



# Notes on the soil ciliate biota (Protozoa, Ciliophora) from the Shimba Hills in Kenya (Africa): diversity and description of three new genera and ten new species

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A very diverse ciliate community was found in nine soil samples from the Shimba Hills Nature Reserve in Kenya, equatorial Africa. The ciliates, respectively, their resting cysts, were re-activated from air-dried samples using the non-flooded Petri dish method. Species were determined from life and by silver impregnation. 34 (27%) of the 125 taxa identified had not yet been described in 1985, when the samples were collected and investigated. The richest samples, each containing 59 species, were those from a deciduous primary forest and a young secondary pine forest. The most remarkable species discovered in the Shimba Hills were *Krassniggia auxiliaris*, *Bresslauides terricola*, *Gigantothrix herzogii*, and *Afrothrix darbyshirei*. They are “flagships” with a very distinct morphology and easy to recognise due to their extraordinarily large body size. *Krassniggia auxiliaris* occurs also in Australia and probably has a restricted Gondwanan distribution, like some other ciliates. *Bresslauides terricola* was later found in soils from all main biogeographical regions, except for Antarctica. *Gigantothrix herzogii* and *Afrothrix darbyshirei* are still unique to the Shimba Hills. The following taxa are described in detail: *Sikorops woronowiczae* nov. gen., nov. spec., *Arcuospathidium multinucleatum* nov. spec., *Dileptus similis* Foissner, 1995, *Plagiocampa bitricha* nov. spec., *Drepanomonas exigua exigua* Penard, 1922, *D. exigua bidentata* nov. spec., *Parafurgasonia protectissima* (Penard, 1922) nov. comb., *P. terricola* nov. spec., *Brachyosoma brachypoda mucosa* nov. spec., *Gigantothrix herzogii* nov. gen., nov. spec., *Afrothrix darbyshirei* nov. gen., nov. spec., *Oxytricha africana* nov. spec., and *O. elegans* nov. spec.

**Keywords:** biodiversity; new species; soil ciliates; soil protozoa; tropical Africa.

## Introduction

In a paper recently published in this journal, Foissner (1997a) estimated that global soil ciliate diversity amounts to at least 1330–2000 species, 70–80% of which have not yet been described. I also emphasized that I have about 500 new species at my disposal, whose full description will require years of work (Foissner, 1997a, 1998). The present paper provides descriptions of some of these species, most of which were discovered in equatorial and southern Africa, where I found 507 species, of which 240 were undescribed (Foissner, 1997a). Other species of this region, which is extremely rich in soil ciliates, have been described previously (Foissner, 1988, 1993, 1998).

## Materials and methods

### *Samples*

Samples were collected in July 1985 in the Shimba Hills Nature Reserve (310 km<sup>2</sup>; E39°25', S5°), that is, in Kenya (equatorial Africa) about 40 km south of Mombasa and about 20 km west of the Indian Ocean coast. The Shimba Hills (highest elevation in sampling area about 450 m above sea level) are a triassic sandstone formation covered by grassland and evergreen primary forest which, according to its structure, might be classified as some sort of coastal rain forest. Mean annual daily maximum temperature is about 30°C, mean annual precipitation is 1200 mm.

In the following sample descriptions, I use the original numbering to avoid later confusion with other samples from Kenya, which have not yet been published. Unfortunately, detailed soil data are not available, but some information is included in the sample descriptions.

Sample no. 8: Forest around picnic site. Collection of the upper 0–5 cm litter and soil layer. Litter layer only about 5 mm thick; soil brown, humic, contains dense root-carpet at 2–4 cm, strongly bleached below 5 cm; pH 6.1.

Sample no. 10: Sheldrick waterfalls. Collection of wet mosses and adhering sandy soil from wall of fall; pH 7.0.

Sample no. 13: Sheldrick waterfalls. Collection of almost dry mosses and adhering sandy soil from rocks in the surroundings of the fall; pH 6.4.

Sample no. 14: Forest surrounding the Sheldrick waterfalls. Collection of the very wet upper 0–5 cm litter and soil layer. Litter layer with much fungal hyphae; soil very sandy; pH 6.5.

Sample no. 15: Grassland downhill path to the Sheldrick waterfalls. Collection of the upper 0–5 cm grass sward and very sandy soil layer; pH 6.6.

Sample no. 16: Near site 14. Collection of the upper 0–5 cm litter and sandy soil layer under a leguminose tree with very impressive, up to 1 m long pods; pH 6.1.

Sample no. 17: Marshy area near site 14. Collection of the upper 0–5 cm soil layer with few roots and litter; soil black, very sandy, and very wet; pH 6.0.

Sample no. 18: Young (about 30 years) secondary pine forest near main gate to Nature Reserve. Collection of the upper 0–5 cm litter and soil layer. Litter layer about 10 mm thick, followed by dark, very sandy and humic soil; pH 5.7.

Sample no. 23: Forest near way to the Sheldrick waterfalls. Collection of litter and greyish, very sandy soil under a mahogany tree; pH 6.9.

The samples were air-dried in the Salzburg laboratory for 1 month and sealed in plastic bags. They were investigated in 1985 and 1986.

Several species occurring in the Shimba Hills samples 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 the Shimba Hills, that is, not contained in the sample 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 the Shimba Hills Nature Reserve, described in the following paragraph.

### *Sample processing and investigation*

All collections were analysed with the non-flooded Petri dish method as described by Foissner (1987a). Briefly, this simple method involves placing 10–50 g terrestrial material

in a Petri dish (10–15 cm in diameter) and saturating but not flooding it with distilled water. Such cultures were analysed for ciliates by inspecting about 2 ml of the run-off on days 2, 7, 14, 21, and 28. The non-flooded Petri dish method is selective, that is, probably only a small proportion of the resting cysts present in a sample is reactivated, and undescribed species or species with specialized demands are very likely undersampled (Foissner 1997a, b). Thus, the real number of species, described and undescribed, in the samples investigated is very likely much higher. Unfortunately, a better method for broad analysis of soil ciliates is not known.

#### *Species identification and taxonomic methods*

Identification, nomenclature and terminology of species followed the literature cited in this paper and in Foissner (1998). Determinations were done mainly on live specimens using a high-power ( $\times 100$ , N.A. 1.32) oil immersion objective and bright field, phase contrast, or differential interference contrast microscopy. However, all “difficult”, new, or supposedly new species were investigated with the silver-staining techniques described by Foissner (1991). The descriptions of the new taxa were based on material obtained with the non-flooded Petri dish method mentioned above, that is, no clonal cultures were set up.

Counts and measurements on silvered specimens were performed at a magnification of  $\times 1000$ . In vivo measurements were made at magnifications of  $\times 40$ – $1000$ . While the latter measurements provide only rough estimates, it is worth giving such data as specimens usually shrink in preparations or contract during fixation. Standard deviation and coefficient of variation were calculated according to statistics textbooks. Illustrations of live specimens were based on freehand sketches and micrographs; those of impregnated cells were made with a camera lucida. All figures were oriented with the anterior end of the organism directed to the top of the page.

## **Results**

### *Faunistic notes*

125 taxa were identified in the nine samples investigated (Table 1). This was a considerable number as compared to other regions of the world, especially when the small number of samples was taken into account: 139 species in 21 samples from Australia (Blatterer and Foissner, 1988), 64 species in 59 samples from Antarctica (Foissner, 1996a), 132 species in 50 samples from five very different sites (xerothermic grasslands, riparian forests, beech forest) in Austria (Foissner *et al.*, 1985), and about 70 species in many samples from spruce forests of Central Europe (Aescht and Foissner, 1993). Thus, soils of tropical Africa are obviously inhabited by a highly diverse ciliate community, like those of Costa Rica, where I found 80 species in a single sample from a seasonal dry forest (Foissner, 1995).

The species numbers listed above were obtained with the same technique (non-flooded Petri dish method) and are thus comparable. However, as explained in the method section, the non-flooded Petri dish method is rather selective. Thus, the number of species would at least double if the same sites were studied over several years and seasons and using larger quantities of soil.

Ten of the 125 taxa found are described here as new species or subspecies. This is a rather low number compared to the total number of new species found in 92 samples collected in various tropical and subtropical regions of Africa, viz. 240 undescribed taxa in

**Table 1.** List of species found in nine soil samples from the Shimba Hills in Kenya. (+) found, (–) not found

Species	Samples								
	8	10	13	14	15	16	17	18	23
<i>Afrothrix darbyshirei</i> nov. gen., nov. spec.	–	–	–	–	+	–	–	–	–
<i>Arcuospathidium cultriforme</i> (Penard, 1922)	–	–	–	+	–	–	–	–	–
<i>Arcuospathidium multinucleatum</i> nov. spec.	+	–	–	–	–	–	–	–	–
<i>Arcuospathidium muscorum</i> (Dragesco & Dragesco–Kernéis, 1979)	–	–	+	–	–	–	+	–	–
<i>Australocirrus octonucleatus</i> Foissner, 1988	+	–	–	–	–	–	–	+	–
<i>Birojimia muscorum</i> (Kahl, 1932)	–	–	–	+	+	+	–	+	–
<i>Blepharisma hyalinum</i> Perty, 1849	+	–	–	+	+	+	+	+	+
<i>Brachyosoma brachypoda mucosa</i> nov. sspec.	–	–	–	–	–	+	–	–	–
<i>Bresslaia vorax</i> Kahl, 1931	–	–	–	–	+	–	–	–	–
<i>Bresslauides terricola</i> (Foissner, 1987)	–	–	–	–	–	–	–	+	–
<i>Bryometopus pseudochilodon</i> Kahl, 1932	+	–	–	–	+	–	–	–	–
<i>Bryophyllum loxophylliforme</i> Kahl, 1931	–	–	–	–	–	–	–	+	–
<i>Chilodontopsis muscorum</i> Kahl, 1931	–	–	–	–	–	–	–	+	–
<i>Cinetochilum margaritaceum</i> (Ehrenberg, 1830)	–	–	–	–	–	–	+	+	–
<i>Circinella filiformis</i> (Foissner, 1982)	–	–	–	+	+	–	–	–	+
<i>Colpoda aspera</i> Kahl, 1926	–	–	–	–	–	–	–	–	+
<i>Colpoda cucullus</i> (Müller, 1773)	–	–	+	–	+	+	+	+	+
<i>Colpoda ellioti</i> Bradbury & Outka, 1967	+	–	–	+	–	–	–	+	–
<i>Colpoda henmeguyi</i> Fabre–Domergue, 1889	+	–	–	–	+	+	+	+	–
<i>Colpoda inflata</i> (Stokes, 1884)	+	–	–	–	+	–	+	+	–
<i>Colpoda lucida</i> Greeff, 1888	+	–	–	–	–	–	–	–	–
<i>Colpoda maupasi</i> Enriques, 1908	+	+	+	+	+	+	+	+	+
<i>Colpoda steinii</i> Maupas, 1883	+	+	+	–	+	–	–	+	+
<i>Colpodidium caudatum</i> Wilbert, 1982	+	–	–	+	–	+	+	–	–
<i>Cyclidium muscicola</i> Kahl, 1931	+	–	–	+	+	+	+	+	–
<i>Cyrtohymena candens</i> (Kahl, 1932)	+	–	–	+	–	–	–	–	+
<i>Cyrtohymena citrina</i> (Berger & Foissner, 1987)	–	–	–	–	–	+	–	–	–
<i>Cyrtohymena quadrinucleata</i> (Dragesco & Njiné, 1971)	–	–	–	–	–	–	–	+	–
<i>Cyrtolophosis acuta</i> Kahl, 1926	+	–	–	+	–	–	+	–	–
<i>Cyrtolophosis elongata</i> (Schewiakoff, 1892)	–	–	–	–	–	+	–	–	–
<i>Cyrtolophosis mucicola</i> Stokes, 1885	+	–	–	+	+	+	+	+	+
<i>Dileptus alpinus</i> Kahl, 1931	–	–	–	+	+	–	–	+	–
<i>Dileptus similis</i> Foissner, 1995	+	–	–	–	–	–	–	–	–
<i>Drepanomonas exigua bidentata</i> nov. sspec.	+	–	–	–	–	–	–	–	–
<i>Drepanomonas muscicola</i> Foissner, 1987	+	–	–	+	–	+	–	+	–
<i>Drepanomonas pauciciliata</i> Foissner, 1987	+	–	–	–	+	+	+	+	–
<i>Drepanomonas revoluta</i> Penard, 1922	+	–	–	+	–	+	+	+	+
<i>Drepanomonas sphagni</i> Kahl, 1931	–	–	–	–	–	+	+	+	–
<i>Enchelyodon lagenula</i> (Kahl, 1930)	–	–	–	–	–	–	–	+	–
<i>Enchelyodon tratzi</i> Foissner, 1987	–	–	–	–	–	–	–	+	–
<i>Engelmanniella mobilis</i> (Engelmann, 1862)	–	–	–	–	–	–	+	–	–
<i>Epispathidium amphoriforme</i> (Greeff, 1888)	–	–	–	–	–	–	–	+	–
<i>Epispathidium ascendens</i> (Wenzel, 1955)	–	–	–	–	–	+	+	+	+
<i>Epispathidium terricola</i> Foissner, 1987	+	–	–	+	–	+	+	+	–



Table 1. (Continued)

Species	Samples									
	8	10	13	14	15	16	17	18	23	
<i>Phialina binucleata</i> Berger, Foissner & Adam, 1984	–	–	–	–	–	–	–	–	+	
<i>Plagiocampa bitricha</i> nov. spec.	–	–	–	–	+	–	–	–	–	
<i>Platyophrya spumacola</i> Kahl, 1927	+	–	–	–	+	–	+	–	–	
<i>Platyophrya vorax</i> Kahl, 1926	–	+	+	–	–	–	–	+	–	
<i>Pleuroplites australis</i> Foissner, 1988	–	–	–	–	–	+	–	+	–	
<i>Protopathidium serpens</i> (Kahl, 1930)	–	–	–	–	–	–	+	–	–	
<i>Pseudochilonopsis mutabilis</i> Foissner, 1981	+	+	+	–	+	–	–	–	–	
<i>Pseudochilonopsis polyvacuolata</i> Foissner & Didier, 1981	–	–	–	–	–	–	–	–	+	
<i>Pseudocyrtolophosis alpestris</i> Foissner, 1980	+	–	–	+	+	–	+	+	–	
<i>Pseudoholophrya terricola</i> Berger, Foissner & Adam, 1984	+	–	–	+	–	–	+	+	+	
<i>Pseudourostyla franzi</i> Foissner, 1987	+	–	–	–	–	+	–	–	–	
<i>Sathrophilus muscorum</i> (Kahl, 1931)	+	–	–	+	+	–	+	+	–	
<i>Sikorops woronowiczae</i> nov. gen., nov. spec.	–	–	–	–	+	–	–	–	–	
<i>Sorogena stoianovitchae</i> Bradbury & Olive, 1980	–	–	–	–	–	–	–	–	+	
<i>Spathidium claviforme</i> Kahl, 1930	+	–	+	–	+	–	–	+	–	
<i>Spathidium longicaudatum</i> (Buitkamp & Wilbert, 1974)	–	–	–	–	+	–	–	–	–	
<i>Spathidium procerum</i> Kahl, 1930	+	–	–	–	–	–	+	–	–	
<i>Spathidium rusticum</i> Foissner, 1981	–	–	–	–	–	–	+	–	–	
<i>Spathidium spathula</i> (Müller, 1773)	–	–	–	–	–	–	+	+	–	
<i>Sterkiella cavicola</i> (Kahl, 1935)	–	+	+	–	–	–	+	–	–	
<i>Sterkiella histriomuscorum</i> (Foissner, Blatterer, Berger & Kohmann, 1991)	+	–	–	–	–	+	–	+	–	
<i>Tachysoma humicola</i> Gellért, 1957	–	–	–	–	–	+	+	–	–	
<i>Tachysoma humicola longisetum</i> Foissner, 1998	–	–	–	+	+	–	–	+	–	
<i>Terricirra matsusakai</i> Berger & Foissner, 1989	–	–	–	+	–	+	+	–	–	
<i>Tetrahymena rostrata</i> (Kahl, 1926)	+	–	–	–	+	–	–	+	–	
<i>Trachelophyllum apiculatum</i> (Perty, 1852)	–	–	–	–	–	–	–	+	–	
<i>Trihymena terricola</i> Foissner, 1988	–	–	–	–	–	–	–	+	–	
<i>Trithigmostoma bavariensis</i> (Kahl, 1931)	+	–	–	–	–	–	–	+	–	
<i>Uroleptus lepisma</i> (Wenzel, 1953)	–	–	–	–	–	–	+	–	–	
<i>Urosoma macrostyla</i> (Wrześniowski, 1866)	–	–	–	–	–	+	+	–	–	
<i>Urosomoida agiliformis</i> Foissner, 1982	+	+	+	+	+	+	+	+	+	
<i>Urosomoida agilis</i> (Engelmann, 1862)	–	–	–	–	–	–	–	–	+	
<i>Vorticella astyliformis</i> Foissner, 1981	+	+	+	+	–	+	+	+	+	
<i>Vorticella infusionum</i> Dujardin, 1841	–	–	–	–	–	+	–	–	–	
<i>Woodruffides metabolicus</i> (Johnson & Larson, 1938)	+	–	–	–	–	–	+	–	–	
Number of taxa identified	59	11	15	38	36	43	46	59	23	
Number of unidentified taxa	2	0	1	3	2	1	1	2	0	

a total of 507 identified (Foissner, 1997a). However, in 1985 when I analysed the samples, 34 (27%) of the 125 species were new, that is, the others have since been described, mainly from tropical and/or Australian soils (Blatterer and Foissner, 1988; Foissner, 1988, 1993, 1998; Hemberger, 1985). Furthermore, a considerable portion (about 10%) of the species could not be identified because they were too rare; very likely, some of them were new taxa, too.

The richest samples were no. 8, 18 (59 species each; primary and secondary forests), 17 (46 species; marshy grassland) and 16 (43 species; primary forest). Apparently, there was no significant loss of species in the secondary forest. However, a firm conclusion was impossible considering the few samples analysed and the methodological problems in general (see above).

The most remarkable species discovered in the Shimba Hills were *Krassniggia auxiliaris*, *Bresslauides terricola*, *Gigantothrix herzogi*, and *Afrothrix darbyshirei*. They are “flag-ships” with a very distinct morphology and easy to recognise due to their extraordinarily large body size. *Krassniggia auxiliaris* occurs also in Australia and probably has a restricted Gondwanan distribution, like some other ciliates (Foissner, 1998). *Bresslauides terricola* was later found in soils from all main biogeographical regions, except for Antarctica (Foissner, 1998). *Gigantothrix herzogi* and *Afrothrix darbyshirei* are still unique to the Shimba Hills.

#### *Description of new and insufficiently known species*

Morphometric data shown in Tables 2–11 are repeated in this section only as needed for clarity. All observations are from field material, that is, not from clonal cultures. Thus, it cannot be excluded that similar, but different species are mixed, although this is unlikely because I exclude specimens which deviate in at least one prominent character. Certainly, this can generate some bias in the data if used too uncritically. However, I usually exclude only such specimens which have, for instance, a different nuclear structure (very likely often postconjugates), a distinctly deviating ciliary pattern (very likely often injured, regenerating or malformed specimens), or an unusually small size (very likely often degenerating, just excysted or divided specimens). The inclusion of such individuals, which might sometimes belong to another species, would artificially increase variability.

#### ***Sikorops* nov. gen.**

*Diagnosis:* Acropisthiidae Foissner and Foissner, 1988 with three dorsal brush rows and fusiform extrusomes in the oral bulge.

*Type species:* *Sikorops woronowiczae* nov. spec.

*Dedication:* Named in honour of Prof. Dr. Jerzey Sikora (Nencki Institute of Experimental Biology, Warszawa) in appreciation of his great, unselfish efforts in editing the international journal “Acta Protozoologica”. The genus name is a composite of Sikora and the Latin noun *ops* (help). It has masculine gender, according to article 30a (ii) of the ICZN (1985).

*Comparison with related genera:* *Sikorops* has an apical cytostome, three brush rows, extrusomes in the oral bulge, and nematodesmal bundles originating from the oral dikinetids and from oralized somatic monokinetids (Fig. 1j, l). Accordingly, it belongs to the family Acropisthiidae, as defined by Foissner and Foissner (1988) and Foissner (1996a).

The family Acropisthiidae contains three genera, which are distinguished mainly by the shape of the extrusomes and the number of brush rows: nail-like and two rows in

*Fuscheria* (Fig. 1i), graver-like and two rows in *Actinorhabdos* (Fig. 1e, h), rod-like and three rows in *Acropisthium* (Fig. 1g). *Sikorops woronowiczae*, in contrast, has fusiform extrusomes and three brush rows (Fig. 1f, m). Furthermore, it very likely has a particular circumoral kinety, possibly composed of two dikinetids each at the anterior end of the ciliary rows (Fig. 1l, m). As this feature needs to be confirmed by transmission electron microscopy, it has not been included in the diagnosis. If my interpretation is correct, then *Sikorops* resembles *Protopathidium*, which, however, lacks oralized somatic monokinetids and thus belongs to another order, the Spathidiida Foissner and Foissner, 1988.

***Sikorops woronowiczae* nov. spec.** (Fig. 1a–d, f, j–m; Table 2)

I studied two populations of this species, one each from Africa and South America. They are very similar, in spite of the geographical spatial distance. Thus, the diagnosis and description comprise both populations. Morphometric data, however, are kept separate (Table 2).

**Diagnosis:** Size in vivo about  $100 \times 15 \mu\text{m}$ ; cylindroid to clavate. Nuclear apparatus usually consisting of two ellipsoidal macronuclear nodules and a single micronucleus in between. Extrusomes  $1\text{--}3 \mu\text{m}$  long. On average 11 somatic kineties and 5 dikinetids in brush row 1, 10 in row 2, and 14 in row 3.

**Type location:** Soil under grass carpet at the Mzima Springs in Tsavo National Park West, Kenya, equatorial Africa ( $38^\circ\text{E}$ ,  $3^\circ\text{S}$ ).

**Type slides:** Two slides (1 holotype and 1 paratype) with protargol-impregnated specimens from the type population and one voucher slide from the Chilean population have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria. The slides contain several specimens, with relevant cells marked by a black ink circle on the cover glass.

