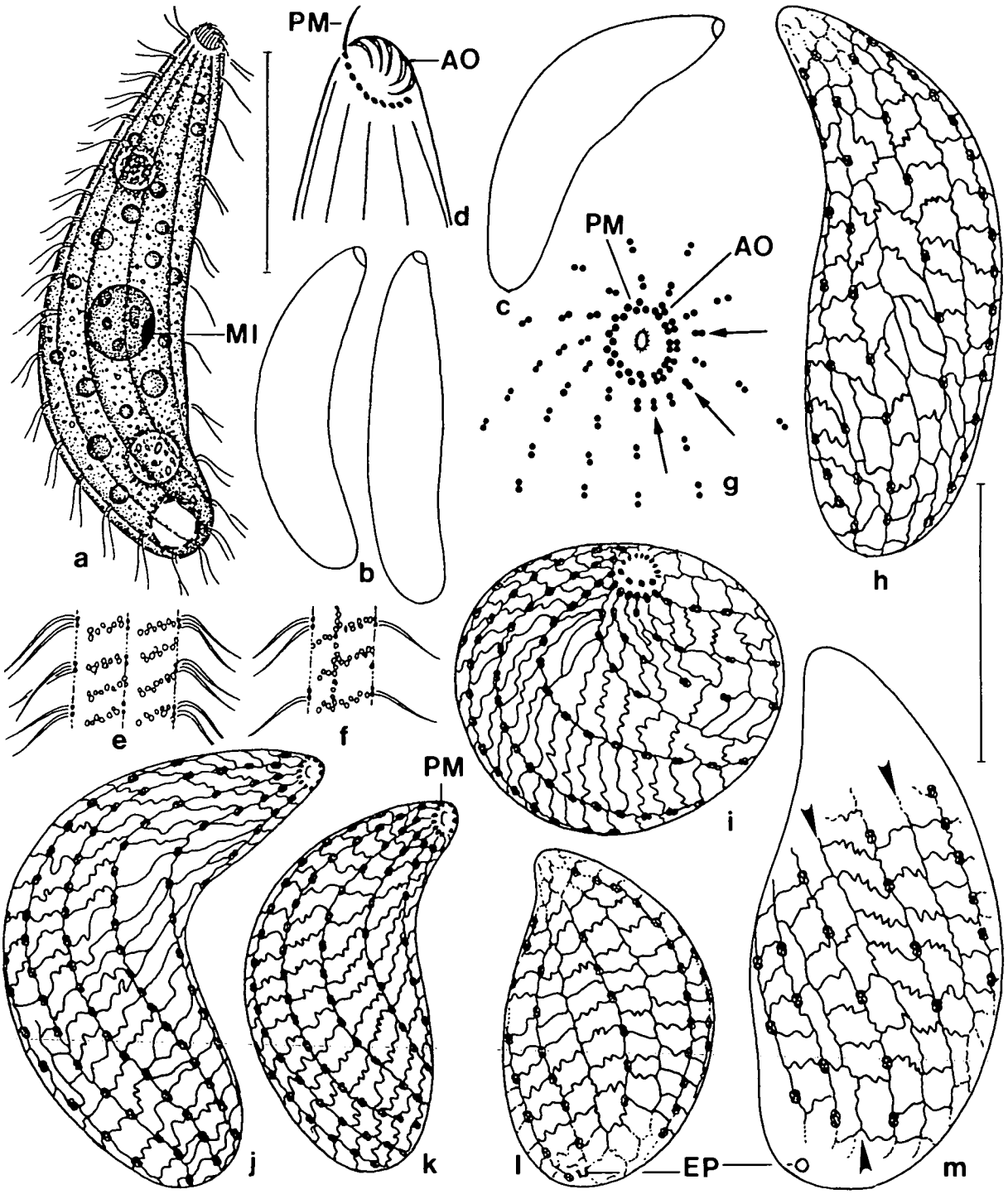

Fig. 220a–m. *Semiplatyophrya acrostoma* from life (a–f), and after silver carbonate (g) and CHATTON-LWOFF silver nitrate (h–m) impregnation. **a:** Right side view of a representative specimen. **b, c:** Extended and slightly contracted shape variants. **d:** The minute oral apparatus is at the anterior end of the cell. The thin ciliary tufts of the adoral organelles are very difficult to recognize. **e, f:** Mucocyst pattern in right and left side cortex. **g:** Oral structures. Arrows mark single dikinetids between the anterior end of the left side kineties. **h–m:** Oblique frontal (i), right lateral (j, k), and left lateral (h, l, m) views of ciliary pattern and silverline system, drawn to scale. Arrowheads mark median silverlines. AO – adoral organelles, EP – excretory pore, MI – micronucleus, PM – paroral membrane. Scale bars 25 µm.