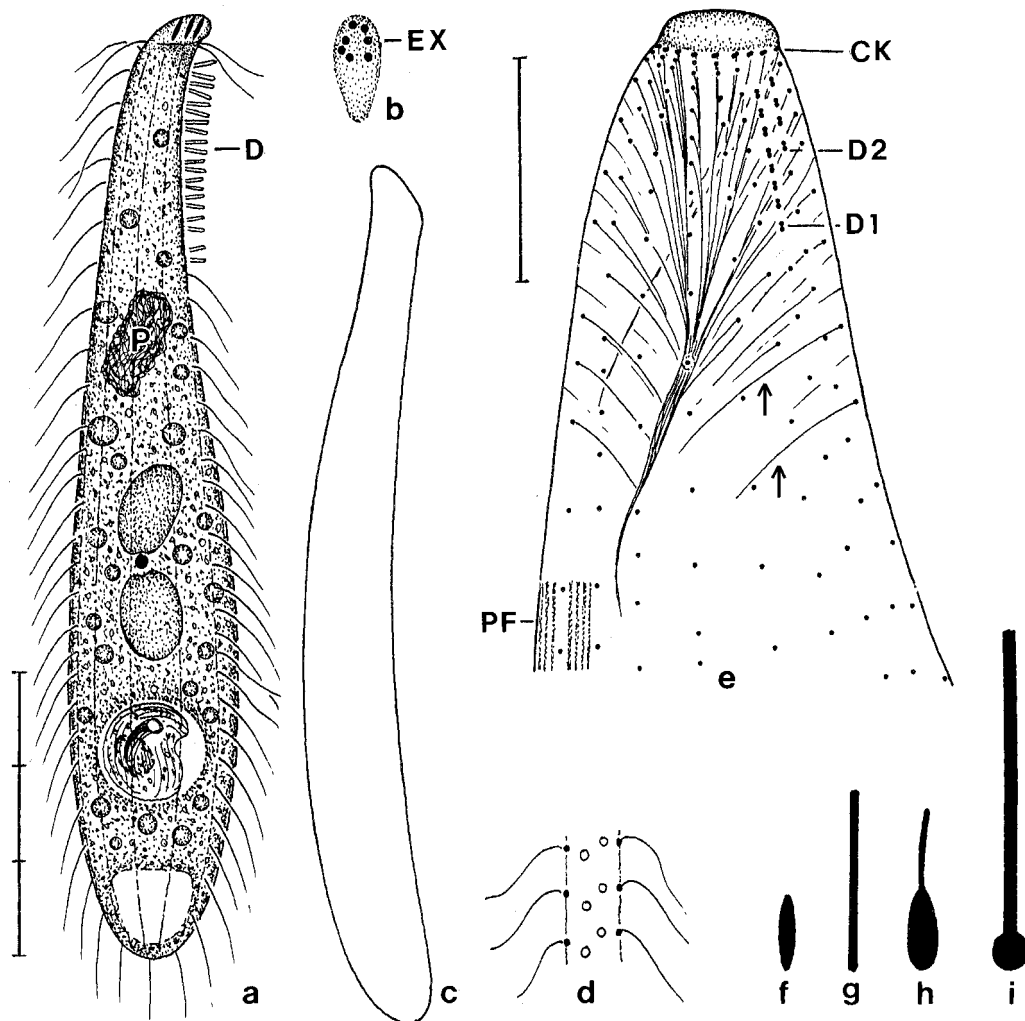
**Dedication:** Named in honour of Miss Małgorzata Woronowicz, managing editor of “Acta Protozoologica” (for details, see genus dedication).

**Description:** Size in vivo  $80\text{--}140 \times 10\text{--}20 \mu\text{m}$ ; unflattened. Shape fairly distinct due to minute, button-like oral bulge on neck-like narrowed anterior body third; overall appearance, however, rather variable, that is, lanceolate (Fig. 1a), cylindroid (Fig. 1c), or clavate (Fig. 1j). Nuclear apparatus subequatorial, usually consisting of two slightly ellipsoidal macronuclear nodules and a single, globular micronucleus in between (Fig. 1a, k); three to four macronuclear nodules form dense clusters in mid-body in about 20% of specimens, very much like in *Enchelyodon lagenula* (Blatterer and Foissner, 1988). Contractile vacuole in posterior body end. Extrusomes mainly in dorsal half of oral bulge, fusiform, minute,  $2\text{--}3 \mu\text{m}$  long in type population,  $1\text{--}2 \mu\text{m}$  in Singapore specimens (Fig. 1a, b, f). Cortex flexible, contains few, loosely arranged, colourless granules about  $0.5 \mu\text{m}$  across (Fig. 1d). Cytoplasm hyaline, contains some small fat globules and large food vacuoles with ingested ciliates, viz. *Pseudochilodonopsis mutabilis* in specimens from type population and *Cyrtolophosis mucicola* in those from Chile. Swims and creeps slowly.

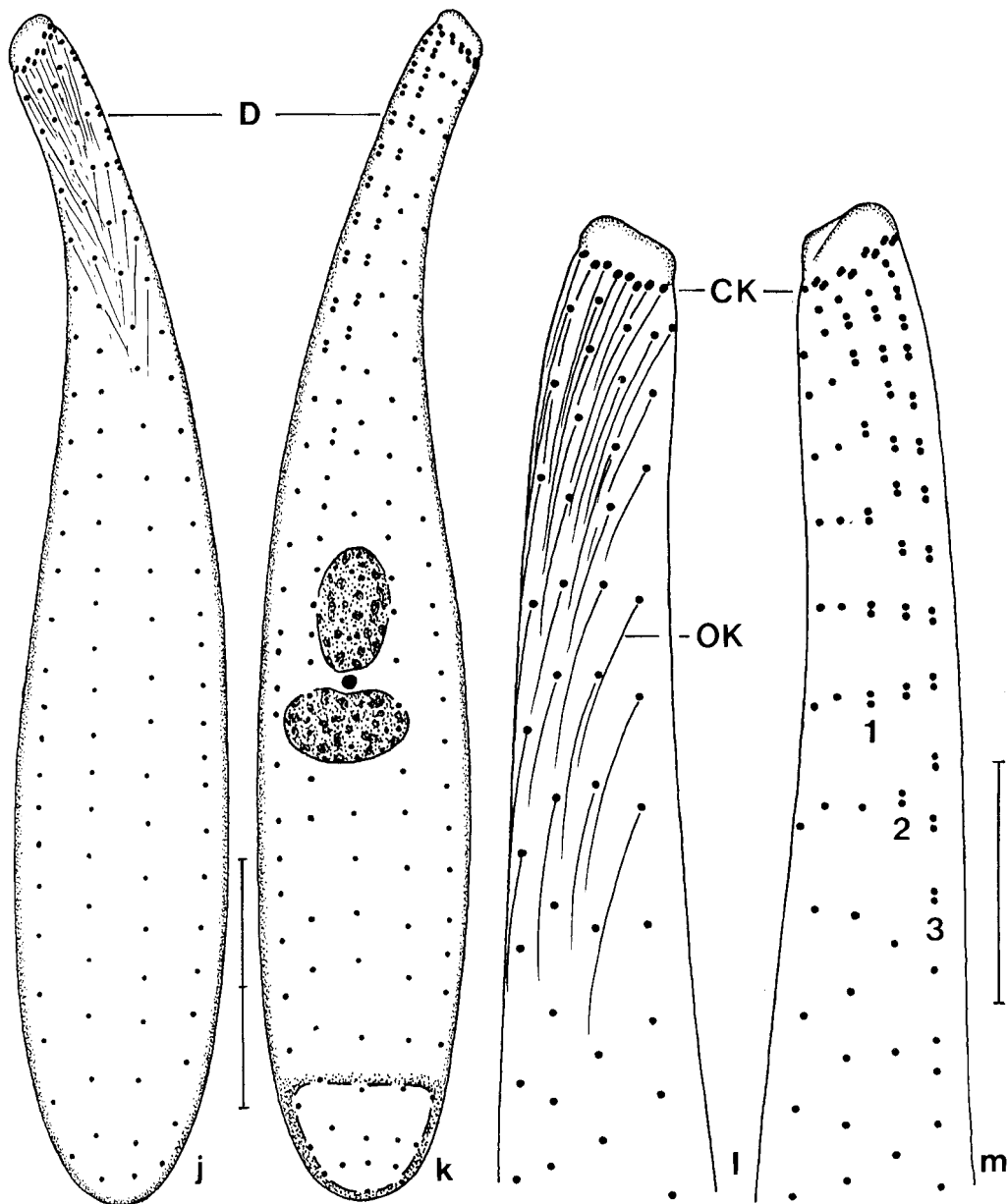
Cilia in vivo about  $8 \mu\text{m}$  long, rather widely spaced, arranged in longitudinal, equidistant rows distinctly separate from circumoral kinety, especially on ventral and right side (Fig. 1j–m). Dorsal brush inconspicuous, about 27% of body length, composed of three rows having up to  $3 \mu\text{m}$  long, paired bristles (Fig. 1a, j, k, m; Table 2).

Oral bulge minute, spathidiform, that is, obliquely truncate occupying anterior body end, broadly cuneate in frontal view, more or less distinctly domed in prepared specimens (Fig. 1a, b, j–m). Circumoral kinety at base of oral bulge, circular, very likely composed of





**Figures 1a–i.** *Sikorops woronowiczae* (a–d, f) and related genera (e, g–i) from life (a–d, f–i) and after protargol impregnation (e). **a:** Left lateral view of a representative specimen from type population. **b:** Frontal view of oral bulge. **c:** Diagram of a specimen from Singapore. Specimens of this population are, like those from Chile (Table 2), on average more slender than those from Kenya. **d:** Surface view showing scattered cortical granules. **e:** Anterior dorsal portion of *Actinorhabdos trichocystifera*, which has, like *S. woronowiczae* (Fig. 1j, l), oralized somatic monokinetids (arrows) contributing to the oral basket with their nematodesmata (from Foissner, 1984). **f–i:** Genera within the family Acropisthiidae are distinguished mainly by the shape of the extrusomes (drawn to scale): fusiform in *Sikorops* (f; 2  $\mu$ m), rod-shaped in *Acropisthium* (g; 4  $\mu$ m), graver-like in *Actinorhabdos* (h; 3  $\mu$ m), and nail-like in *Fuscheria* (i; 8  $\mu$ m). A further important character is the number of brush rows: two in *Actinorhabdos* and *Fuscheria*, three in *Acropisthium* and *Sikorops*. CK – circumoral kinety, D – dorsal brush, EX – extrusomes, P – prey, PF – postciliary fibres. Scale bar division 10  $\mu$ m.



**Figures 1j–m.** *Sikorops woronowiczae*, somatic and oral infraciliature after protargol impregnation. **j, k:** General left and right lateral view of a representative specimen having the micronucleus between two ellipsoidal macronuclear nodules. **l, m:** Anterior ventral and dorsal portion showing details of the oral apparatus and the dorsal brush. Nematodesmata originate not only from the circumoral dikinetids but also from the anterior somatic bodies (=oralized somatic monokinetids), as in the other members of the family (Fig. 1e). *Sikorops woronowiczae* has three brush rows (numbers 1, 2, 3 in Fig. 1m) composed of paired, specialized cilia (Fig. 1a). CK – circumoral kinety, D – dorsal brush, OK – oralized somatic monokinetids. Scale bar division 10  $\mu\text{m}$ .

**Table 2.** Morphometric data from a Kenyan (type, upper line) and a Chilean (lower line) population of *Sikorops woronowiczae*

Character <sup>a</sup>	$\bar{x}$	M	SD	CV	Min	Max	n
Body, length	95.7	91.0	11.1	11.6	81.0	118.0	11
	100.8	95.0	18.9	18.8	74.0	135.0	9
Body, width at circumoral kinety	5.0	5.0	–	–	4.0	6.0	11
	4.2	4.0	–	–	4.0	5.0	9
Body, maximum width	15.8	17.0	2.5	15.9	11.0	20.0	11
	12.1	12.0	2.6	21.2	7.0	15.0	9
Macronuclei, number	2.4	2.0	0.8	34.2	2.0	4.0	11
	2.3	2.0	0.7	30.7	2.0	4.0	9
Macronuclear nodules, length	8.8	9.0	1.6	18.2	6.0	11.0	11
	10.8	10.0	1.6	14.5	9.0	13.0	9
Macronuclear nodules, width	6.2	6.0	1.1	17.5	4.0	8.0	11
	6.9	7.0	0.6	8.7	6.0	8.0	9
Micronuclei, number	1.0	1.0	0.0	0.0	1.0	1.0	11
	1.0	1.0	0.0	0.0	1.0	1.0	8
Micronucleus, largest diameter	1.4	1.4	–	–	1.4	1.6	11
	1.6	1.6	–	–	1.2	2.0	7
Somatic kineties, number	10.8	11.0	0.8	6.9	10.0	12.0	11
	10.5	10.5	1.7	16.1	9.0	14.0	8
Basal bodies in a right lateral kinety, number	32.2	33.0	5.8	17.9	21.0	43.0	11
	36.2	32.0	9.1	25.2	27.0	50.0	6
Dorsal brush rows, number	3.0	3.0	0.0	0.0	3.0	3.0	11
	3.0	3.0	0.0	0.0	3.0	3.0	8
Dorsal brush kinety 1, length <sup>b</sup>	17.5	17.0	3.4	19.5	15.0	24.0	11
	8.4	8.5	2.3	27.0	5.0	11.0	8
Dorsal brush kinety 2, length <sup>b</sup>	23.2	22.0	3.2	13.6	17.0	28.0	11
	22.0	20.0	4.1	18.5	17.0	31.0	9
Dorsal brush kinety 3, length <sup>b</sup>	27.4	27.0	3.8	14.0	22.0	35.0	11
	25.8	24.0	6.3	24.3	18.0	36.0	9
Dorsal brush kinety 1, number of dikinetids	6.5	6.0	0.9	14.3	5.0	8.0	11
	3.0	3.0	0.8	25.2	2.0	4.0	8
Dorsal brush kinety 2, number of dikinetids	10.1	10.0	1.6	15.6	7.0	12.0	11
	10.0	9.0	2.6	26.5	7.0	15.0	9
Dorsal brush kinety 3, number of dikinetids	13.1	13.0	2.0	15.5	10.0	16.0	11
	13.7	14.0	3.9	28.5	9.0	20.0	9

<sup>a</sup> Data based on protargol-impregnated, mounted specimens from field (protocol A in Foissner, 1991). Measurements in  $\mu\text{m}$ . CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation,  $\bar{x}$  – arithmetic mean.

<sup>b</sup> Measured as distance from anterior body end to proximal end of row.

oblique pairs of dikinetids, as indicated by the nematodesmata and the slightly increased size and elliptical outline of the granules; thus, the circumoral kinety of *S. woronowiczae* can be considered to be composed of very short kinetofragments attached to the anterior end of the somatic kineties (Fig. 1m), as in *Protospathidium*. Oral basket inconspicuous, hardly recognisable in live specimens, composed of fine, scarcely bundled nematodesmata

originating from circumoral dikinetids and 5–6 basal bodies at anterior end of somatic kineties (Fig. 1j–m; oralized somatic monokinetids, Foissner and Foissner, 1988).

*Occurrence and ecology:* As yet found at type location (soil under grass carpet on old lava-stream, pH 6.9; collected on 8.5.1985), at site 15, in Chile (near Lago Chungará, 4500 m above sea-level, dark soil under cushion plants, mixed with some surface mosses, pH 6.2; collected by Dr. Müller in 1987; Table 1), and in Singapore (Bukit Timah National Park, mosses mixed with some soil on granitic rocks, pH 3.9; collected on 26.2.1987). These data indicate that *S. woronowiczae* is very likely cosmopolitan, possibly occurring in both soil and moss.

*Comparison with related species:* There are several species in the literature which resemble *S. woronowiczae*, mainly because they have a similar size, shape, and nuclear apparatus: *Arcuospathidium japonicum* Foissner, 1988 has spinous, 4–5 µm long extrusomes and a distinctly longer oral bulge; *A. atypicum* Wenzel, 1953 (redescribed by Foissner, 1988 as *A. australe*, a junior synonym; see Foissner, 1998) has rod-shaped extrusomes and a distinctly longer oral bulge; *Enchelyodon lagenula* (Kahl), as redescribed by Blatterer and Foissner (1988), is stouter, has a conspicuous, hemispherical oral bulge containing rod-shaped extrusomes, and lacks oralized somatic monokinetids; *Trachelophyllum falciforme* Penard, 1922 is similar to *S. woronowiczae* in many respects and might belong to this genus or to *Protospathidium*, but is only 40–60 µm long and has two or three distinctly elongated brush cilia at the anterior dorsal end. Furthermore, *S. woronowiczae* resembles several pleurostomatids, like *Litonotus* spp. and *Acineria* spp., because of its lanceolate shape and characteristic nuclear apparatus. Accordingly, identification of *S. woronowiczae* is difficult and requires careful live observation of the extrusomes and brush cilia, which are usually not or only insufficiently impregnated by silver compounds.

***Arcuospathidium multinucleatum* nov. spec.** (Fig. 2a–m; Table 3)

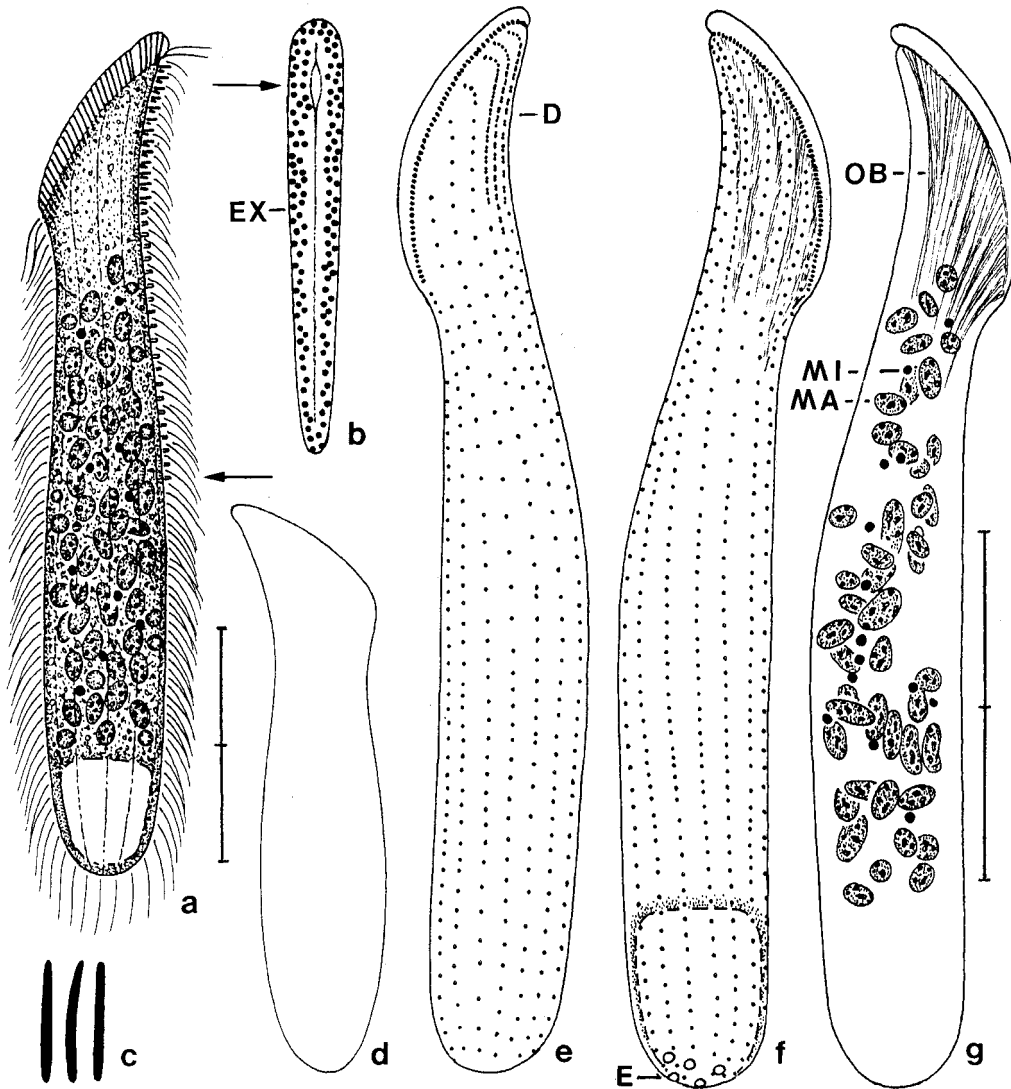
I studied three populations of this species in detail, and several others cursorily (see occurrence and ecology section). They agree in the main characters (size, slender shape, many macronuclear nodules, short extrusomes, 10–20 ciliary rows), but differ in some details, especially morphometric characteristics (Table 3), which might be considered by some workers to be of significance for splitting the species into several subspecies. Thus, the diagnosis contains only the type population. Differing features from the other populations are mentioned, if important, in the description and figure explanations.

*Diagnosis:* Size in vivo about 140 × 20 µm, slenderly spatulate. Oral bulge distinctly cuneate and inclined to ventral side, 22% of body length on average, with minute conical depression near dorsal end. Extrusomes rod-shaped, 4–5 µm long. On average 47 macronuclear nodules and 15 somatic kineties.

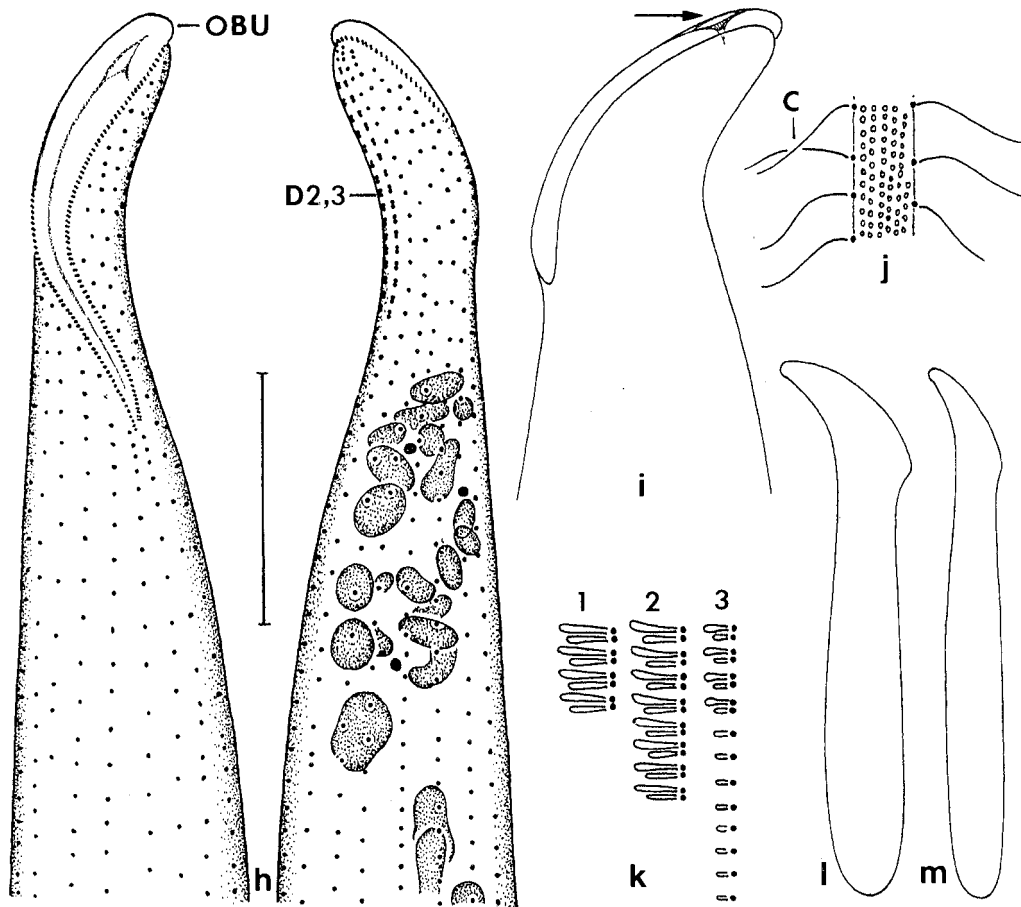
*Type location:* Forest soil near the village of Limuru, about 25 km NE of Nairobi, Kenya, equatorial Africa (36°50'E, 1°S).

*Type slides:* Two slides (1 holotype and 1 paratype) with protargol-impregnated specimens have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria. Voucher slides from the populations found in sample 8 and in Australia have also been deposited. The slides contain several specimens, with relevant cells marked by a black ink circle on the cover glass.

*Etymology:* “multinucleatum” (Lat., many nuclei) refers to the main species character, that is, the numerous macronuclear nodules.



**Figures 2a–g.** *Arcuospathidium multinucleatum* from life (a–d) and after protargol impregnation (e–g). **a:** Left lateral view of a representative specimen from type population. Note brush row 3 (arrow), which extends with minute, monokinetidal bristles to mid-body. **b:** Frontal view of oral bulge, which is packed with extrusomes. Arrow marks minute conical depression near dorsal bulge end (cp. Fig. 2i). **c:** Extrusomes are rod-shaped, slightly curved, and 4–5  $\mu\text{m}$  long. **d:** Diagram of a representative specimen from sample 8. Specimens of this population are, on average (Table 3), stouter than those from type location (Fig. 2a, e). **e–g:** Infraciliature of left and right side, and nuclear apparatus and oral basket of a representative specimen from type population. D – dorsal brush, E – excretory pores of contractile vacuole, EX – extrusomes (toxicysts), MA – macronuclear nodule, MI – micronucleus, OB – oral basket. Scale bar division 20  $\mu\text{m}$ .



**Figures 2h–m.** *Arcuospathidium multinucleatum* from life (j–m) and after protargol impregnation (h, i). **h:** Infraciliature of anterior ventral and dorsal side of a specimen from type population. The oral bulge (OBU) is distinctly cuneate. **i:** Anterior portion of a specimen from sample 8, showing the minute conical depression near the dorsal end of the oral bulge (arrow). **j:** Surface view showing cortical granules. **k:** Posterior end of dorsal brush of Venezuelan population; length of largest bristles 4  $\mu\text{m}$ . **l, m:** Diagram of representative individuals from Australia. Specimens of this population are, on average (Table 3), more slender than those from type population (Fig. 2a). C – cilia, D – dorsal brush rows 2 and 3, OBU – oral bulge. Scale bar 20  $\mu\text{m}$ .

**Description:** Size in vivo 100–200  $\times$  15–40  $\mu\text{m}$ , usually 130–170  $\times$  20–30  $\mu\text{m}$ , depending on population (Table 3). Spatulate, length:width ratio 5:1–10:1, likewise depending on specimen and population (Fig. 2a, d, l, m; Table 3). Oral area distinctly flattened laterally and set off from cylindroidal postoral portion by narrowed neck, often conspicuously axe-shaped and occasionally curved laterally. Cells very flexible and rather fragile, those from Australian population contracted by up to 50% under cover glass pressure. Macronuclear nodules scattered throughout trunk, ellipsoidal, number highly variable, depending on specimen and population (Fig. 2a, g; Table 3); rarely, nodules obtain moniliform

**Table 3.** Morphometric data from three populations (Pop) of *Arcuospathidium multinucleatum*: KT (Kenya, type), KS (Kenya, Shimba Hills, sample 8), AU (Australia)

Character <sup>a</sup>	Pop	$\bar{x}$	M	SD	CV	Min	Max	n
Body, length	KT	124.1	124.5	10.7	8.6	103	138	10
	KS	141.0	140.0	15.2	10.8	120	165	10
	AU	156.4	159.5	25.4	16.3	118	192	10
Body, width	KT	16.7	17.0	1.2	6.9	15	18	10
	KS	29.3	30.0	4.9	16.6	20	35	10
	AU	15.6	15.5	2.4	15.5	12	19	10
Oral bulge (circumoral kinety), length	KT	27.2	28.0	3.4	12.5	21	31	10
	KS	41.6	42.5	5.4	12.9	35	50	10
	AU	37.0	35.0	7.7	20.9	26	47	10
Macronuclei, number	KT	46.9	45.0	11.2	23.8	30	65	10
	KS	39.6	38.0	10.2	25.8	24	55	10
	AU	32.6	33.0	9.7	29.9	14	44	10
Macronuclear nodules, length	KT	5.5	5.3	2.3	41.7	3	11	10
	KS	8.9	10.0	2.3	25.6	5	12	10
	AU	6.5	6.0	1.4	22.1	5	9	10
Macronuclear nodules, width	KT	2.7	2.7	0.6	22.2	2	4	10
	KS	4.4	4.0	1.1	24.4	3	7	10
	AU	4.3	4.0	1.2	27.0	3	6	10
Micronuclei, number	KT	12.3	11.5	2.7	21.7	8	17	10
	KS	12.0	13.0	3.3	27.8	5	17	10
	AU	8.8	8.5	2.6	30.2	5	12	10
Micronuclei, largest diameter	KT	1.6	1.6	0.1	7.2	1.4	1.8	10
	KS	2.0	2.0	0.0	0.0	2	2	10
	AU	1.8	2.0	0.2	12.9	1.3	2	10
Somatic kineties, number	KT	14.6	15.0	1.7	11.7	11	17	10
	KS	17.5	18.0	1.4	8.2	15	19	10
	AU	12.8	12.0	1.1	8.9	12	15	10
Basal bodies in a right lateral kinety, number	KT	60.3	57.5	15.1	25.1	40	90	10
	KS	57.3	57.5	7.4	12.9	45	68	10
	AU	50.7	46.0	13.9	27.5	34	72	10
Dorsal brush rows, number	KT	3.1	3.0	–	–	3	4	10
	KS	3.0	3.0	–	–	3	3	10
	AU	3.1	3.0	–	–	3	4	10
Dorsal brush kinety 1, length <sup>b</sup>	KT	21.4	21.5	2.9	10.8	17	25	10
	KS	29.5	30.0	4.4	14.9	22	35	10
	AU	20.4	19.5	3.9	19.4	15	30	10
Dorsal brush kinety 2, length <sup>b</sup>	KT	21.8	22.0	3.1	14.3	15	25	10
	KS	31.6	30.5	4.4	13.9	25	40	10
	AU	24.2	23.5	3.8	15.6	19	32	10
Dorsal brush kinety 3, length <sup>b</sup>	KT	18.1	18.0	3.0	16.4	11	22	10
	KS	25.7	25.0	5.8	22.5	17	35	10
	AU	23.3	22.5	3.9	16.7	19	31	10

<sup>a</sup> Data based on protargol-impregnated, mounted specimens from field (protocol A in Foissner, 1991). Measurements in  $\mu\text{m}$ . CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation,  $\bar{x}$  – arithmetic mean.

<sup>b</sup> Measured as distance from circumoral kinety to proximal end of row.

configuration, i.e., are connected by fine strands. Micronuclei scattered between macronuclear nodules, globular and heavily impregnated by protargol. Contractile vacuole in posterior body end, several excretory pores in pole area. Extrusomes very similar in all populations, rod-shaped to slightly fusiform, 4–5 µm long, densely spaced in oral bulge and scattered in cytoplasm (Fig. 2c); about 3 µm long and more or less heavily impregnated in protargol slides. Cortex very flexible, contains about 5 rows of colourless granules (<1 µm across) between each two ciliary rows (Fig. 2j), pellicle of Australian population partially covered by 2–3 µm long bacterial rods. Cytoplasm, except for flat and hyaline oral portion, more or less densely packed with 1–7 µm sized fat globules, depending on nutrition state. Very likely feeds mainly on ciliates. Swims rather clumsily but creeps versatily on soil particles, showing great flexibility.

Somatic cilia about 10 µm long, fairly widely spaced, arranged in longitudinal rows anteriorly curved dorsally and distinctly separate from circumoral kinety; monokinetidal anterior tail of dorsal brush kineties curved ventrally, occasionally abutting to circumoral kinety (Fig. 2e, f, h). Dorsal brush 16%–24% of body length, depending on population (Table 3), consists of 3 (rarely 4) rows of narrowly spaced dikinetids having 2–4 µm long, distally slightly inflated cilia; row 3 continues with about 1 µm long, monokinetidal bristles to mid-body (Fig. 2a, e, h, k).

Oral bulge distinctly inclined to ventral side and slenderly cuneate, bright because packed with extrusomes, base surrounded by cuneate circumoral kinety composed of closely spaced dikinetids, contains minute conical depression near dorsal end, very similar to that found in *Spathidium seppelti* Petz and Foissner, 1997; depression occasionally marked by minute notch on bulge surface, lined by fine fibres recognisable only in excellently prepared specimens, more distinct in Australian than in African type population (Fig. 2a, b, h, i). Nematodesmata very fine, originate from oral dikinetids, form inconspicuous basket (Fig. 2g).

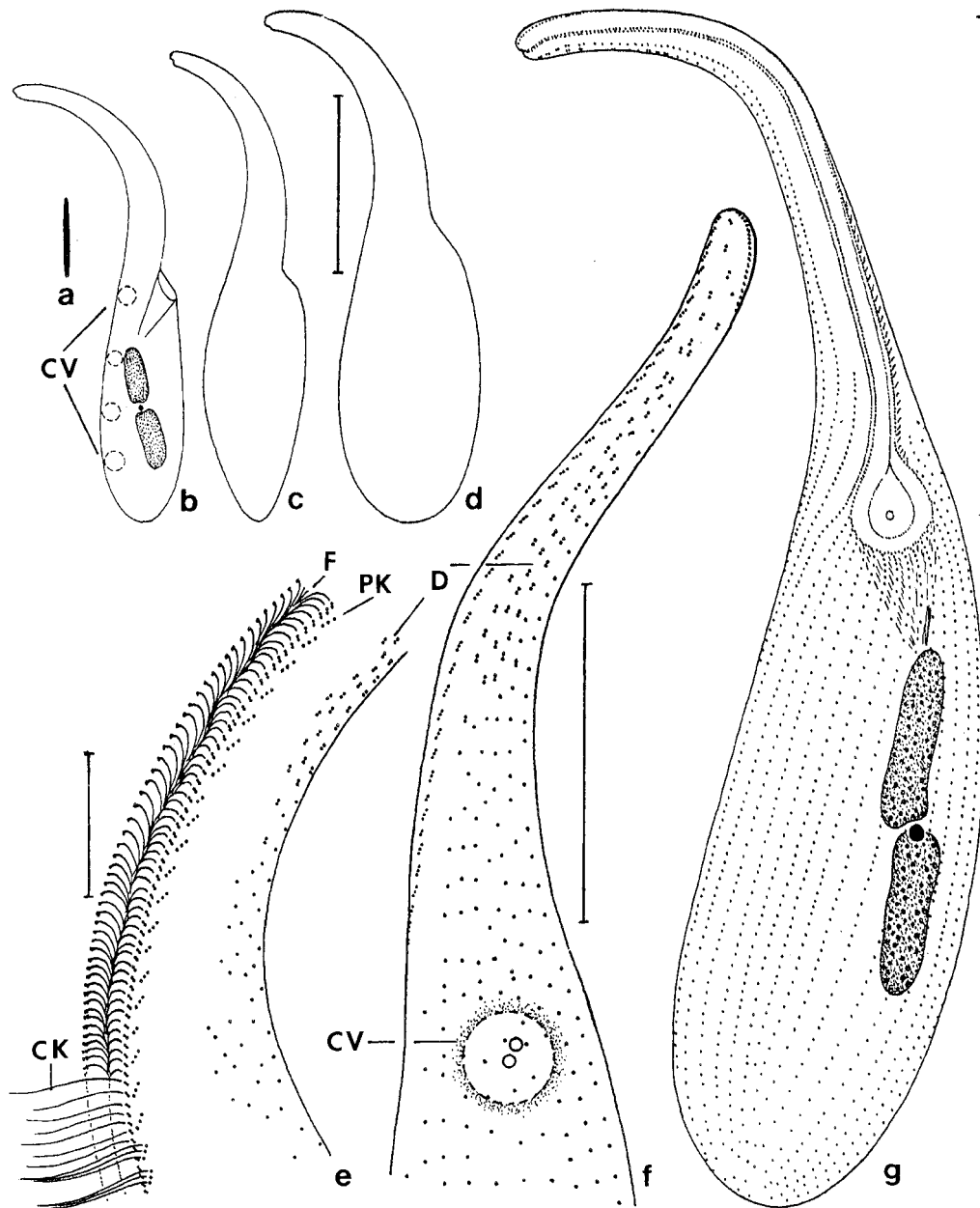
**Occurrence and ecology:** As yet found at type location (forest in the Escarpment Mountains near Nairobi, mixture of leaf litter and red soil, pH 6.6), in the Shimba Hills Nature Reserve (sample 8; Table 3), in Australia (Green Island near Cairns, mixture of litter and brownish soil from the Palm-girdle about 30 m inshore, pH 7.1; collected on 8.2.1987; Table 3), and in Venezuela (0–5 cm very sandy Savannah soil near Puerto Ayacucho, pH 6.0; collected on 6.2.1996). These data indicate that *A. multinucleatum* is very likely cosmopolitan, possibly preferring circumneutral conditions.

**Comparison with related species:** *Arcuospathidium multinucleatum* is a typical member of the genus, as diagnosed by Foissner (1984): most ciliary rows are distinctly separate from the circumoral kinety, the oral bulge is cuneate, and the body is large and slender. *Arcuospathidium multinucleatum* is easily distinguished from the congeners by the numerous macronuclear nodules; all other species have a filiform or reniform macronucleus or two large nodules (Foissner, 1984, 1996b). No *Spathidium* species was found in the older literature which might be identical with *A. multinucleatum*.

#### ***Dileptus similis* Foissner, 1995 (Fig. 3a–g; Table 4)**

When I described this species from Costa Rica in 1995, I overlooked that I had found it previously in Kenya. However, this is a fortunate circumstance because the independent observations eliminate my concern about synonymy of *D. similis* and *D. mucronatus*. Obviously, both are distinct species, differing mainly in the shape of the body, namely the presence (in *D. mucronatus*) vs. the absence (in *D. similis*) of a tail.





**Figures 3a–g.** *Dileptus similis* from life (a–d) and after protargol impregnation (e–g). **a:** Extrusome, length 7–8  $\mu\text{m}$ . **b–d:** Shape and size variability, scale bar 100  $\mu\text{m}$ . **e, f:** Infraciliature of left and dorsal side of proboscis, scale bars 10  $\mu\text{m}$ , respectively, 30  $\mu\text{m}$ . **g:** Total ventral view of somatic and oral infraciliature, scale bar 100  $\mu\text{m}$ . CK – circumoral kinety, CV – contractile vacuoles, D – dorsal brush, F – fibres, PK – preoral kineties.

**Table 4.** Morphometric data from *Dileptus similis*. Upper line: type population from Costa Rica (from Foissner, 1995). Lower line: population from the Shimba Hills Nature Reserve in Kenya

Character <sup>a</sup>	$\bar{x}$	M	SD	CV	Min	Max	n
Body, length	218.7	210	27.4	12.5	170	280	12
	245.1	240	20.6	8.4	216	288	11
Body, width	56.7	55	13.9	24.6	37	83	12
	43.0	44	4.8	11.2	36	50	11
Anterior somatic end to proximal vertex of circumoral kinety	104.3	103	19.2	18.4	80	140	12
	121.5	120	11.5	9.4	112	152	11
Macronuclear nodules, length	36.8	39	7.1	19.3	22	45	12
	32.1	32	3.9	12.0	26	38	11
Macronuclear nodules, width	10.5	10	1.6	15.5	8	13	12
	9.4	10	0.8	8.6	8	10	11
Micronucleus, diameter	2.8	3	0.6	22.6	1.5	3.5	12
	2.6	2.4	–	–	2.4	3.0	11
Somatic kineties, number	28.7	28	2.6	9.2	25	32	7
	31.5	31	2.2	7.0	28	35	11
Macronuclear nodules, number	2.0	2	0.0	0.0	2	2	12
	2.0	2	0.0	0.0	2	2	11
Micronuclei, number	1.0	1	0.0	0.0	1	1	12
	1.0	1	0.0	0.0	1	1	11

<sup>a</sup>Data based on protargol-impregnated, mounted specimens from field (protocol A in Foissner, 1991). Measurements in  $\mu\text{m}$ . CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation,  $\bar{x}$  – arithmetic mean.

The population from the Shimba Hills (sample 8) matches the original description very well. Some small differences, for instance, in body size and shape, need not to be detailed because they are evident from Figures 3a–g and the morphometric data compiled in Table 4. Two voucher slides have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria.

***Plagiocampa bitricha* nov. spec.** (Fig. 4a–m; Table 5)

I studied three populations of this species (see occurrence and ecology section). They are very similar, in spite of the great geographical distance between them. Thus, the diagnosis and description comprise all populations. Morphometric data, however, are kept separate (Table 5).

**Diagnosis:** Size in vivo about  $40 \times 23 \mu\text{m}$ ; ellipsoidal. Extrusomes mainly in oral area, slightly fusiform, 2–3  $\mu\text{m}$  long. 2 caudal cilia. 18 somatic kineties and 14 oral dikinetids (flaps) on average.

**Type location:** Canary Islands, Tenerife (W17°, N28°), soil near beach of Candelaria.

**Type slides:** Two slides (1 holotype and 1 paratype) with protargol-impregnated specimens from the type location have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria. One voucher slide each with Chatton-Lwoff silver nitrate-impregnated specimens from the Australian populations has also been deposited. The

slides contain several specimens, with relevant cells marked by a black ink circle on the cover glass.

*Etymology*: “bitricha” (Lat., two hairs) refers to the two caudal cilia, a main species character of *P. bitricha*.

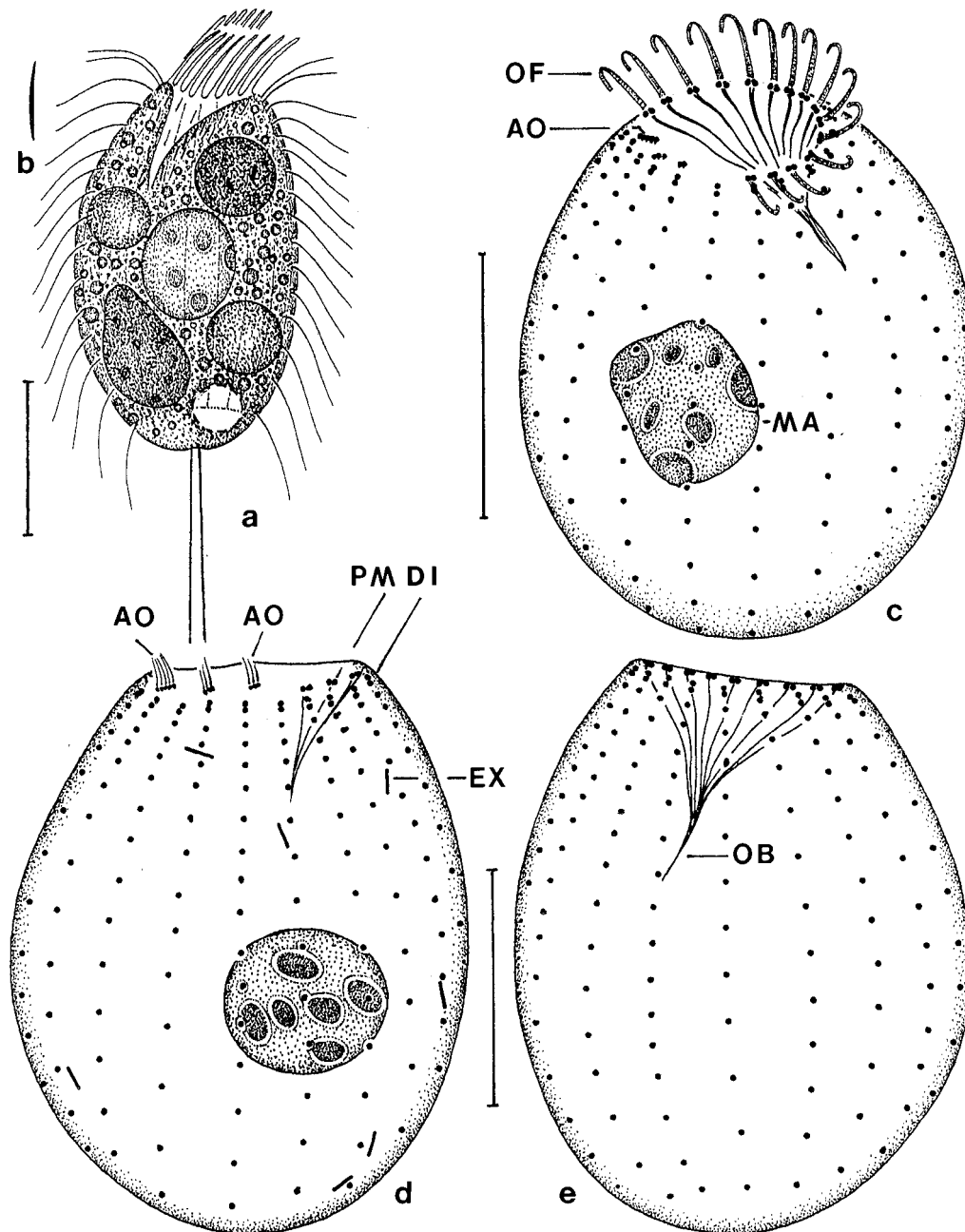
*Description*: Size in vivo  $30\text{--}50 \times 20\text{--}30\ \mu\text{m}$ . Shape fairly variable, depending on nutrition state; usually ellipsoidal and slightly asymmetrical because laterally up to 1.5:1 flattened and dorsal side more distinctly vaulted than ventral (Fig. 4a, f–h, k–m); overfed specimens bluntly fusiform and unflattened (Fig. 4i). Macronucleus in or near body centre, spherical, contains small and large globular nucleoli. Micronucleus not seen, not stained by protargol. Excretory pore of contractile vacuole on ventral side subterminal at border of ciliated/unciliated body portion. Cytopyge near contractile vacuole. Cortex flexible, without extrusomes. Extrusomes mainly around pharyngeal basket, slender and inconspicuous,  $2\text{--}3\ \mu\text{m}$  long and slightly fusiform (Fig. 4a, b, f). Usually rather dark at low ( $\leq \times 100$ ) magnification due to many  $0.5\text{--}1\ \mu\text{m}$  sized, compact (not ring-shaped as in some congeners) globules and some up to  $10\ \mu\text{m}$  sized food vacuoles containing protozoan prey (Fig. 4a, k, l). I observed a specimen ingesting a naked amoebae by putting the widely opened mouth over the prey and engulfing it whole. Swims rather fast and shakily, frequently changing direction.