Table 202. Morphometric data on *Semiplatyophrya acrostoma*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	44.5	47.0	7.5	1.7	16.9	30.0	55.0	19
Body, width	17.4	17.0	3.5	0.8	20.2	12.0	25.0	19
Oral opening, width [b]	3.8	4.0	0.5	0.1	13.6	3.0	5.0	24
Anterior body end to macronucleus, distance	23.4	25.0	4.0	0.9	17.3	14.0	29.0	19
Macronucleus, length	6.6	7.0	0.8	0.2	12.5	5.0	8.0	19
Macronucleus, width	5.7	6.0	0.8	0.2	14.0	4.0	7.0	19
Right side kineties, distance in between	4.7	5.0	1.2	0.3	26.2	3.0	8.0	19
Left side kineties, distance in between	6.4	6.0	1.4	0.4	22.1	4.0	9.0	16
Somatic ciliary rows, number [c]	9.5	9.0	0.8	0.2	8.9	8.0	11.0	19
Dikinetids in a right side kinety, number [c]	18.7	19.0	1.8	0.4	9.8	16.0	22.0	19
Dikinetids in a left side kinety, number [c]	8.9	8.0	1.5	0.4	16.8	7.0	12.0	19
Paroral dikinetids, number [c]	8.8	9.0	1.0	0.5	10.9	8.0	10.0	4
Adoral organelles, number [c]	4.3	4.0	–	–	–	4.0	5.0	7

[a] Data based, if not otherwise stated, on CHATTON-LWOFF silver nitrate-impregnated and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

[b] Outer margin of paroral to outer margin of adoral organelles.

[c] Partially from silver carbonate-impregnated specimens.

end also in some small *Platyophrya* species, the contractile vacuole is subterminal. *Sagittaria* species have, like *S. acrostoma*, a polar oral opening and a terminal contractile vacuole, but are stout, unflattened organisms. However, all these and some other species are so similar in shape and size that only very experienced workers will be able to distinguish them in vivo. Thus, silver impregnation is indispensable to look for the presence/absence of a postoral pseudomembrane and, especially, the silverline pattern, which is colpodid in *Sagittaria*. *Semiplatyophrya* is unique in having a *Colpoda* silverline pattern on the right side and a *Platyophrya* pattern on the left.

Semiplatyophrya acrostoma differs from *S. foissneri*, type and as yet sole species of the genus, mainly by the apical location of the oral opening. In the two populations of *S. foissneri* studied so far, the oral opening is larger and subapical on the ventral side. Furthermore, the adoral organelles are larger, that is, consist of six to nine basal bodies vs. only four in *S. acrostoma*. All other features and the habitats are very similar in both species (FOISSNER 1993c).

Pseudokreyella FOISSNER, 1985

Pseudokreyella belongs to the family Tectohymenidae FOISSNER, 1993c, a highly aberrant group of soil colpodids as yet comprising only two genera with three species altogether;

however, most species of this group are still undiscovered because they are small, infrequent, and hardly ever reach high abundances. Thus, we are happy to report on a further "good" *Pseudokreyella* species, where we could clear the structure of the paroral membrane which, according to FOISSNER's genus diagnosis "consists of a single row of dikinetids or monokinetids". The excellent preparations from → *P. etoschensis* show clearly that the paroral consists of dikinetids which, however, may appear as monokinetids depending on the angles by which the membrane is viewed; as the membrane becomes more or less distinctly twisted due to its U-like shape, an observer usually sees a more or less large portion in profile, where the obliquely arranged dikinetids appear as elliptical monokinetids (Fig. 221b, c; 443a–i).

Accordingly, the genus diagnosis can be improved as follows: "Very small Tectohymenidae with dikinetidal paroral membrane". The second genus of the family, *Tectohymena* FOISSNER, 1993c has a conspicuous field of paroral kineties.

Pseudokreyella etoschensis nov. spec. (Fig. 221a–e; 443a–k; Table 203)

Diagnosis: Size about 20 × 18 µm in vivo; ovoid. Somatic kinety 1 composed of ordinarily spaced kinetids. Three adoral organelles, organelle 1 minute and distinctly separated from almost abutting organelles 2 and 3, each composed of three vertically orientated basal body row.

Type location: Highly saline soil from margin of Etosha Pan, Namibia, 19°S 15°50'E (site 54 in figures 2, 3 and chapter 2.1.2).

Etymology: Named after the region discovered.