Normal somatic cilia  $8\text{--}10\ \mu\text{m}$  long, arise from distinct cortical pits, more narrowly spaced anteriorly than posteriorly, number of cilia per kinety distinctly lower in one of the two Australian populations (Table 5); caudal cilia about  $20\ \mu\text{m}$  long, very fragile and frequently shed when cells are immobilized by cover glass pressure. Ciliary rows extend meridionally and equidistantly, commence close underneath oral opening with a pair of basal bodies, slightly shortened posteriorly, leaving blank small pole area containing 2, occasionally 3 caudal cilia (Fig. 4a–i, k, m).

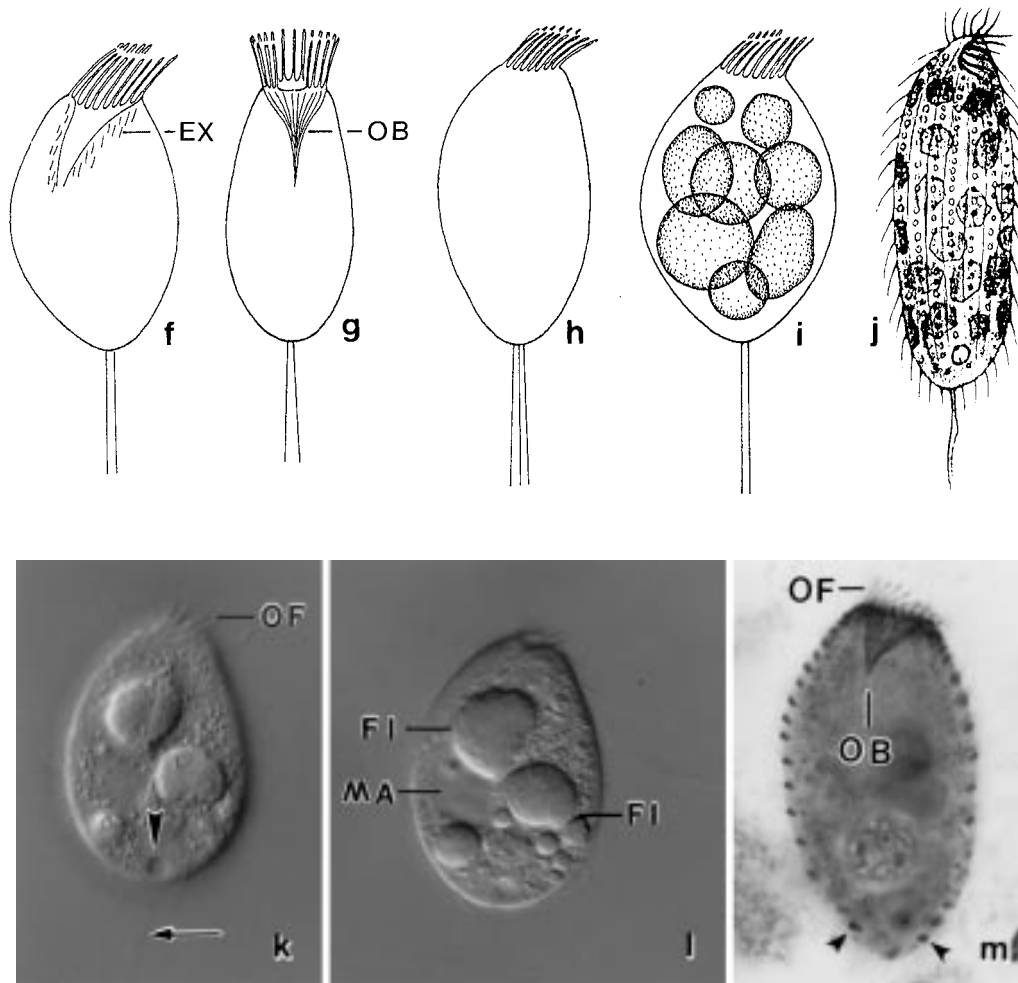
Oral opening occupies anterior body end, almost entirely surrounded by dikinetids (undulating membrane) associated with about  $8\ \mu\text{m}$  long, ventrally curved flaps that frequently beat up and down, giving the impression of a digitate membrane (Fig. 4a, f, g, k). Adoral organelles (brosse) minute, side by side at end of three ventral somatic kineties, interrupt dikinetidal undulating membrane, very likely composed of dikinetids, right organelle with 4–5 short cilia, middle and left organelle each with 2–3 cilia (Fig. 4c, d). Pharyngeal basket oblique-conical, that is, ventrally longer than dorsally, open on ventral (brosse) side, basket rods distinct and originating from dikinetids comprising undulating membrane (Fig. 4a, e, f, g, m).

*Occurrence and ecology*: As yet found at type location (Tenerife, 0–3 cm lightgrey, non-saline soil layer mixed with very few roots and litter, pH 8.2; collected by Dr. B. Krassnigg in 1987), in the Shimba Hills Nature Reserve (sample 15), and at two sites in Australia (0–5 cm reddish soil and litter layer from the semi-desert near Erldunda, E133°, S26°, pH 6.2, collected on 31.1.1987; dark mud from rock-pools at bank of Shoalhaven River near Bungonia, E149°, S35°, pH 7.0, collected on 10.11.1994 by Dr. I. Foissner). These data indicate that *P. bitricha* is cosmopolitan with a wide ecological range, occurring in both true terrestrial and semiterrestrial (rock-pools) habitats.

*Comparison with related species*: At first glance, *P. bitricha* resembles *P. atra* Grandori and Grandori, 1934, which also has two caudal cilia and was discovered in soil from a sewage-irrigated field in Italy. However, Grandori and Grandori (1934) state (Fig. 4j): “Caratteristica è la presenza nell’ectoplasma di serie regolarissime di *perle*, granuli lucenti, considerati come organi filogeneticamente collegati ai *tricocisti* e all’altro tipo di organelli



**Figures 4a–e.** *Plagiocampa bitricha* (type population) from life (a, b) and after protargol impregnation (c–e). **a:** Right lateral view of a representative specimen containing four large food inclusions. **b:** Extrusome, 2–3  $\mu\text{m}$  long. **c–e:** Infraciliature of ventral and dorsal side. AO – adoral organelles, DI – dikinetid at anterior end of somatic kineties, EX – extrusome, OB – oral basket, OF – oral flaps, MA – macronucleus, PM – paroral membrane. Scale bars 15  $\mu\text{m}$ .



**Figures 4f–m.** *Plagiocampa bitricha* (f–i, k–m, population from Erldunda, Australia) and *P. atra* (j; from Grandori and Grandori, 1934) from life (f–l) and after Chatton-Lwoff silver nitrate impregnation (m). **f, g:** Right lateral and ventral view of a representative specimen. Note lateral flattening. **h:** Specimen without food vacuoles and three caudal cilia. **i:** A broadly fusiform specimen with many food inclusions. **j:** *Plagiocampa atra* differs from *P. bitricha* mainly by the pearl-like extrusomes (protrichocysts) between the ciliary rows and the small, closed oral opening. **k, l:** Slightly squeezed specimen at different focal planes. Note large food inclusions and lack of cortical granules (“pearls”). The oral flaps are upright in (k) and curved above the oral opening in (l). Arrow marks caudal cilia; arrowhead denotes contractile vacuole. **m:** Lateral view showing shape and oral structures. Arrowheads mark last basal body of kineties, which end subterminally leaving blank the posterior pole area, in the centre of which two caudal cilia arise. EX – extrusomes, FI – food inclusions, MA – macronucleus, OB – oral basket, OF – oral flaps.

che il Klein ha proposto di chiamare *prototricocisti*. Il Kahl ci segnala che perle così nettamente visibili come nella nostra *P. atra* furono da lui trovate soltanto in forme marine.” Such pearls are definitely absent in *P. bitricha* (Fig. 4k, l). Another, even more

**Table 5.** Morphometric data from three populations (Pop) of *Plagiocampa bitricha*: TE (Tenerife, type), AE (Australia, Erldunda), AB (Australia, Bungonia)

Character <sup>a</sup>	Me <sup>b</sup>	Pop	$\bar{x}$	M	SD	CV	Min	Max	n
Body, length	P	TE	33.1	33	2.1	6.3	30	36	11
	CHL	AE	33.0	33	3.6	10.9	27	38	15
	CHL	AB	31.3	30	2.3	8.8	27	37	15
Body, width	P <sup>c</sup>	TE	24.7	25	2.4	9.6	21	29	11
	CHL	AE	19.2	19	2.7	14.1	15	23	15
	CHL	AB	19.5	19	2.0	10.2	16	24	15
Macronucleus, length	P	TE	10.1	10	0.8	8.2	9	11	11
Macronucleus, width	P	TE	8.6	9	0.9	10.7	7	10	11
Somatic kineties, number	P	TE	18.1	18	0.5	3.0	17	19	11
	CHL	AE	16.7	17	0.8	4.8	15	18	15
	CHL	AB	19.9	20	0.8	4.2	18	21	15
Basal bodies in a dorsal kinety, number <sup>d</sup>	P	TE	16.4	17	2.1	12.9	13	19	11
	CHL	AE	14.3	14	1.3	9.4	12	16	15
	CHL	AB	11.8	12	1.3	11.2	9	13	15
Oral dikinetids, number <sup>e</sup>	P	TE	14.4	14	–	–	14	15	12

<sup>a</sup> Data based on protargol-impregnated, mounted specimens from field (protocol A in Foissner, 1991). Measurements in  $\mu\text{m}$ . CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation,  $\bar{x}$  – arithmetic mean.

<sup>b</sup> Methods: CHL – silver nitrate impregnation after Chatton-Lwoff, as described by Foissner (1991), P – protargol impregnation (Foissner's protocol).

<sup>c</sup> Body rather distinctly inflated by preparation procedures.

<sup>d</sup> Dikinetids counted as 1 basal body.

<sup>e</sup> Number similar (about 12–16) in Australian populations, as charged from basket rods.

distinct difference, concerns the oral opening, which appears small and closed in *P. atra*, while it is always wide open and very conspicuous in *P. bitricha*. Thus, *P. atra* and *P. bitricha* are very likely different species. *Plagiocampa ovata*, discovered by Gelei (1954) in a temporary pool in Hungary, and redescribed by Fauré-Fremiet and André (1965) from moss in France, is similar to *P. bitricha* in almost every respect, except for the single caudal cilium – a difference widely used as species character because of its low variability (Foissner and Pfister, 1997). *Plagiocampa caudata* Alekperov, 1993, also a terrestrial species, has a tuft of 12–15 caudal cilia and only about 8 oral flaps.

#### ***Drepanomonas exigua exigua* Penard, 1922 (Fig. 5a–t; Table 6)**

Although I have not yet found *D. exigua exigua* in Africa, it is redescribed here to make distinct the differences to a new subspecies, *D. exigua bidentata* (described below), which I discovered in Kenya and later found in terrestrial habitats worldwide.

*Neotype material:* No type material of *D. exigua exigua* has been mentioned in the literature. Thus, I deposit two neotype slides with protargol-impregnated cells and two neotype slides with silver nitrate-impregnated specimens (Klein-Foissner method) from the Hanneck Kogel in Austria in the Oberösterreichische Landesmuseum in Linz (LI). The slides contain many specimens, with relevant cells marked by a black ink circle on the cover glass.

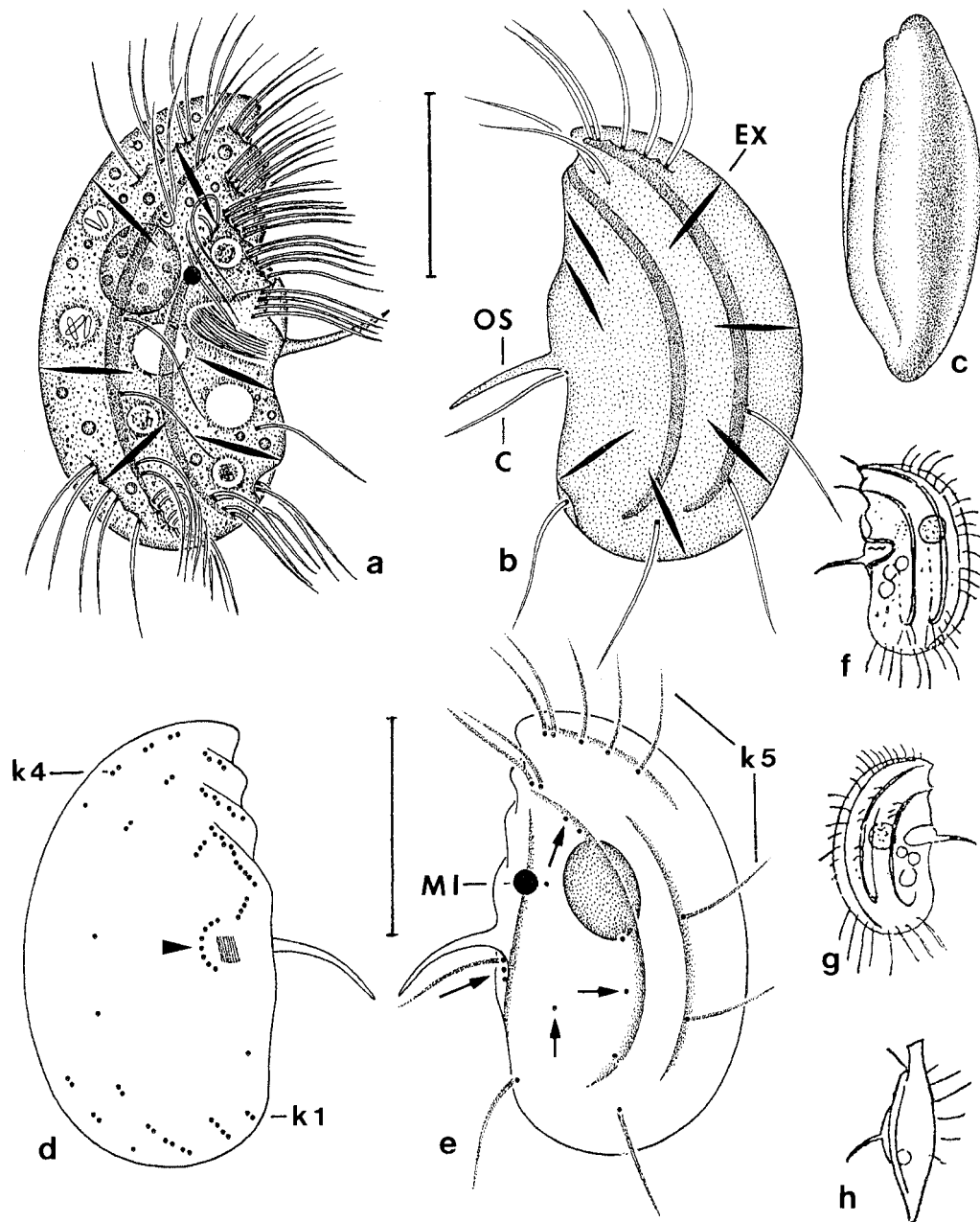
*Redescription:* Size in vivo about  $20\text{--}25 \times 10\text{--}15 \mu\text{m}$ ; laterally flattened up to 2:1, thus ellipsoidal when viewed from dorsal and ventral (Fig. 5c, h, q). Lateral outline rounded triangular, ventral side roughly straight, dorsal distinctly convex, anterior end tapered, posterior broadly rounded. Right and left side each with two conspicuous ridges right and left of midline, that is, along kineties 2 and 3 and, respectively, 5 and 6; ridges commence at anterior end of cell, extend parallel to dorsal curvature, and end subterminally with posterior portion distinctly curved ventrally (Fig. 5a, b, f, g, k, l, s). Ventral side sculptured by clefts containing preoral kineties, oral apparatus, and species-specific oral spine originating from left margin of oral opening slightly underneath mid-body; spine in vivo  $3\text{--}5 \mu\text{m}$  long, straight or slightly curved upward or downward, immobile (Fig. 5a, b, d–i, l, m, q, r, t). Macronucleus slightly ellipsoidal, in vivo about  $5 \mu\text{m}$  in diameter, usually slightly above mid-body right of buccal cavity, contains many globular, pale nucleoli. Micronucleus about  $2 \mu\text{m}$  in diameter, near macronucleus (Fig. 1a, e). Contractile vacuole slightly underneath mid-body near proximal end of buccal cavity in midline of cell (Fig. 5a, j). Cytopyge underneath buccal cavity near ventral margin of cell, in vivo usually marked by a hyaline vacuole, after silver impregnation by a minute, angular silverline (Fig. 5a, n, o). Extrusomes (trichocysts) conspicuous because about  $5 \times 0.8 \mu\text{m}$  in size, fusiform (Fig. 5a, b, j). Cortex colourless, glossy, rigid, cells thus inflexible. Cytoplasm bright, without particular inclusions; food vacuoles  $2\text{--}3 \mu\text{m}$  in diameter, contained bacteria. Glides moderately rapidly on surface of slides and soil particles.

Cilia in vivo  $7 \mu\text{m}$  long, rather stiff, arise at margin of cortical ridges having neat crenellation directed to left in kineties 1–3 and to right in kineties 4 and 5. Ciliary pattern very constant (Table 6) and as shown in Figures 5a, b, d, e, l, n–s; left side sparsely ciliated because about half of basal bodies barren. Four cilia between paroral membrane and preoral kinety 1 form membranous structure; three basal bodies close underneath oral spine, of which only the uppermost is ciliated (Fig. 5b, e, m, q, t). Kinety 3 distinctly more densely ciliated in Marion Island (Fig. 5s) than in Austrian (Fig. 5a, d) population.

Oral opening about  $5 \times 2.5 \mu\text{m}$ , reniform, in mid-body of ventral side (Fig. 5a, d, i, n, q, r, t). Buccal cavity conspicuous because extending almost to midline of cell and broadly horn-shaped. Adoral membranelles at bottom of cavity, minute and compact, details could thus not be recognised. Paroral membrane also within buccal cavity, semicircular, composed of about 8 basal bodies (Fig. 5d).

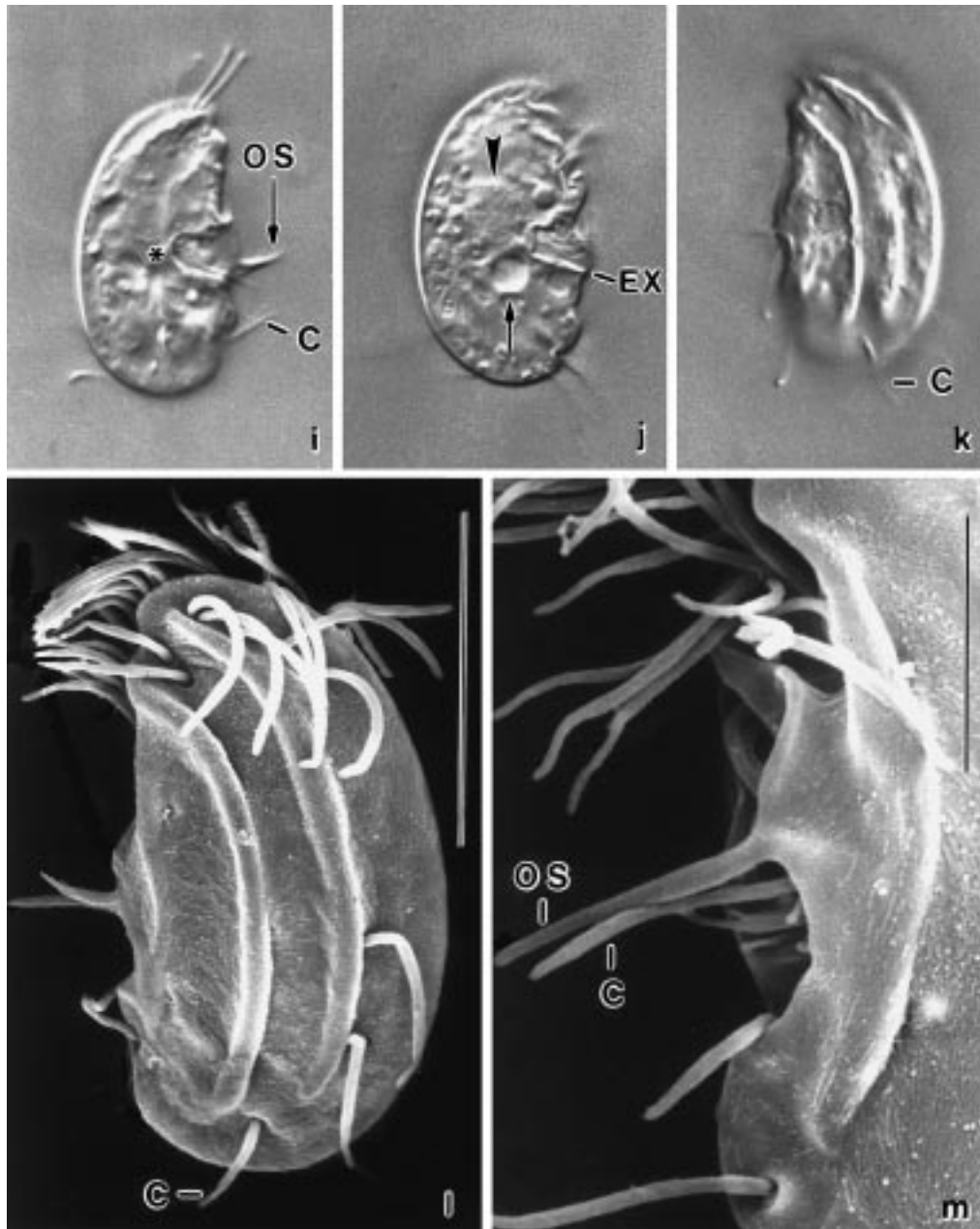
*Occurrence and ecology:* Penard (1922) discovered *D. exigua exigua* in a *Sphagnum* pond in Switzerland, where it occurred together with *D. dentata* and *D. obtusa*. I found it in Austria, Germany, and on an island in the Indian ocean, indicating that it is very likely cosmopolitan. Brief site descriptions: Austria (neotype population), on top of the Hanneck Kogel (about 1800 m above sea-level) near the village of Thumersbach (Salzburg, Zell am See), collected on 2.8.1988 by H. Augustin, mainly spruce needles mixed with some dark humus, mosses, lichens, and grass roots; Germany, litter from a beech forest near Munich, collected on 30.8.1987; Marion Island in the southern Indian ocean, near meteorological station, grass (*Poa* sp.) sward with many roots and black soil, pH 6.3 [detailed site description in Foissner (1996a), where the species was, unfortunately, misidentified as *D. exigua bidentata*].

*Comparison with literature data:* My observations match those mentioned in the original description (Penard, 1922) very well. Thus, identification is beyond any reasonable doubt (cp. Fig. 5a–h). The ciliary pattern was not yet studied in detail previously. It is, like the general body organization, very similar to that of *D. revoluta*, as redescribed by Kahl

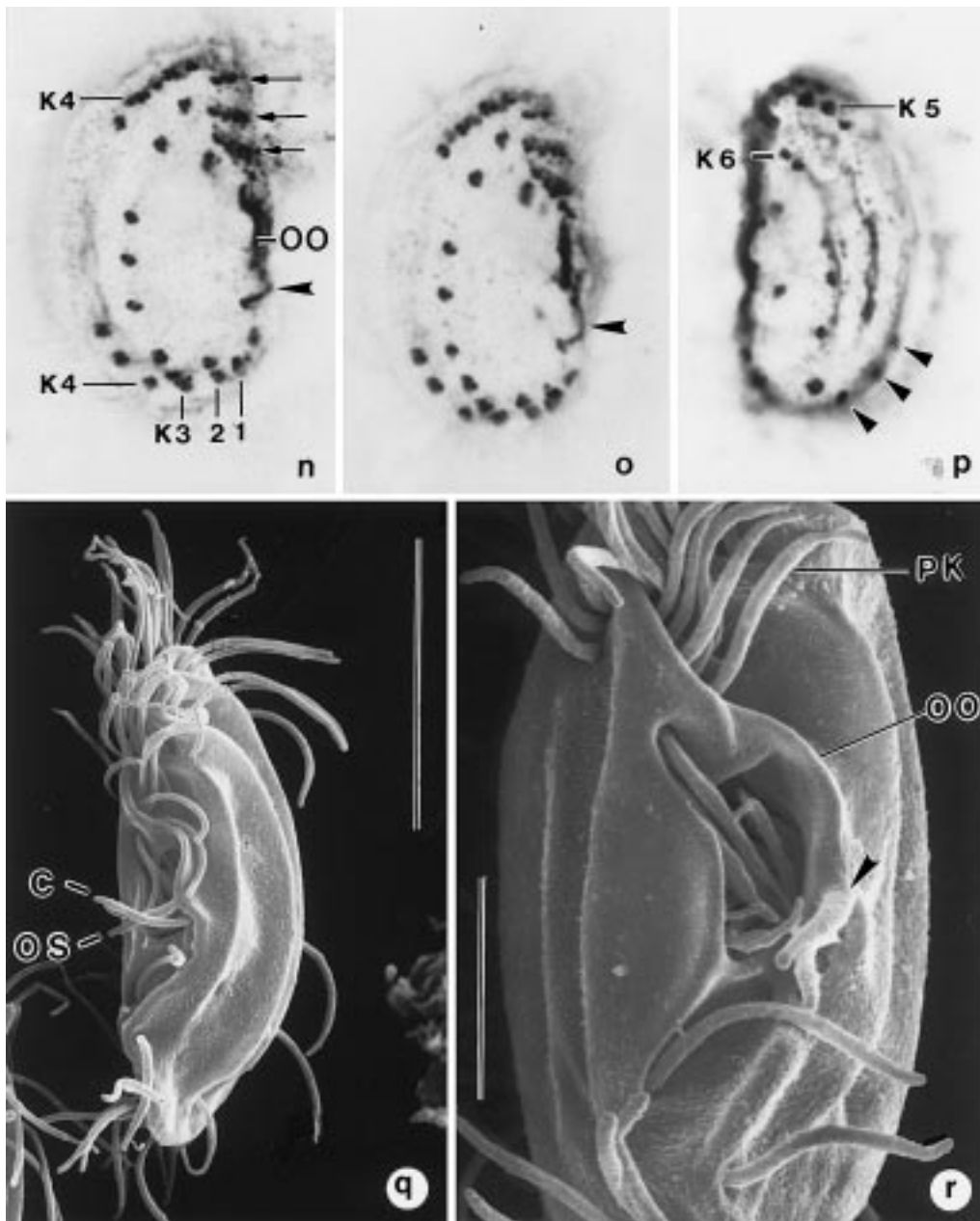


**Figures 5a–h.** *Drepanomonas exigua exigua*, Austrian neotype (a–e) and original (f–h; from Penard, 1922) population from life (a–c, f–h) and after protargol impregnation (d, e). **a, b, f, g:** Right and left lateral views of representative specimens. Note the species-specific oral spine and two distinct ridges each in midline of right and left side (cp. Fig. 5l, s). **c:** Dorsal view (after a SEM micrograph). **d, e:** Infraciliature of right and left side. All basal bodies of the right side are ciliated, on left some are barren (arrows). Arrowhead marks paroral membrane. **h:** Ventrolateral view. C – cilium, EX – extrusome, K 1, 4, 5 – kineties (ciliary rows), MI – micronucleus, OS – oral spine. Bars 10 µm.

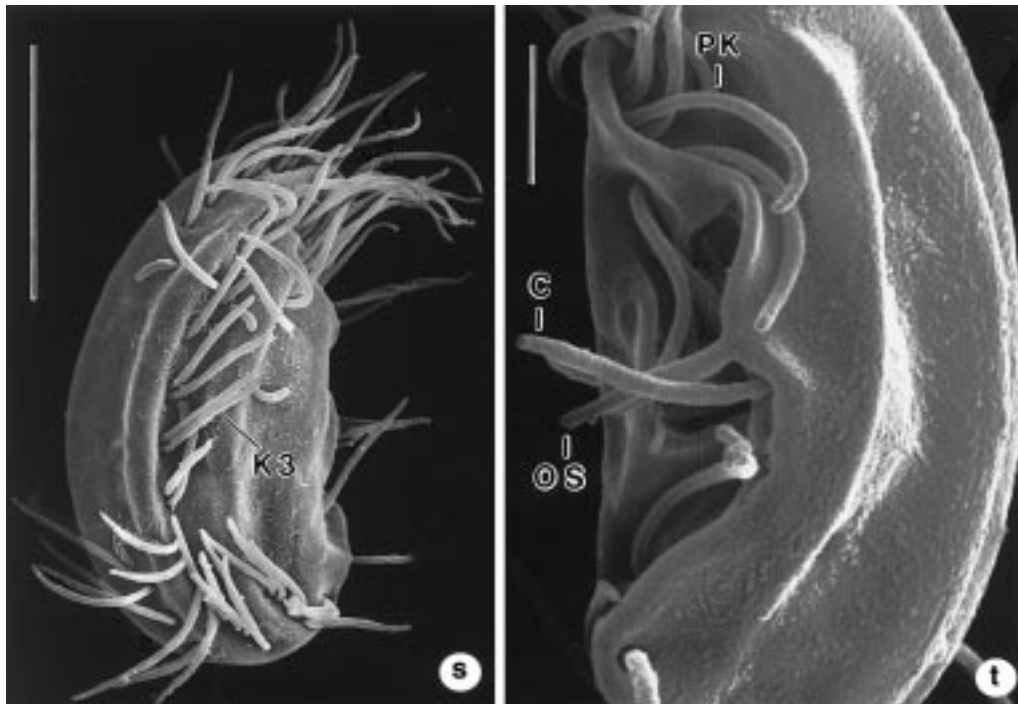




**Figures 5i–m.** *Drepanomonas exigua exigua*, Austrian neotype population from life (i–k) and Marion Island population in the scanning electron microscope (l, m). **i, j:** Right side views of same specimen at different focal planes. Asterisk marks proximal margin of buccal cavity; arrow denotes contractile vacuole, arrowhead marks macronucleus. **k–m:** Left side views showing two conspicuous ridges in midline of cell and oral spine close beneath which a cilium arises. C – cilium, EX – extrusome, OS – oral spine. Bars 10  $\mu$ m and 4  $\mu$ m.



**Figures 5n–r.** *Drepanomonas exigua exigua*, Austrian neotype population after Klein-Foissner silver nitrate impregnation (n–p) and Marion Island population in the scanning electron microscope (q, r). **n, o:** Right side views. Arrows mark preoral kineties, arrowheads denote silverline marking cytophyge. **p:** Left side view. Arrowheads mark kinetids from kinety 4 on right side. **q, r:** Ventral views showing the highly sculptured cell surface. Arrowhead marks oral spine. C – cilium, K1–6 – kineties (ciliary rows), OO – oral opening, OS – oral spine, PK – preoral kinety. Bars 10  $\mu$ m and 4  $\mu$ m.



**Figures 5s, t.** *Drepanomonas exigua exigua*, scanning electron micrographs from Marion Island population. **s:** Right side view. Note that kinety 3 (K3), which extends between distinct ridges, is more densely ciliated in the Marion Island than in the Austrian population (cp. Fig. 5d, n, o). **t:** Oral area of cell shown in Figure 5q at higher magnification. C – cilium, K3 – kinety (ciliary row) 3, OS – oral spine, PK – preoral kinety. Bars 10  $\mu$ m and 2  $\mu$ m.

(1932) and Foissner (1987b). Accordingly, these species are easily confused because the characteristic spine of *D. exigua exigua* is recognisable only at rather high magnification and does not impregnate with protargol. Thus, identification of *D. exigua*-like populations requires careful observation of live specimens because *D. exigua bidentata* differs from *D. exigua exigua* only by the minute spine on the posterior left surface.

***Drepanomonas exigua bidentata* nov. spec.** (Fig. 6a–i; Table 6)

**Diagnosis:** With about 5  $\mu$ m long spine near posterior end of left side.

**Type location:** Gum tree (*Ficus* sp.) litter in the Nairobi Arboretum, Kenya, equatorial Africa (36°50'E, 2°20'S).

**Type slides:** Two slides (1 holotype and 1 paratype) with protargol-impregnated specimens and two slides (1 holotype and 1 paratype) with silver nitrate-impregnated specimens have been deposited in the Oberösterreichische Landesmuseum in Linz (LI). The slides contain many specimens, with relevant cells marked by a black ink circle on the cover glass.

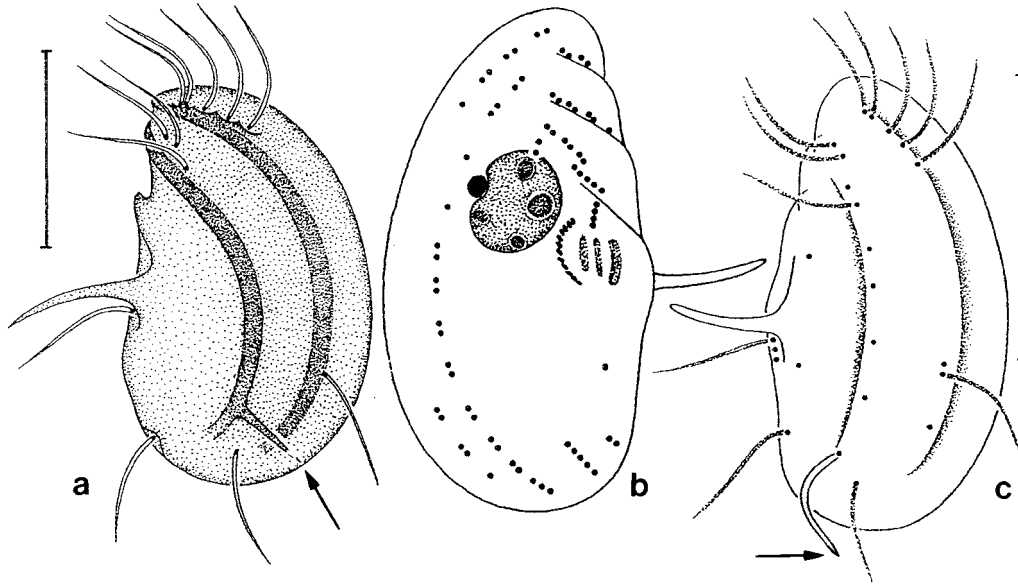
**Etymology:** “bidentata” (Lat., two teeth) because of two spines, that is, an oral and a left lateral spine.

**Table 6.** Morphometric data from *Drepanomonas exigua exigua* (upper line) and *D. exigua bidentata* (lower line)

Character <sup>a</sup>	$\bar{x}$	M	SD	CV	Min	Max	n
Body, length	20.1	20	1.9	9.4	17	23	13
	16.2	16	0.8	4.6	15	17	11
Body, maximum width	10.5	11	0.7	6.3	9	11	13
	8.6	9	0.8	9.1	7	10	11
Anterior end to macronucleus, distance	6.3	7	1.4	21.9	4	8	13
	4.7	5	–	–	4	5	11
Anterior end to paroral, distance	8.2	8	1.2	14.2	6	10	13
	6.3	6	–	–	6	7	11
Macronucleus, length	4.9	5	0.8	16.6	4	7	13
	4.2	4	0.3	7.8	3.5	5	11
Macronucleus, width	3.6	4	0.4	11.6	3	4	13
	3.1	3	0.3	9.1	2.7	3.5	11
Basal bodies in kinty 1, number	1.8	2	–	–	1	2	13
	2.0	2	0.0	0.0	2	2	11
Basal bodies in kinty 2, number	7.0	7	0.0	0.0	7	7	13
	6.5	7	–	–	6	7	11
Basal bodies in kinty 3, number	13.1	13	1.3	9.6	11	15	13
	22.2	22	1.3	6.0	20	25	11
Basal bodies in kinty 4, number	11.6	12	1.0	8.3	10	13	13
	12.4	12	0.9	7.5	11	14	11
Basal bodies in kinty 5, number	8.0	8	0.0	0.0	8	8	13
	8.0	8	0.5	6.3	7	9	9
Basal bodies in kinty 6, number	7.0	7	0.0	0.0	7	7	13
	7.4	7	1.0	13.6	6	9	9
Basal bodies in preoral kinty 1, number	11.0	11	0.0	0.0	11	11	13
	11.0	11	0.0	0.0	11	11	11
Basal bodies in preoral kinty 2, number	7.0	7	0.0	0.0	7	7	13
	7.0	7	0.0	0.0	7	7	11
Basal bodies in preoral kinty 3, number	4.0	4	0.0	0.0	4	4	13
	4.0	4	0.0	0.0	4	4	11
Basal bodies in somatic plus preoral kineties, total number	72.5	73	1.8	2.5	69	75	13
	82.3	82	2.8	3.4	78	88	9

<sup>a</sup> Data based on protargol-impregnated, mounted specimens from field (protocol A in Foissner, 1991). Measurements in  $\mu\text{m}$ . CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation,  $\bar{x}$  – arithmetic mean.

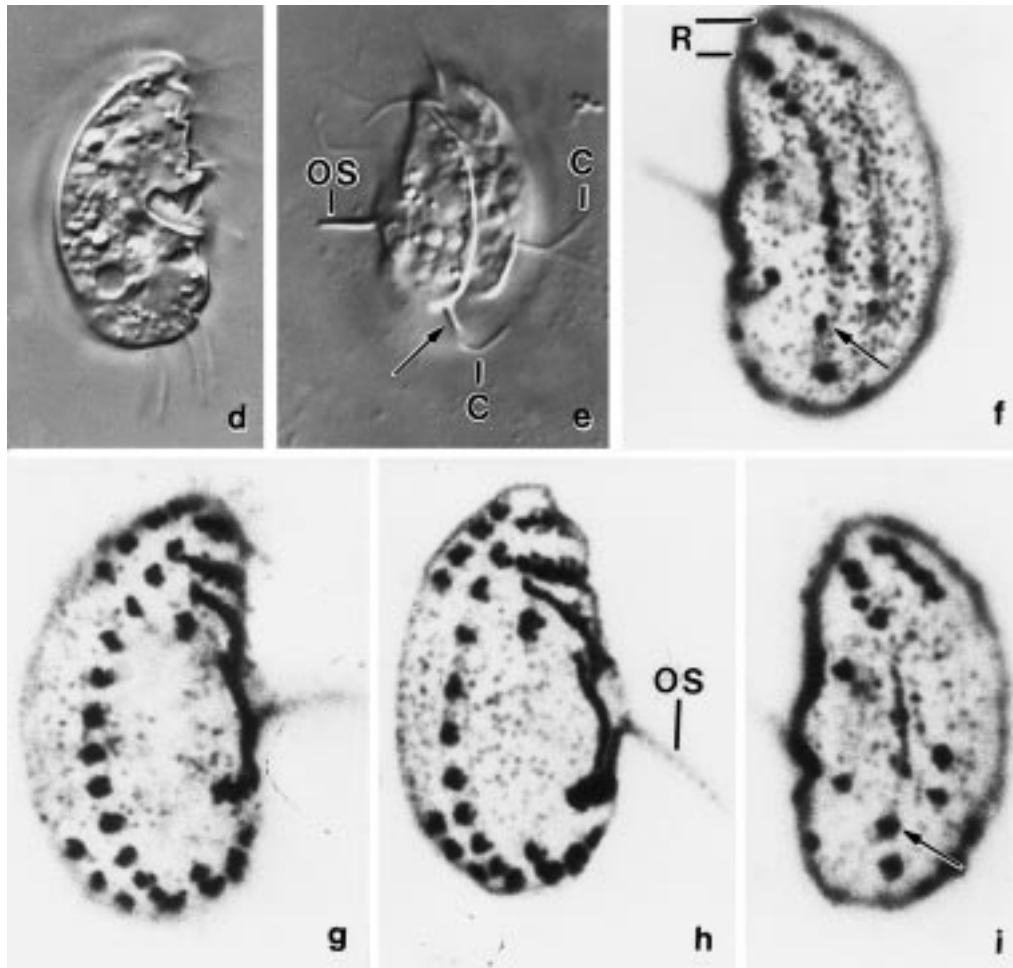
*Description and comparison with related species:* A detailed description of this new subspecies is not necessary because it is very similar to *D. exigua exigua*, as redescribed above; thus, the figures and morphometric data should suffice. The subspecies-specific spine invariably originates from the right ridge near the posterior end of the left side. The spine is not easy to recognise because it is very hyaline and near the last cilium of kinty 6; at or very near to the spine there is an unciliated basal body (Fig. 6c, f, i).



**Figures 6a–c.** *Drepanomonas exigua bidentata* from life (a) and after protargol impregnation (b, c). **a:** Left side view showing the subspecies-specific spine (arrow) originating from the right ridge. **b, c:** Infraciliature of right and left side. All basal bodies of the right side are ciliated, on left some are barren. Arrow marks spine close beneath which is a cilium. For detailed labelling, see *D. exigua exigua* and following figures. Bars 10  $\mu$ m.

*Drepanomonas exigua bidentata* differs from *D. exigua exigua*, as redescribed above, by the spine on the left surface, the slightly smaller size (in vivo about  $17\text{--}22 \times 8\text{--}14$  vs.  $20\text{--}25 \times 10\text{--}15$   $\mu$ m; Table 6), and the more densely ciliated kinety 3 (Fig. 6b, g, h; Table 6). However, ciliation of *Drepanomonas* spp., although being usually very stable within a certain morphotype (Table 6; Foissner, 1987b), is highly variable between populations, possibly due to microspecies formation. For instance, the population of *D. exigua exigua* from Marion Island has, like *D. exigua bidentata*, a densely ciliated kinety 3. Thus, the only reliable difference between these populations is the minute lateral spine, suggesting that they should be separated not at species but at subspecies level.

**Occurrence and ecology:** Over the years, I found populations of *D. exigua bidentata* in soil samples from Africa, Australia, and Europe, indicating that it is cosmopolitan inhabiting a wide range of habitats. Brief site descriptions: Kenya (Africa), Nairobi Arboretum (type population), upper (0–2 cm) litter layer under a gum tree, pH 7.5, collected on 30.6.1985; Kenya (Africa), Shimba Hills (sample 8); South Australia, surroundings of Adelaide, upper (0–5 cm) litter and soil layer of a secondary pine forest (pH 5.1) and of a *Eucalyptus* forest (pH 5.7) in the Belair National Park, collected in February 1987 (for details, see sites 10 and 14 in Blatterer and Foissner, 1988); Denmark, litter, roots and soil under coastal plants at Aarhus, slightly saline, pH 7.2, collected on 14.8.1987; Austria, upper (0–10 cm) litter and soil layer of a beech forest in the surroundings of the city of Salzburg, pH 6.4, collected in May 1997.



**Figures 6d–i.** *Drepanomonas exigua bidentata* from life (d, e) and after Klein-Foissner silver nitrate impregnation (f–i). **d, e:** Right and left side view. The arrow marks the subspecies-specific spine originating from the right ridge; close underneath the spine is the last cilium of kinety 6. **f–i:** Infraciliature of right (g, h) and left (f, i) side. Arrows mark unciliated basal body at site where the spine originates. C – cilia, OS – oral spine, R – ridges.

***Parafurgasonia protectissima* (Penard, 1922) nov. comb.** (basonym: *Nassula protectissima*; Fig. 7a–x, 8a–p; Table 7)

Over the years, I studied, albeit with varying precision, four populations of this species collected in edaphic habitats from Africa, Australia and South America (see occurrence and ecology section). Although they differ in some details, all belong very likely to the same species because they have distinct trichocysts, a rather short paroral membrane and pharyngeal basket, and a single hypostomial organelle. The following diagnosis and redescription are based on the original description and on the populations from the Republic of South Africa (neotype population) and the Cape Verde Islands, which are so similar that conspecificity is beyond reasonable doubt.