Description: Size 25–40 × 15-25 µm in vivo, usually about 30 × 18 µm. In lateral view ovoid with dorsal margin more distinctly convex than ventral, dorsal and ventral view ellipsoidal because cells laterally flattened about 1.5:1 (Fig. 221a, b, e). Nuclear apparatus in posterior half of cell, usually neighboured ventral side. Macronucleus globular, contains some large nucleoli. Micronucleus slightly flattened, attached to macronucleus. Contractile vacuole in posterior body end; excretory pore and cytopyge not impregnated. Cortex flexible, without specific granules, slightly furrowed by ciliary rows, especially preorally. Cytoplasm hyaline, contains up to 5 µm-sized food vacuoles with bacterial remnants. Glides rather rapidly on microscope slide and soil particles.

Cilia about 8 µm long and paired throughout, usually arranged in 10 rather sparsely ciliated rows, about half of which commence postorally and along preoral suture. Kinetids closely spaced in distinctly curved anterior portion of rows 1–3, those of rows 1 and 2 additionally obliquely arranged; row 2 with wide break in mid-portion (Fig. 221a, b, e; 443a, d, f, j).

Oral apparatus in second quarter of cell, conspicuous in silver preparations, while inconspicuous in vivo because oral structures almost entirely covered by U-shaped roof of buccal cavity. Buccal cavity deepening from anterior to posterior, guides into an inconspicuous pharyngeal basket commencing at right margin of last adoral organelle (Fig. 221a, b; 443j). Paroral membrane U-shaped, composed of (ciliated?) dikinetids, middle portion appears monokinetidal, as explained in genus introduction, because seen in profile when specimen is viewed ventrally; at right end a short, third row of basal bodies in about one third of specimens (Fig.