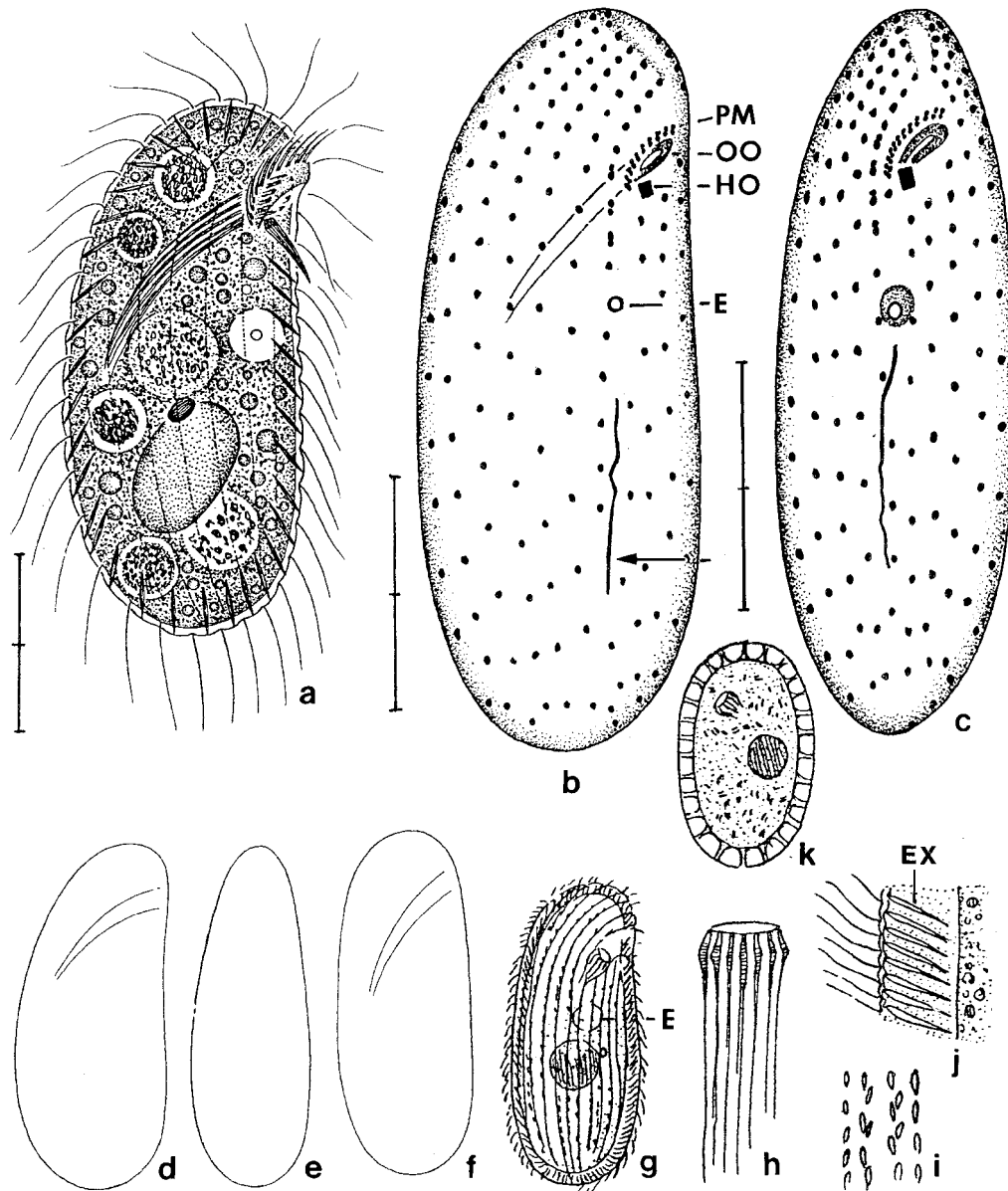
*Improved diagnosis:* Size in vivo about  $60 \times 25 \mu\text{m}$ , ellipsoidal with ventral side flattened and dorsal vaulted. Contractile vacuole in to distinctly above mid-body. Two kinds of extrusomes: trichocysts in distinct rows, fusiform,  $4\text{--}7 \mu\text{m}$  long; mucocysts scattered, about  $1 \mu\text{m}$  in diameter, form voluminous coat when extruded. 16–22, usually 17–20 somatic kineties. Oral opening distinctly subapical, pharyngeal basket composed of about 10 slightly curved rods obliquely extending to mid-body. Hypostomial organelle usually composed of three kineties with three ciliated monokinetids each. Paroral membrane curved, extends along right and anterior margin of oral opening, composed of about 12 dikinetids.

*Neotype material:* No type material of *P. protectissima* has been mentioned in the literature. Thus, I deposit two neotype slides with Chatton-Lwoff silver nitrate-impregnated specimens and two neotype slides with protargol-impregnated cells from the Kruger National Park (Republic of South Africa) in the Oberösterreichische Landesmuseum in Linz (LI). The slides contain many specimens, with relevant cells marked by a black ink circle on the cover glass.

*Redescription:* Size in vivo  $50\text{--}70 \times 20\text{--}30 \mu\text{m}$ ; slightly to distinctly (up to 2:1) flattened laterally, dorsal, respectively, ventral view elongate oval (Fig. 7e). Shape very susceptible to changing environmental conditions and depending on specimen and population: lateral outline of South African specimens usually ellipsoidal with ventral side flattened and dorsal rather distinctly vaulted (Fig. 7a), Cape Verde population reniform (Fig. 7d), Australian specimens parallel-sided with both ends broadly rounded (Fig. 7f); preorally usually slightly projecting due to hyaline lip covering right half of oral area (Fig. 7a, g). Macronucleus ellipsoidal, in vivo about  $15 \times 8 \mu\text{m}$ , location rather variable, usually, however, in middle third or posterior half of cell; nucleoli large, globular. Micronucleus ellipsoidal, attached to macronucleus. Contractile vacuole at to distinctly above mid-body, with conspicuous excretory pore invariably between first postoral kinety and ciliary row facing undulating membrane (Fig. 7a–c, g, u, 8a, b, g–j, p; Table 7). Cytopyge close underneath excretory pore, extends to near posterior body end. Extrusomes (trichocysts) in distinct rows along somatic kineties, obliquely attached to pellicle, compact and fusiform, length depending on population ( $4 \mu\text{m}$  in Cape Verde specimens,  $4\text{--}6 \mu\text{m}$  in South African specimens,  $7 \mu\text{m}$  in Australian specimens); released trichocysts up to  $50 \times 1.5 \mu\text{m}$ , hyaline, anterior region frequently curved hook-like (Fig. 7a, g, j, o, p, s, u, 8a, d, f). Mucocysts irregularly arranged,  $0.8\text{--}1.2 \mu\text{m}$  in diameter, very hyaline and thus difficult to recognise in living cells; are extruded when methyl green-pyronin is added, swelling to voluminous, fibrous coat eventually forming membranous structures after some time (Fig. 7t, 8e). Cortex about  $1 \mu\text{m}$  thick, bright, distinctly punctate by extrusomes and about  $1 \mu\text{m}$  deep ciliary pits. Cells colourless, cytoplasm filled with  $1\text{--}3 \mu\text{m}$  sized fat globules and up to  $15 \mu\text{m}$  large food vacuoles with fluffy content, possibly bacterial residues. Creeps and/or swims moderately fast by rotation about main body axis, jerky when trichocysts are extruded.

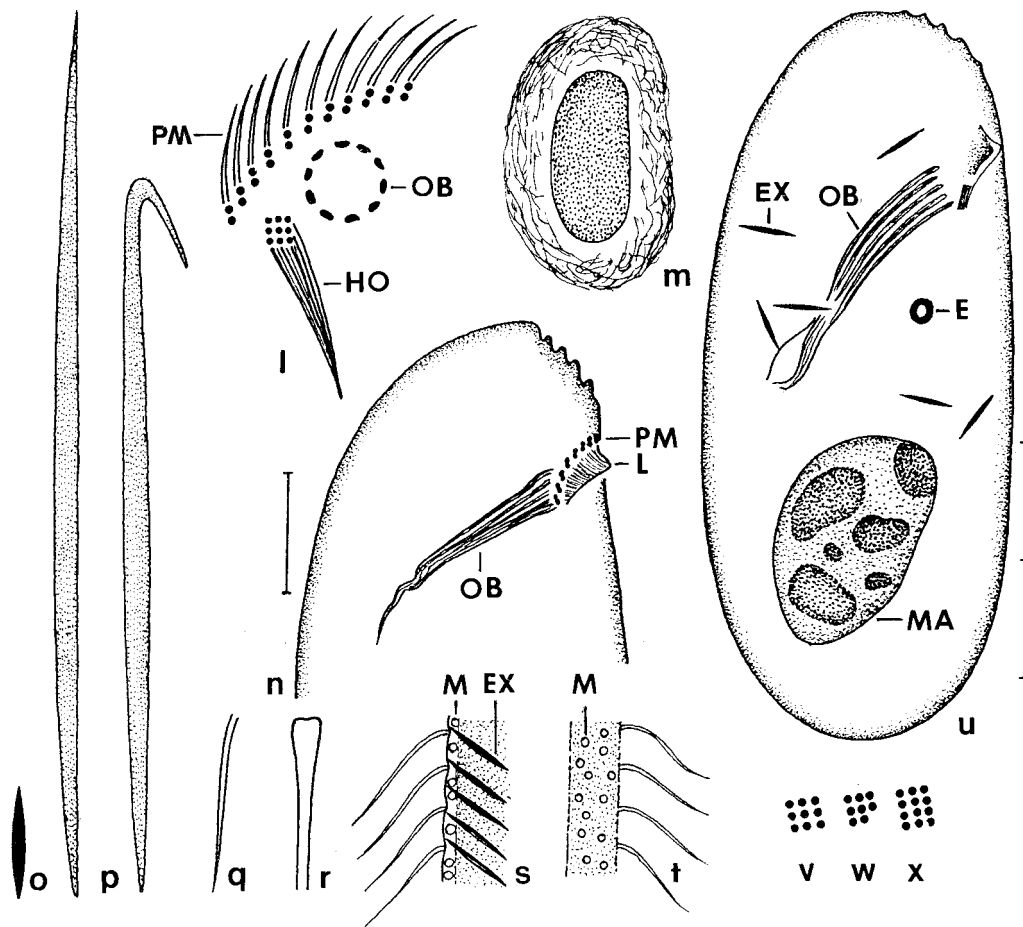
Cilia in vivo  $8\text{--}10 \mu\text{m}$  long, distances between individual cilia increase from anterior to posterior, arranged in equidistant, longitudinal rows forming distinct preoral suture and small, unciliated posterior pole area (Fig. 7a–c, g, 8h–l; Table 7); some dikinetids in anterior region of kinety facing undulating membrane (Fig. 7b, c, 8c, m, p).

Oral opening distinctly subapical on ventral side, in vivo about  $4 \mu\text{m}$  in diameter, slit-like in prepared specimens. Pharyngeal basket inconspicuous in live specimens but distinct after protargol impregnation, extends obliquely to mid-body, composed of about 10



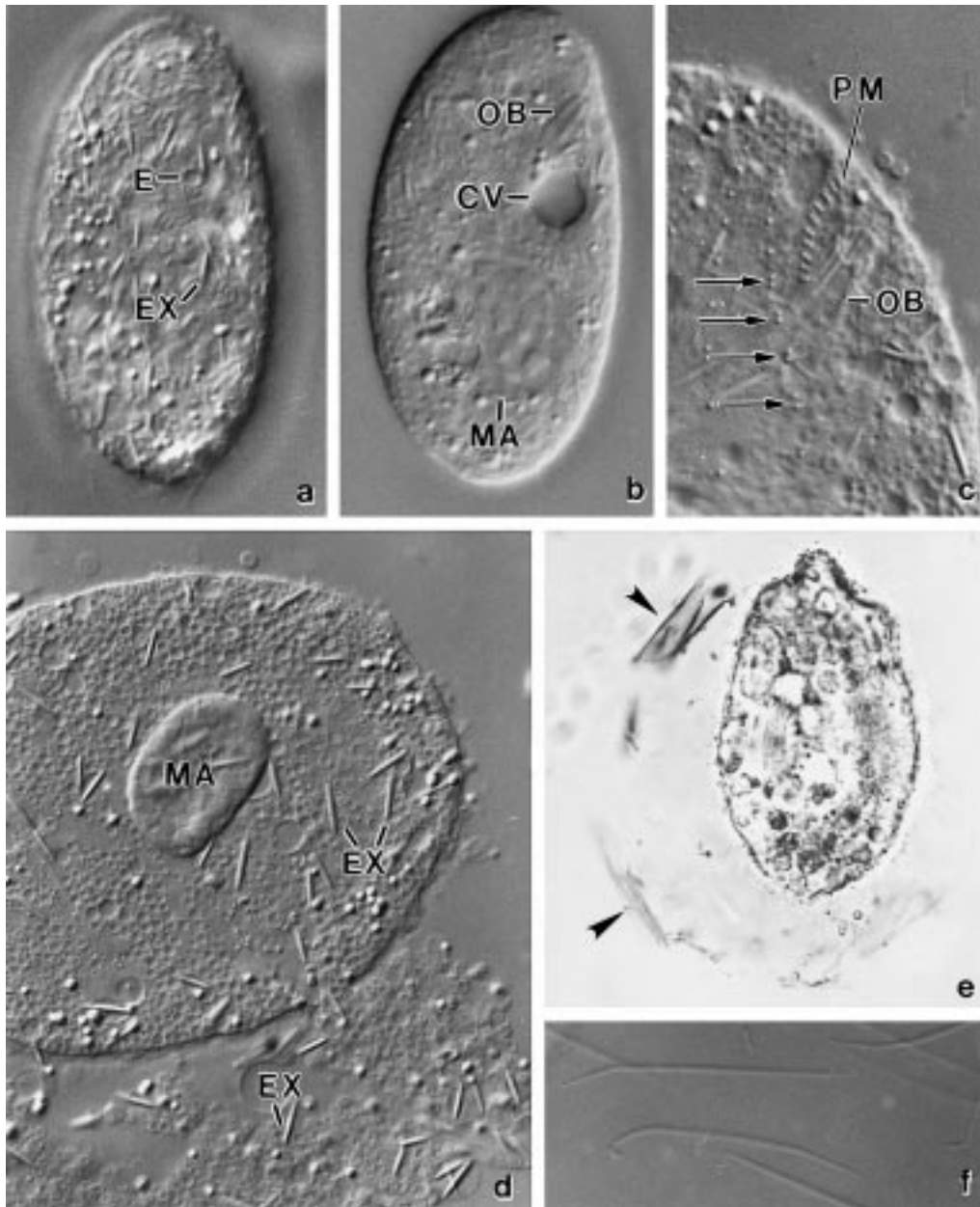
**Figures 7a–k.** *Parafurgasonia protectissima*, South African neotype population (a–c, e), Cape Verde specimen (d), Australian specimen (f), and Swiss type population (g–k; from Penard, 1922) from life (a, d–k) and after Chatton-Lwoff silver nitrate impregnation (b, c). **a, d, f, g:** Right lateral views showing general organization and shape variability. **b, c:** Infraciliature of right and ventral side. Arrow marks cytophyge. **e:** Dorsal view of specimen shown in figure (a). **h:** Oral basket. **i, j:** Surface view and optical section of cortex showing arrangement of extrusomes. **k:** Resting cyst. E – excretory pore of contractile vacuole, EX – extrusomes, HO – hypostomial organelle, OO – oral opening, PM – paroral membrane. Scale bar division 10 µm.



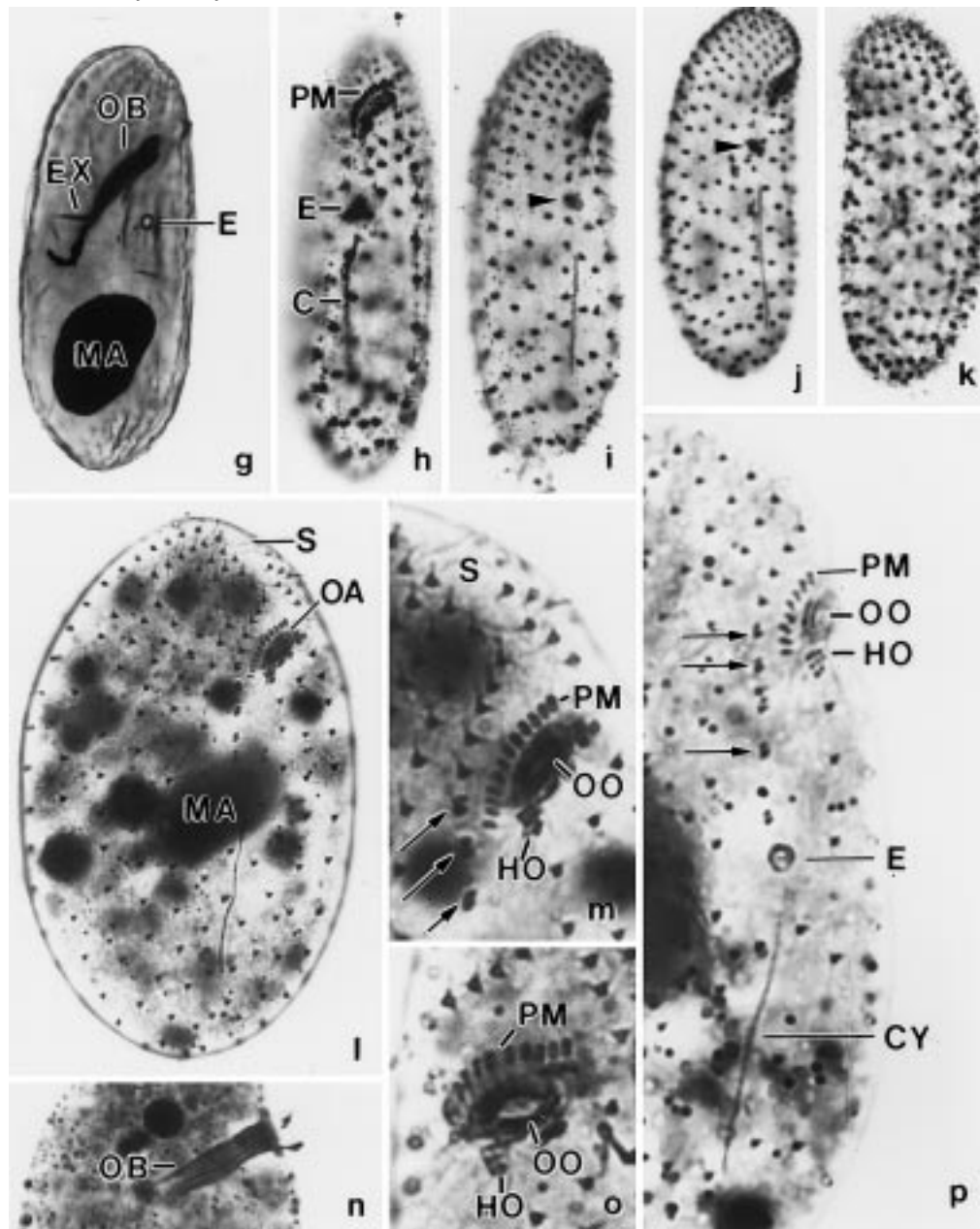


**Figures 7l–x.** *Parafurgasonia protectissima*, South African neotype (l–w) and Australian (x) population from life (l, o–t, x), after methyl green-pyronin staining (m), protargol impregnation (n, u), and silver carbonate impregnation (v, w). **l**: Surface view of oral structures in interference contrast. **m**: When methyl green-pyronin is added, *P. protectissima* releases many mucocysts, which form a voluminous, fibrous coat. **n, u**: Lateral views showing main cell organelles. **o, p**: Resting (4 µm) and extruded trichocysts (up to 50 µm), drawn to scale. **q**: Somatic cilium, 7 µm long. **r**: Anterior region of pharyngeal rod. **s, t**: Optical section and surface view of cortex showing arrangement of trichocysts and mucocysts. **v–x**: Structure of the hypostomial organelle in the South African (v, w) and Australian (x) population. E – excretory pore of contractile vacuole, EX – extrusomes, HO – hypostomial organelle, L – lip (hyaline cortical process), M – mucocysts, MA – macronucleus, OB – oral basket, PM – paroral membrane. Scale bar division 10 µm.

slightly curved rods with broadened anterior end (Fig. 7a, g, h, n, r, u, 8b, c, g, n). Hypostomial organelle close underneath right end of oral opening, square, oriented obliquely to main body axis, in South African population usually composed of three kineties each having three basal bodies with about 7 µm long cilia forming distinct, cone-shaped bundle; lower leftmost basal body sometimes lacking (Fig. 7a–c, l, v, w, 8m, o, p); hypostomial



**Figures 8a–f.** *Parafurgasonia protectissima*, South African population from life (a–d, f) and after methyl green-pyronin staining (e). **a, b:** Right lateral surface view and optical section of a slightly squeezed specimen. **c:** Details of oral apparatus and dikinetids (arrows) in subapical region of kinety facing paroral membrane. **d, f:** Squashed specimen showing many fusiform, 4  $\mu$ m long extrusomes, which can extend to up to 50  $\mu$ m long rods. **e:** The mucocysts from a voluminous, fibrous coat eventually forming membranous structures (arrowheads). CV – contractile vacuole, E – excretory pore of contractile vacuole, EX – extrusomes, MA – macronucleus, OB – oral basket, PM – paroral membrane.



**Figures 8g–p.** *Parafurgasonia protectissima*, South African population after protargol (g, n), silver nitrate (h–k), and silver carbonate (l, m, o, p) impregnation. **g, n:** Right lateral views showing main cell organelles. The pharyngeal basket ends in mid-body. **h–k:** Infraciliature of ventral (h), right (i, j) and left (k) side. Arrowheads mark excretory pore of contractile vacuole. **l:** General ventrolateral view. **m, o, p:** Details of the oral and somatic infraciliature. Arrows mark dikinetids in anterior region of kinety facing paroral membrane. CY – cytophyge, E – excretory pore, EX – extrusome, HO – hypostomial organelle, MA – macronucleus, OA – oral apparatus, OB – oral basket, OO – oral opening, PM – paroral membrane, S – preoral suture.

organelle of Australian population composed of three kineties each having four basal bodies (Fig. 7x). Paroral membrane at base of triangular lip covering right half of oral field, extends right and above oral opening, distinctly curved and separate from postoral

**Table 7.** Morphometric data from *Parafurgasonia protectissima* and *P. terricola*

Character <sup>a</sup>	Sp <sup>b</sup>	Pop <sup>c</sup>	Me <sup>d</sup>	$\bar{x}$	M	SD	CV	Min	Max	n
Body, length	PP	1	CHL	60.4	60	5.1	8.5	51	69	21
	PP	2	SC	61.4	63	4.0	6.6	55	65	5
	PT	1	CHL	31.8	32	2.5	7.8	28	36	12
	PT	2	CHL	34.7	35	5.0	14.4	28	44	11
	PT	3	CHL	55.4	58	8.3	15.0	40	65	9
Body, width in lateral view	PP	1	CHL	26.0	26	2.4	9.3	22	30	21
	PT	1	CHL	14.3	14	1.4	9.6	12	17	12
	PT	2	CHL	15.0	15	2.2	14.6	13	20	11
Body, width in ventral view	PT	3	CHL	23.2	22	2.9	12.3	19	27	9
	PP	1	CHL	21.8	22	2.8	12.7	17	25	21
Anterior somatic end to hypostomial organelle, distance	PP	1	CHL	14.7	15	1.3	9.2	12	17	21
	PT	1	CHL	3.8	4	—	—	3	4	12
	PT	2	CHL	5.6	5	0.9	16.5	5	8	11
	PT	3	CHL	14.0	15	—	—	10	17	3
Anterior somatic end to excretory pore, distance	PP	1	CHL	25.4	25	2.8	10.9	22	32	21
	PP	2	SC	30.2	30	3.1	10.3	27	35	5
	PT	1	CHL	17.3	17	1.7	9.6	14	21	12
	PT	2	CHL	14.4	14	2.1	14.7	11	18	11
	PT	3	CHL	18.8	19	2.3	12.1	15	22	9
Anterior somatic end to macronucleus, distance	PP	1	CHL	27.5	29	6.6	23.8	17	40	21
	PT	1	CHL	13.3	14	2.2	16.9	10	17	11
	PT	2	CHL	18.3	20	3.7	20.5	13	23	11
	PT	3	CHL	26.9	26	7.4	27.6	16	40	9
Paroral membrane, length	PP	1	CHL	7.9	8	0.7	9.2	7	9	21
	PT	1	CHL	5.0	5	0.7	14.8	4	6	12
Macronucleus, length	PP	1	CHL	14.1	14	1.8	12.7	11	20	21
	PT	1	CHL	5.3	5	0.9	17.2	4	7	11
	PT	2	CHL	6.1	6	1.2	20.0	5	8	11
	PT	3	CHL	10.1	10	1.2	11.6	9	13	9
Macronucleus, width	PP	1	CHL	7.6	8	1.0	12.8	6	9	21
	PT	1	CHL	5.1	5	0.7	13.8	4	6	11
	PT	2	CHL	5.4	5	—	—	5	7	11
	PT	3	CHL	9.1	9	0.9	10.2	8	10	9
Somatic kineties, number	PP	1	CHL	20.1	20	1.1	5.4	19	22	21
	PP	2	SC	17.0	17	0.6	3.7	16	18	6
	PT	1	CHL	11.2	11	—	—	11	12	12
	PT	2	CHL	13.5	14	—	—	13	14	11
	PT	3	CHL	19.3	19	0.7	3.6	18	20	9
Basal bodies in a dorsal kinety, number	PP	1	CHL	19.4	20	2.2	11.1	15	23	21
	PP	2	SC	26.0	25	2.4	9.4	24	30	6
	PT	1	CHL	12.3	13	1.2	10.0	11	15	12
	PT	2	CHL	13.2	14	1.4	10.6	10	15	11
	PT	3	CHL	40.3	40	3.8	9.4	35	46	9

**Table 7.** (Continued)

Character <sup>a</sup>	Sp <sup>b</sup>	Pop <sup>c</sup>	Me <sup>d</sup>	$\bar{x}$	M	SD	CV	Min	Max	n
Hypostomial organelles, number	PP	1	CHL	1.0	1	0.0	0.0	1	1	21
	PP	2	SC	1.0	1	0.0	0.0	1	1	5
	PT	1	CHL	1.0	1	0.0	0.0	1	1	12
	PT	2	CHL	1.0	1	0.0	0.0	1	1	11
	PT	3	CHL	1.0	1	0.0	0.0	1	1	9

<sup>a</sup> Data based on mounted specimens from field. Measurements in  $\mu\text{m}$ . CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation,  $\bar{x}$  – arithmetic mean.