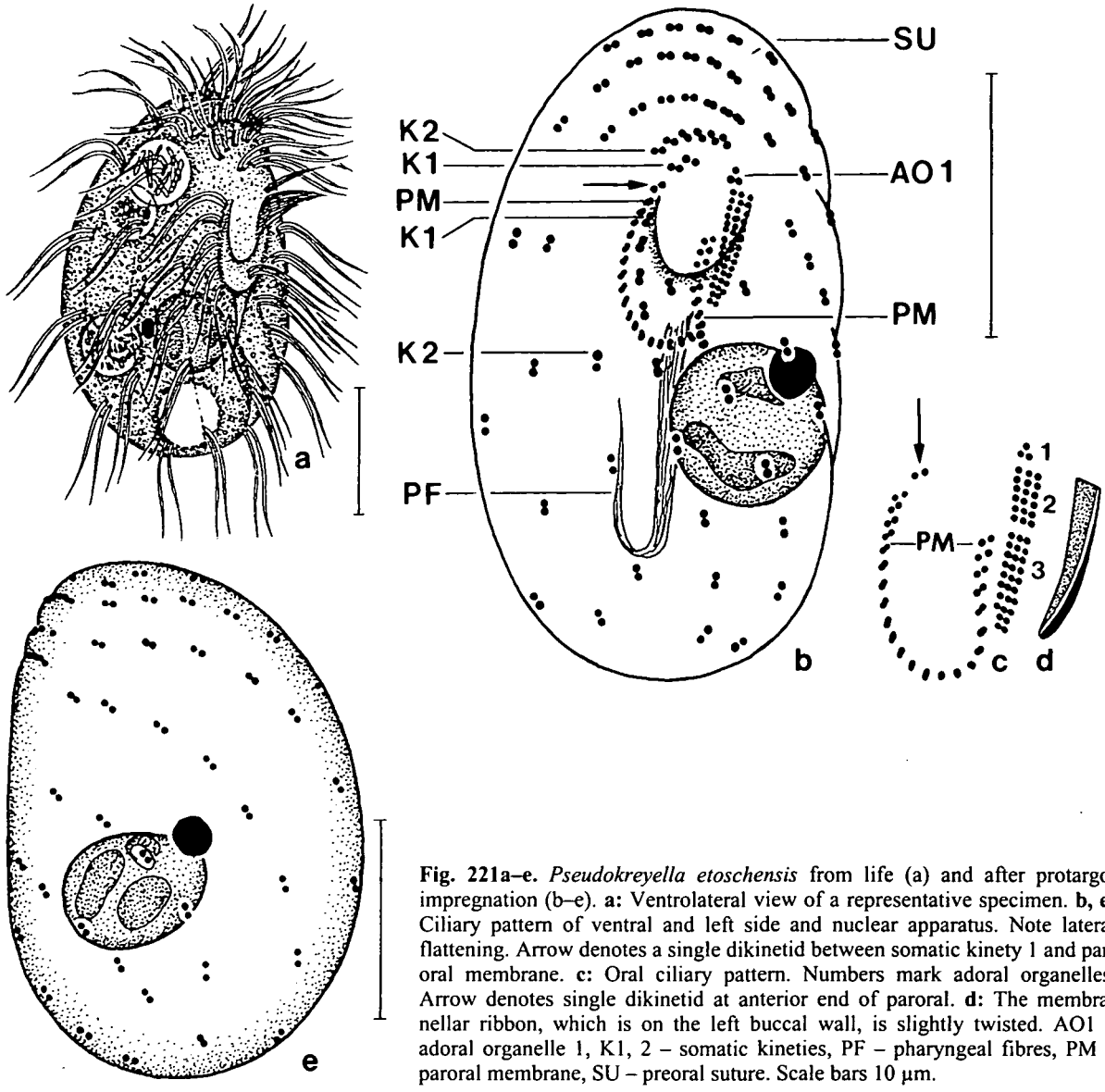

Fig. 221a–e. *Pseudokreyella etoschensis* from life (a) and after protargol impregnation (b–e). **a:** Ventrolateral view of a representative specimen. **b, e:** Ciliary pattern of ventral and left side and nuclear apparatus. Note lateral flattening. Arrow denotes a single dikinetid between somatic kinety 1 and paroral membrane. **c:** Oral ciliary pattern. Numbers mark adoral organelles. Arrow denotes single dikinetid at anterior end of paroral. **d:** The membranellar ribbon, which is on the left buccal wall, is slightly twisted. AO1 – adoral organelle 1, K1, 2 – somatic kineties, PF – pharyngeal fibres, PM – paroral membrane, SU – preoral suture. Scale bars 10 μm.

443h); at anterior end invariably a single dikinetid separated from other paroral dikinetids by a slightly increased distance. This kinetid, which is near the right end of the anterior portion of somatic kinety 1, is at an intermediate focal plane, and thus we could not decide whether it belongs to kinety 1 or the paroral. Three adoral organelles form a narrow, slightly twisted ciliary plate on left wall of buccal cavity: organelle 1 minute consisting of only three to four cilia; organelles 2 and 3 almost abutting, each composed of three vertical basal body rows; at posterior end of organelle 3 some additional basal bodies, possibly representing a minute fourth organelle (Fig. 221a–d; 443a–k).

Occurrence and ecology: To date found only at type location. *Pseudokreyella etoschensis* is the first member of the family living in saline soil.

Comparison with related species: *Pseudokreyella etoschensis* differs from *P. terricola* by the number (3 vs. 4–5) and structure (3 vs. 5–7 vertical rows of basal bodies in last organelle) of the adoral organelles and the distinct gap in kinety 2. *Pseudokreyella australis* has four distinct adoral organelles and a conspicuous condensation of cilia in the middle portion of somatic kinety 1. Thus, *P. etoschensis* is a very distinct species easily identified in silver preparations. In vivo, however, it may be confused with the congeners and other small colpodids because all features are difficult to recognize due to the minuteness of the organism. See FOISSNER (1993c) for a detailed description of all species mentioned.

Table 203. Morphometric data on *Pseudokreyella etoschensis*.

Characteristics [a]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	27.1	27.0	2.9	0.7	10.8	22.0	32.0	17
Body, width	17.1	16.0	2.5	0.6	14.7	13.0	24.0	17
Anterior body end to first adoral organelle, distance	6.5	6.0	1.0	0.2	15.5	5.9	9.0	17
Anterior body end to paroral vertex, distance	13.9	14.0	1.3	0.3	9.7	12.0	17.0	17
Anterior body end to macronucleus, distance	12.4	13.0	2.5	0.6	20.0	6.0	15.0	17
Macronucleus, length	6.2	6.0	0.8	0.2	13.4	5.0	8.0	17
Macronucleus, width	5.8	6.0	0.7	0.2	12.5	5.0	7.0	17
Micronucleus, length	2.4	2.5	–	–	–	2.0	3.0	17
Micronucleus, width	2.1	2.0	–	–	–	2.0	2.5	17
Somatic kineties postoral, number	10.4	10.0	–	–	–	10.0	12.0	17
Kinetids in anterior portion of kinety 1, number	2.1	2.0	–	–	–	2.0	4.0	17
Adoral organelles, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	17
Macronuclei, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	17
Micronuclei, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	17

[a] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

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5. SYSTEMATIC INDEX

Bonafide (valid, acceptable, "good" – in our judgment) species (taxa) names appear in *italics*; invalid species names (junior homonyms, synonyms, outdated combinations, and misspellings) are given in *italics* too, but put in *parentheses*. Bonafide generic names are in ***boldface italics*** print; invalid generic names are given in ***boldface italics*** too, but put in *parentheses*. Acceptable names of the suprageneric taxa (family, order ...) are printed in spaced type.

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