<sup>b</sup> Species: PP – *Parafurgasonia protectissima*, PT – *Parafurgasonia terricola*.

<sup>c</sup> Populations: 1 (types, see species descriptions) – Republic of South Africa, respectively, Kenya; 2 – Cape Verde Islands, respectively, Austria; 3 – Venezuela.

<sup>d</sup> Methods: CHL – silver nitrate after Chatton-Lwoff, SC – silver carbonate.

somatic kineties, composed of about 12 dikinetids whose anterior basal bodies bear 5  $\mu\text{m}$  long, rather slowly beating cilia (Fig. 7a–c, l, n, 8c, h, l, m, o, p).

**Occurrence and ecology:** Penard (1922) discovered *P. protectissima* in forest mosses from Switzerland. I found it in the following samples: Republic of South Africa (neotype population), Kruger National Park, 7.2.1995, mud from granitic rock-pools on the Kruger Tablets, pH 6.5; Cape Verde Islands, Sao Vicente, Ribeira do Juliao, collected on 13.10.1985 by H. Franz, litter and red soil under xerophytes, pH 8.3, Table 7; Australia, Green Island near Cairns, 8.2.1987, mixture of litter and brownish soil under palm trees about 30 m inshore, pH 7.1; South America, north coast of Venezuela, Henry Pittier National Park, cloud rain forest at Rancho Grande, 5–10 cm soil layer with humic, darkbrown, very sandy soil containing fine roots, pH 6.3. These data indicate that *P. protectissima* is cosmopolitan and possibly prefers circumneutral environments. Abundances were low, except in the rock-pools of South Africa, which indicates that this species possibly prefers ephemeral limnetic habitats.

**Generic classification and comparison with literature data and related species:** Penard (1922) assigned the present species to *Nassula*, which was later split into several genera (Foissner and Adam, 1981). The genus *Parafurgasonia* Foissner & Adam, 1981, with *P. sorex* (Penard, 1922) as type and single species so far, differs from the other members of the family by having only a single hypostomial organelle and a distinctly curved paroral membrane extending along the anterior half of the oral opening. *Parafurgasonia protectissima* and *P. terricola*, described below, perfectly match the main character of the genus, that is, have only a single hypostomial organelle. The paroral membrane, however, is as in other nassulids, viz. at the right side of the oral opening, especially in *P. terricola*. There is obviously a transformation of this character from *P. terricola* (paroral right of oral opening; Fig. 9c, s) over *P. protectissima* (paroral right and above oral opening; Fig. 7c, 8h) to *P. sorex* (paroral extends along anterior half of oral opening; Foissner & Adam, 1981). Thus, this is a weak genus character and should be removed from the genus diagnosis. Likewise it should not be used to separate *P. protectissima* and *P. terricola* from *P. sorex* at genus level.

My observations on *P. protectissima* match those of Penard (1922) in every detail. Thus, identification is beyond any reasonable doubt. However, Grolière (1974) identified as *Nassula protectissima* a species with three adoral organelles. Unfortunately, he studied only silver-impregnated specimens, making a reasonable comparison with Penard's description impossible. Grolière's species was very likely *Furgasonia rubens*, as indicated by the body size (47–70 µm), the number of the ciliary rows (31–32), and the arrangement of the adoral organelles (cp. Dragesco and Dragesco-Kernéis, 1986; Fauré-Fremiet, 1967; Foissner, 1989). Indeed, species of the genera *Furgasonia* and *Parafurgasonia* are very similar in vivo, and thus it is impossible to know what Penard (1922), who never used oil immersion objectives and did not have the advantages of silver techniques, really saw because he could not provide the details of the oral structures necessary for a correct generic classification. Thus, it is crucial to fix the species by a neotype (article 75b of the ICZN, 1985), as done above, even if the population is not from the type region (locality), as it should be (article 75d(5) of the ICZN).

As concerns the congeners, *P. protectissima* is easily distinguished from *P. terricola*, described below, by the conspicuous trichocysts, and from *P. sorex*, which also has conspicuous trichocysts, by the much smaller oral basket and hypostomial organelle (3 × 3 vs. about 3 × 7 basal bodies; Foissner & Adam, 1981) as well as by the location of the paroral membrane (see generic classification discussed above) and the number of somatic ciliary rows (16–22 vs. 23–26).

***Parafurgasonia terricola* nov. spec.** (Fig. 9a–v; Table 7)

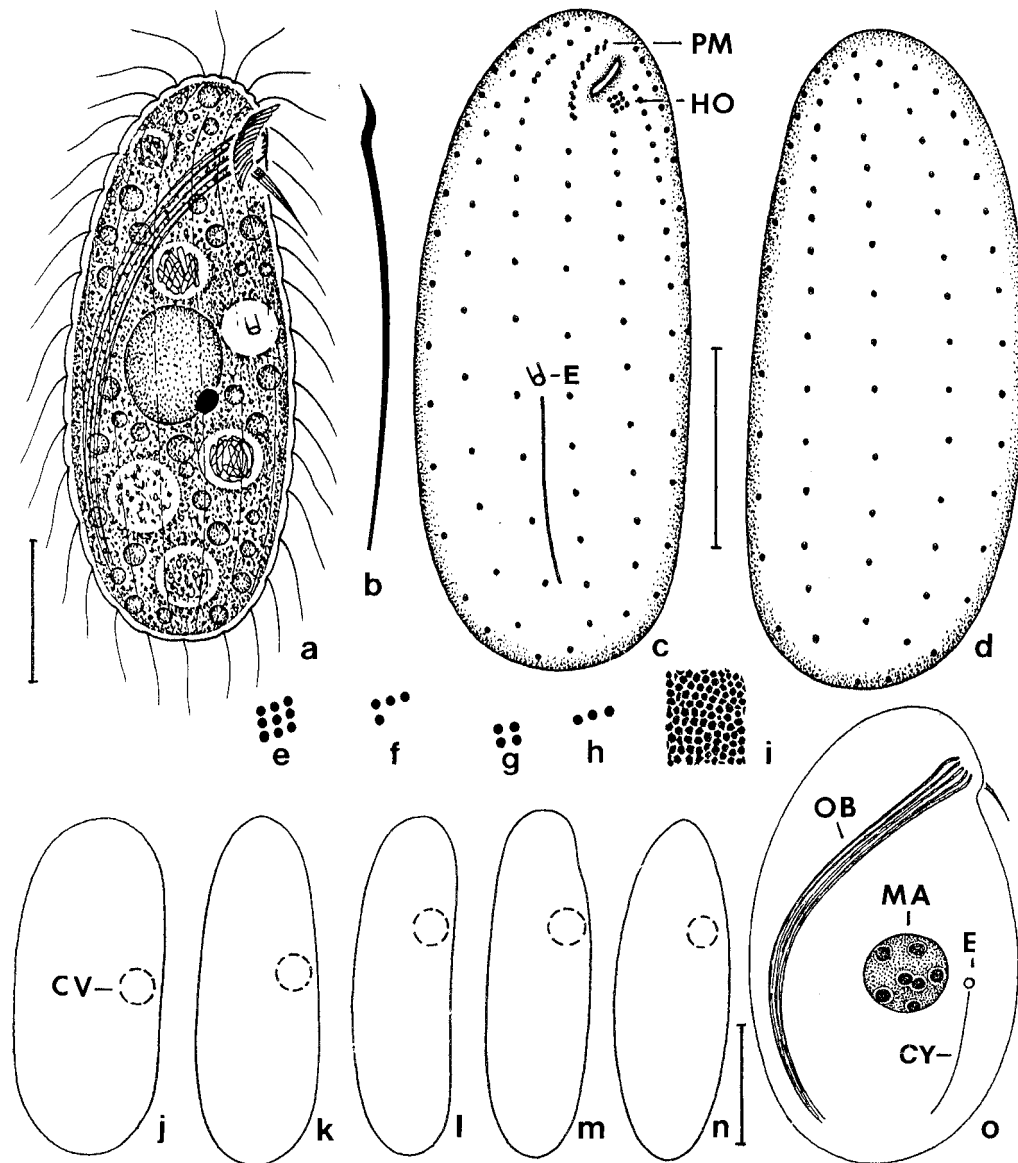
I studied, albeit with varying precision, nine populations of this species collected in edaphic habitats world-wide (see occurrence and ecology section). Although a few of them differ in some details, all very likely belong, at the present state of knowledge, to the same species because they lack extrusomes and have a single hypostomial organelle and a slightly curved, short paroral membrane right of the oral basket. The following diagnosis and description are based on the populations from Kenya (type), Israel, China, and Austria, which are so similar that conspecificity is beyond reasonable doubt (Table 7). Differing features of the other populations will be mentioned after the description of the type material.

**Diagnosis:** Size in vivo about 35 × 15 µm, ellipsoidal to elongate oval. Contractile vacuole slightly above to slightly below mid-body. 11–14 somatic kineties. Oral opening subapical, pharyngeal basket composed of 10–12 curved rods extending dorsally to posterior end of cell. Hypostomial organelle square, composed of 3 kineties with three ciliated monokinetids each. Paroral membrane extends along right margin of oral opening, slightly curved, composed of about 7–10 dikinetids.

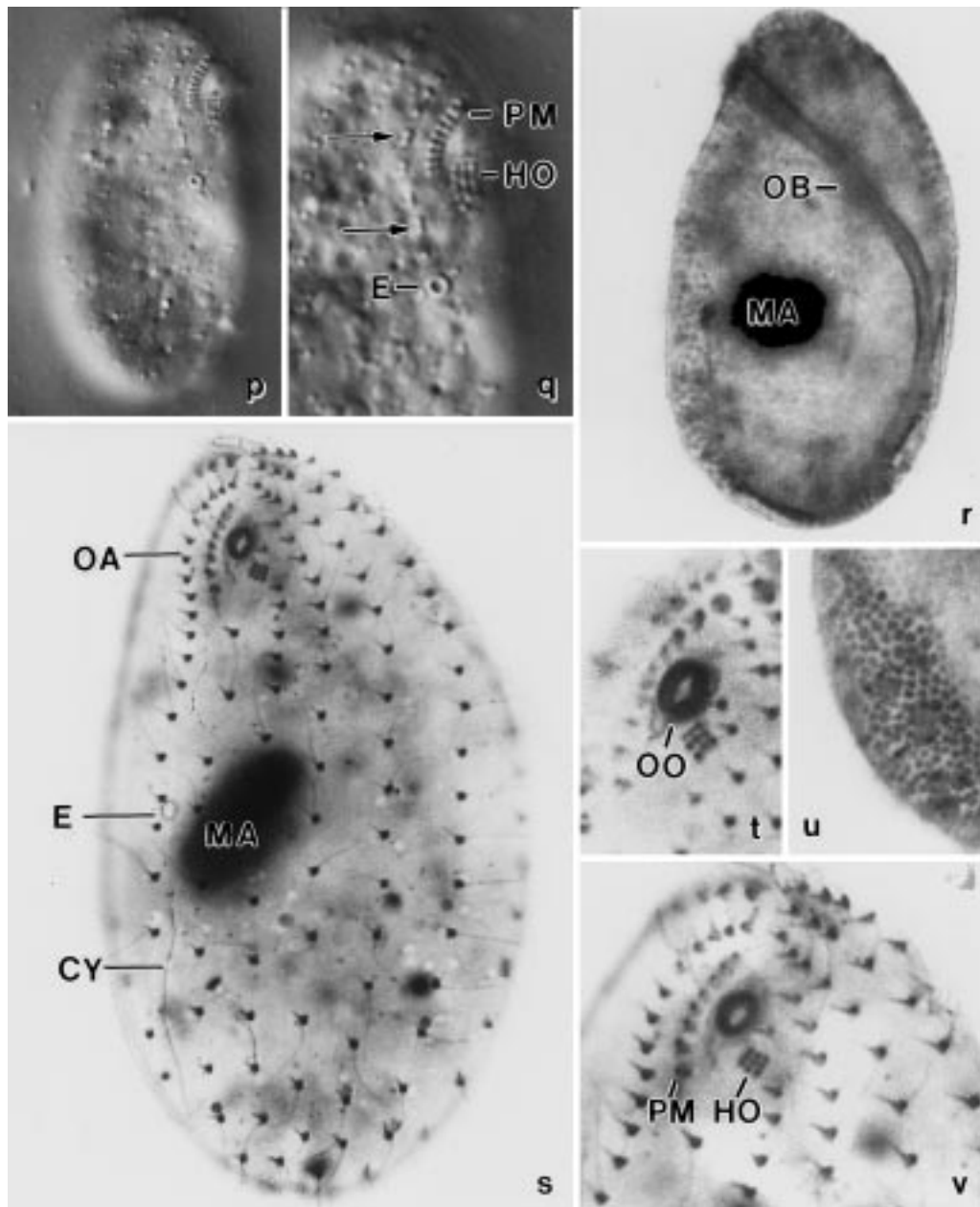
**Type location:** Litter layer of leguminous forest surrounding the Mzima Springs in Tsavo National Park West, Kenya, equatorial Africa (38°E, 3°S).

**Type slides:** Two slides (1 holotype and 1 paratype) with Chatton-Lwoff silver nitrate-impregnated specimens and one holotype slide with protargol-impregnated cells from the type location have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria. One voucher slide each with Chatton-Lwoff silver nitrate-impregnated specimens of the Austrian and Venezuelan population has also been deposited. The slides contain several specimens, with relevant cells marked by a black ink circle on the cover glass.

**Etymology:** “*terricola*” (Latin) because living in terrestrial habitats.



**Figures 9a–o.** *Parafurgasonia terricola*, Kenyan type (a, c–e, i, o) and other (b, f–h, j–n) populations from life (a, b, e–h, j–n), after Chatton-Lwoff silver nitrate (c, d), silver carbonate (e), and protargol (i, o) impregnation. **a:** Right lateral view of a representative specimen. **b:** Pharyngeal rod from Austrian population. **c, d:** Infraciliature of ventral and dorsal side. **e–h:** Structure of the hypostomial organelle in populations from Kenya (type), Austria and China (e), Venezuela (f), Spain (g), and the Maldives (h). **i:** Cortical alveoli. **j–n:** Shape variants in populations from China and Israel (j), China (k), Kenya (sample 8), the Maldives and Venezuela (l), Kenya (sample 8) and Venezuela (m), and Spain (n). **o:** Main cell organelles. CY – cytophyge, CV – contractile vacuole, E – excretory pore of contractile vacuole, HO – hypostomial organelle, MA – macronucleus, OB – oral basket, PM – paroral membrane. Bars 10  $\mu\text{m}$ .



**Figures 9p–v.** *Parafurgasonia terricola*, Kenyan type (r–v) and Chinese (p, q) population from life (p, q) and after protargol (r, u) and silver carbonate (s, t, v) impregnation. **p, q:** Right lateral view of a slightly squeezed specimen. Arrows mark dikinetids in kinety facing paroral membrane. **r:** Left lateral view showing conspicuously curved pharyngeal basket extending to near body end. **s, t, v:** Ventral views of somatic and oral infraciliature. **u:** Cortical alveoli. CY – cytopyge, E – excretory pore of contractile vacuole, HO – hypostomial organelle, MA – macronucleus, OA – oral apparatus, OB – oral basket, OO – oral opening, PM – paroral membrane.



*Description:* Size in vivo  $30\text{--}50 \times 12\text{--}20\text{ }\mu\text{m}$ ; slightly to distinctly (up to 2:1) flattened laterally. Shape, depending on specimen and population, in lateral view elongate oval (Kenya, Austria, China) or parallel-sided with broadly rounded ends (Israel, China), usually slightly indented at oral opening (Fig. 9a, j–n). Macronucleus in vivo about  $8\text{ }\mu\text{m}$  in diameter, location rather variable, usually, however, in middle third of cell; nucleoli globular. Micronucleus in vivo about  $1.5\text{ }\mu\text{m}$  in diameter, attached to macronucleus. Contractile vacuole slightly above or below mid-body, with distinct excretory pore invariably between kinety bearing undulating membrane and neighbouring right lateral ciliary row (Fig. 9a, c, j–q, s; Table 7). Cytopyge close underneath excretory pore, extends to near posterior body end, food remnants leave cell through small, fusiform opening as stream of mucous material (Fig. 9c, o, s). No extrusomes recognisable, either in vivo or after methyl green-pyronin staining and silver impregnation. (A population very recently found in a beech forest soil in the surroundings of Salzburg City had mucocysts about  $1\text{ }\mu\text{m}$  in diameter.) Cortex about  $1\text{ }\mu\text{m}$  thick, bright, slightly punctate by about  $1\text{ }\mu\text{m}$  deep ciliary pits; contains about 10 rows of very small ( $< 1\text{ }\mu\text{m}$ ), polygonal alveoli between each two kineties, recognisable after protargol impregnation and methyl green-pyronin staining (Fig. 9i, u). Cells colourless, cytoplasm filled with fat globules  $0.5\text{--}3\text{ }\mu\text{m}$  across and  $5\text{--}10\text{ }\mu\text{m}$  sized food vacuoles very likely containing bacteria. Creeps and/or swims moderately fast by rotation about main body axis.

Cilia in vivo  $7\text{--}8\text{ }\mu\text{m}$  long, distances between individual cilia increase from anterior to posterior, arranged in equidistant, longitudinal rows forming inconspicuous preoral suture; some ciliated dikinetids in anterior region of kinety facing undulating membrane (Fig. 9a, c, d, p, q, s; Table 7).

Oral opening subapical on ventral side, circular in vivo, slit-like in prepared specimens. Pharyngeal basket difficult to recognise in live specimens but distinct after protargol impregnation, extends obliquely to dorsal side and posterior end of cell, composed of about 10–12 fine rods with curved, tapered anterior end (Fig. 9a, b, o, r). Hypostomial organelle close underneath oral opening, square, oriented obliquely to main body axis, consists of three kineties, each having three basal bodies with about  $4\text{ }\mu\text{m}$  long cilia forming conical bundle. Paroral membrane right of oral opening, continuous with first somatic kinety right of oral opening, slightly curved, consists of 7–10 oblique dikinetids whose anterior basal bodies bear  $5\text{ }\mu\text{m}$  long, slightly mobile cilia (Fig. 9a, c, e, q, s, t, v).

Main differences of the populations from Kenya (Shimba Hills, sample 8), the Maldives, Venezuela, and Spain: length  $40\text{--}80\text{ }\mu\text{m}$ ; unflattened. Shape elongate ellipsoidal, reniform, or fusiform like *Tetrahymena rostrata* (Fig. 9n). Macronucleus of Spanish population in vivo about  $15\text{ }\mu\text{m}$  in diameter and with reticulate nucleolus. Contractile vacuole frequently distinctly above mid-body, i.e. rather close underneath oral opening (Fig. 9l, m, n; Table 7). About 16, and respectively, 18–20 ciliary rows in Maldivan and Venezuelan (Table 7) populations. Hypostomial organelle of rather variable composition (Fig. 9e–h); however, as I studied only live specimens, I can not exclude having overlooked unciliated basal bodies, i.e., that the organelle has the same structure as in the type population; nevertheless, this would indicate that some basal bodies are unciliated, i.e., that the fine structure of the organelle is highly variable. This is supported by observations on *P. protectissima*, where similar variations occur (see above), indicating that details of the hypostomial organelle should not be used to split the species.

*Occurrence and ecology:* Over the years, I found *P. terricola* in nine soil samples from Africa, South America, Asia, and Europe, showing that it is cosmopolitan. Abundances

were always low and all samples measured had a circumneutral pH, indicating that *P. terricola* prefers the litter layer and mull soil. Brief site descriptions: Kenya (type), Mzima Springs in Tsavo National Park, 8.5.1985, strongly decayed litter with many fungal hyphae from leguminous trees, pH 7.0; Kenya, Shimba Hills (sample 8); Israel, about 10 km south of Nazareth, collected on 13.2.1985 by H. Augustin, irrigated wheat field, soil brownish and clayic; Israel, Golan mountains, collected on 14.2.1985 by H. Augustin, sward and dark soil from uncultivated grassland; South America, north coast of Venezuela, Henry Pittier National Park, gallery forest some km south of Choroni village, 21.2.1996, litter and very sandy, brownish soil near bank of river, pH 6.7, Table 7; Maldives, North Male Atoll, collected on 15.12.1990 by W. Petz, litter and some sand under coastal shrubs, very saline, pH 7.7; China, Beijing area, entrance to Great Wall, 22.9.1995, litter and humic, brown soil under shrubs near toilet; Spain, Toledo, 7.9.1991, moss and soil from rock-pool at bank of river Tajo, pH 7.3; Austria, Tyrol, near town of Brixlegg, collected on 8.7.1991 by A. Berthold; Table 7.

*Generic classification and comparison with related species:* For generic classification, see discussion by *P. protectissima*. As concerns the congeners, *P. terricola* is easily distinguished from *P. protectissima* (redescribed above) and *P. sorex* (redescribed by Foissner and Adam, 1981) by the lack of extrusomes; from the latter species also by the smaller adoral organelle and paroral membrane, which does not curve around the upper half of the oral opening. Furthermore, *P. terricola* differs from *P. protectissima* in the oral basket, which extends to the posterior end in the former and only to mid-body in the latter (Fig. 7u, 8n, 9o, r). The number of somatic kineties (11–14 vs. 16–22), the body length (30–50 µm vs. 50–70 µm) and the location of the contractile vacuole (near mid-body vs. underneath oral opening) are also different in *P. terricola* and *P. protectissima* (Table 7); however, the Venezuelan population of *P. terricola* is intermediary in these characters (19 kineties, 60 µm long, contractile vacuole distinctly above mid-body), indicating that they must be used with care (Table 7). Possibly, the Venezuelan population should be separated at subspecies level.

***Brachyosoma brachypoda mucosa* nov. sspec.** (Fig. 10a–v, 11a–g; Table 8)

*Diagnosis:* Body covered by thick layer of mucilaginous material.

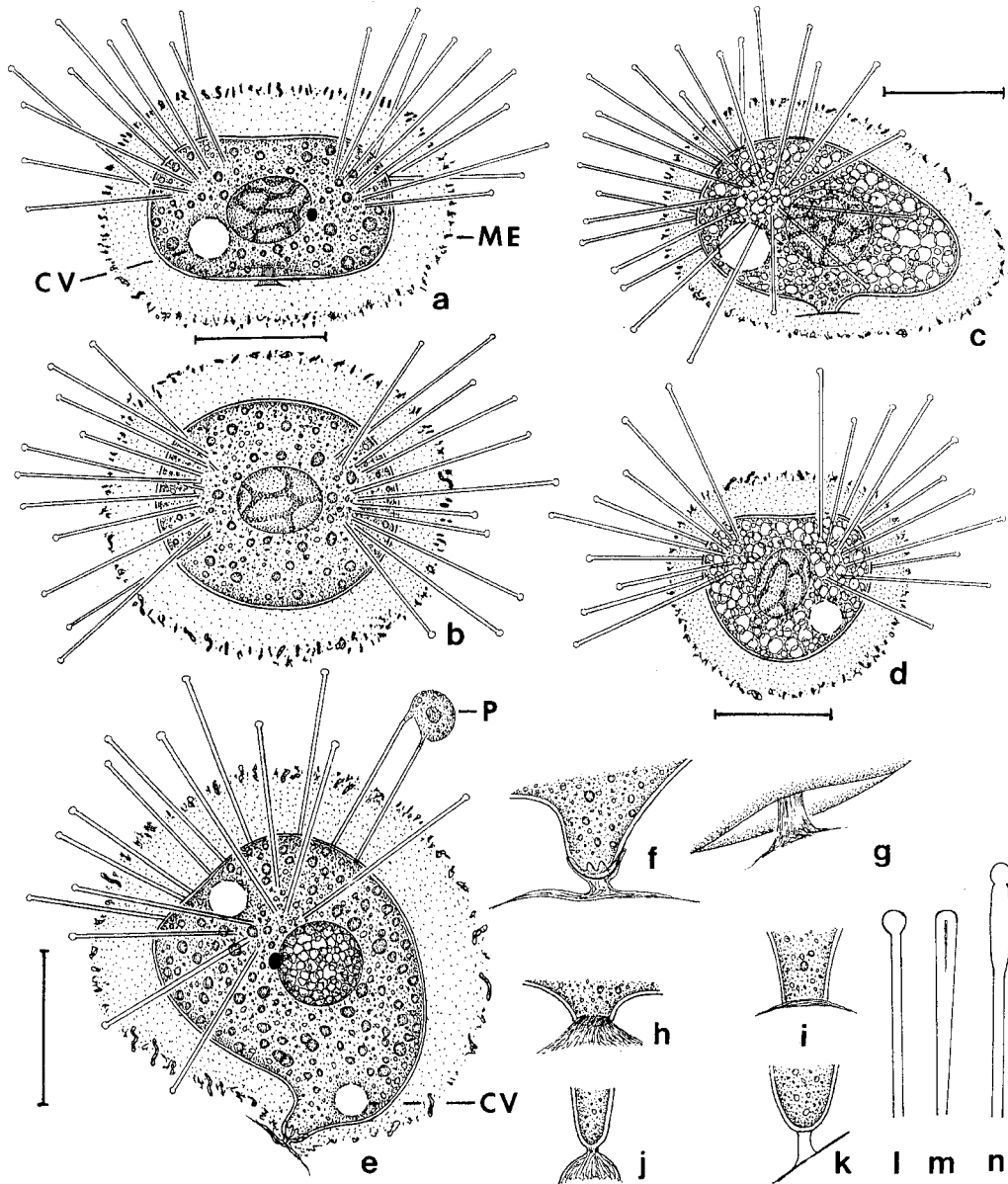
*Type location:* Soil from Hortobágy Puszta near the town of Debrecen in NE-Hungary (E21°, N47°).

*Type slides:* Four slides (1 holotype and 3 paratypes) with protargol-impregnated morphostatic and budding specimens have been deposited in the Oberösterreichische Landesmuseum in Linz (LI). The slides contain several specimens, with relevant cells marked by a black ink circle on the cover glass.

*Etymology:* “mucosa” (Lat., slimy) refers to the mucilaginous envelope.

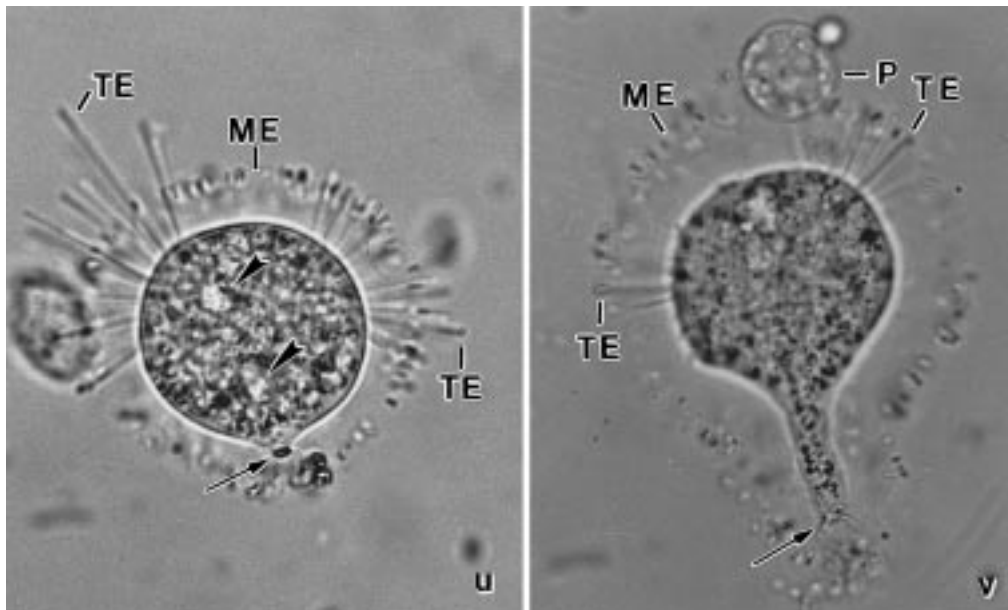
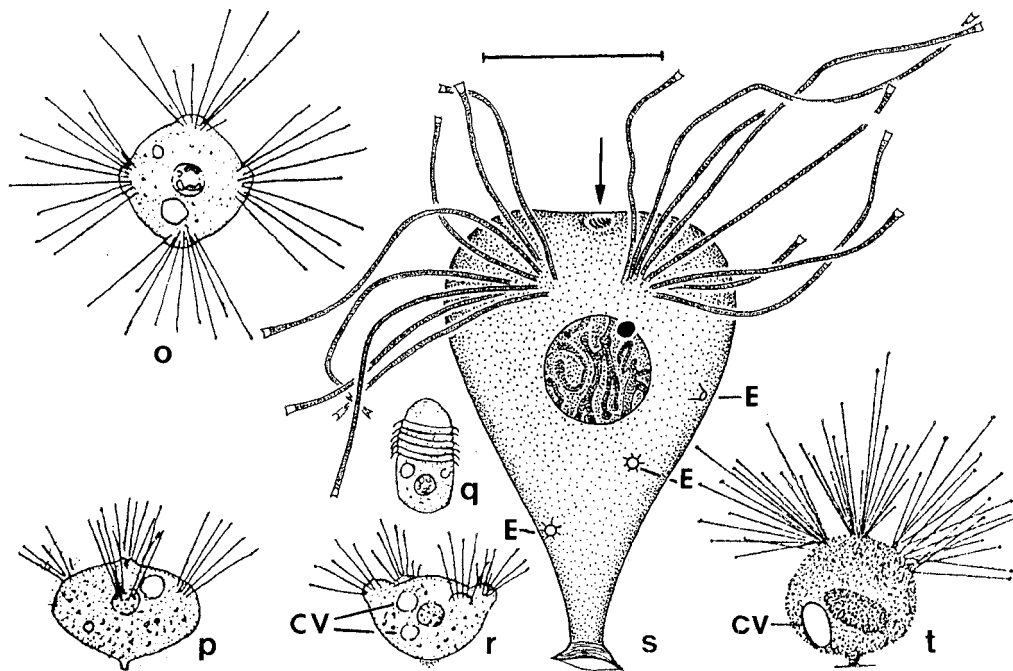
*Description:* Adult specimens were studied from four populations found in Hungary (type), North America, Australia, and Antarctica. All were very similar, except for some details which will be mentioned where appropriate.

**Adult cell** (Fig. 10a–n, s, u, v; Table 8): Size in vivo 30–60 µm ( $\bar{x}$  41 µm, n 9; without mucilaginous coat), prepared specimens considerably shrunk (Table 8). Shape globular to inverted pyriform, anterior body centre occasionally depressed dish-like, type and American population usually slightly to distinctly flattened along anterior-posterior axis, Australian specimens often more or less distinctly flattened laterally. Mucilaginous envelope 3–9 µm thick ( $\bar{x}$  6.7, n 7), covers body and proximal portion of tentacles, very



**Figures 10a–n.** *Brachyosoma brachypoda mucosa*, Hungarian type (a–d, i, l), American (g, l, m), and Australian (e, f, h, j, k, l, n) population from life. **a, b:** Same specimen in lateral and top view. **c, d:** Shape and size variability. Note absence of holdfast in (d). **e:** The Australian population differs from the Hungarian type in having two contractile vacuoles. **f–k:** Variability of holdfast (stalk/basal plate). **l, m:** Distal end of tentacles. **n:** Contracting tentacle. CV – contractile vacuole, ME – mucilaginous envelope, P – prey (heterotrophic flagellate). Scale bars 20  $\mu$ m.

hyaline but usually easily recognisable due to adhering bacteria and soil particles (Fig. 10a–e, u, v); does not stain with protargol. Holdfast (stalk/basal plate) minute (up to 6 µm, Table 8), fibrous, sometimes yellowish, lacking or not recognisable (Fig. 10d),



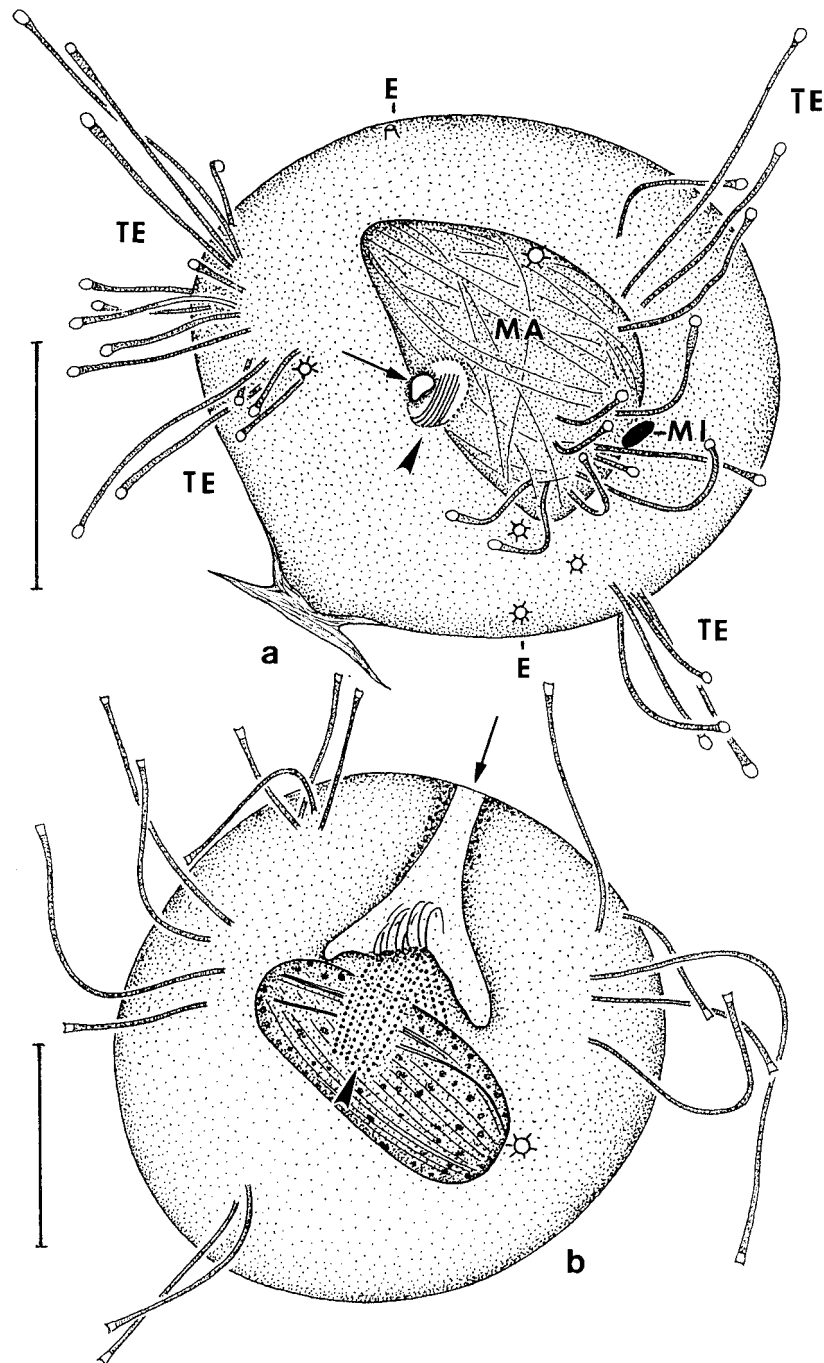
frequently projecting from more or less distinct posterior body elongation, distal end usually adhering to soil particles (Fig. 10a, c, e–k, u, v). Macronucleus in centre of cell, slightly ellipsoidal, with reticulate nucleolus. Micronucleus globular, attached to macronucleus. Specimens from type population with single contractile vacuole in posterior body half, however, further (inactive?) vacuoles very likely occur because all cells have at least two rather distant excretory pores (Fig. 10a, c, d, s, 11a; Table 8), and swimmers invariably possess two contractile vacuoles (Fig. 11d, e, g); American and Australian specimens have two active contractile vacuoles one near the anterior and one near the posterior body end (Fig. 10e, u). One to four, usually two, tentacle fascicles at anterior body end, 12 tentacles per fascicle on average (Table 8); no actinophores. Tentacles about as long as body, 0.9–1.2  $\mu\text{m}$  thick, distal end distinctly capitate in type and Australian population, cuneate or capitate in American specimens (Fig. 10a–e, l–n, u, v). Cortex thin ( $\leq 1 \mu\text{m}$ ) and flexible. Cytoplasm with few to many fat globules, depending on nutrition state. Feeds on ciliates, heterotrophic flagellates and naked amoebae.

**Budding and swarmer** (Fig. 10s, 11a–g; Table 8): *Brachyosoma brachypoda mucosa* produces a typical tokophryid swarmer by invaginative endogenous budding. The events observed are very similar to those described, for instance, by Hascall and Rudzinska (1970) in *Tokophrya infusionum* and by Bardele (1970) in *Acineta tuberosa*. Thus, I refrain from an elaborate description and refer to the Figures 10s and 11a–c, which show the process in detail. The swimmers have a size of about  $40 \times 25 \mu\text{m}$ , are pyriform in shape, and possess 2 contractile vacuoles, 5 1/2 ciliary rows with 15  $\mu\text{m}$  long cilia in the anterior half, and a posterior tuft with about 20  $\mu\text{m}$  long cilia (Fig. 11d–g; Table 8).

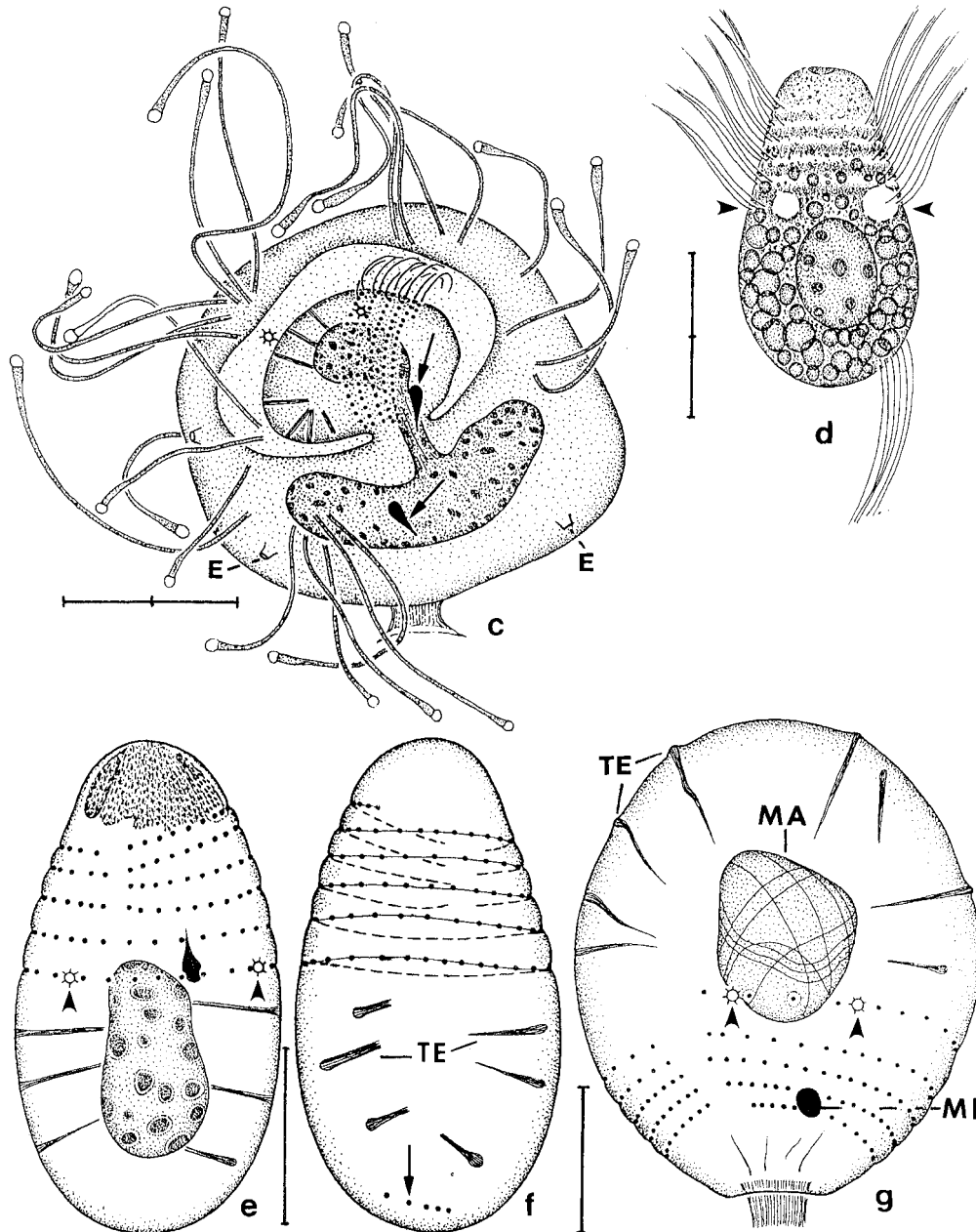
**Occurrence and ecology:** As yet found at type location (Hortobágy Pusztá in Hungary, mixture of greyish, dusty soil, litter, moss, and grass roots from the upper 0–5 cm, pH 7.0; collected by W. Heinisch on 28.7.1987), in the Shimba Hills Nature Reserve (sample 16), in Australia (Tasmania, hop field near Mt. Fields National Park, 0–5 cm red soil layer mixed with litter and roots, pH 7.0; collected on 23.2.1987; see Blatterer and Foissner, 1988, sample 6), and in North America (near entrance to Grand Canyon, juniper litter mixed with red soil and grass roots, pH 6.7; collected on 22.6.1989). These data indicate that *B. brachypoda mucosa* is very likely cosmopolitan with a wide ecological range. This is supported by a record from the mud of a pond of the McMurdo Ice Shelf, Antarctica (sample kindly provided by P. Broady, University of Canterbury, New Zealand). These specimens also possess a mucilaginous envelope, are flattened along the anterior-posterior axis, and have a size of 45–65  $\mu\text{m}$ , 2 contractile vacuoles, 2–3 tentacle fascicles, and a slimy holdfast.

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**Figures 10a–v.** *Brachyosoma brachypoda brachypoda* (o–r, t) and *B. brachypoda mucosa* (s, u, v) from life (o–r, t–v) and after protargol impregnation (s). **o–r:** Adults and swarmer of *Trichophrya melo*, a junior synonym of *B. brachypoda brachypoda*, size 30–40  $\mu\text{m}$  (from Penard, 1920). **s:** Pyriform specimen from Hungarian population. Arrow marks budding anlage (cp. Fig. 10a, b). Scale bar 20  $\mu\text{m}$ . **t:** Type figure from Stokes (1885), diameter 34–42  $\mu\text{m}$ . **u, v:** Specimens from Australian population. Note the two contractile vacuoles (arrowheads), the minute holdfast (arrows), and the voluminous mucilaginous envelope recognisable due to adhering bacteria and soil particles. CV – contractile vacuoles, E – excretory pores, ME – mucilaginous envelope, P – prey (heterotrophic flagellate), TE – tentacles.



**Figures 11a–b.** *Brachyosoma brachypoda mucosa*, swarmer genesis in Hungarian type population (protargol impregnation). Arrows mark birth canal, arrowheads denote ciliary rows of forming swarmer. E – excretory pores, MA – macronucleus, MI – micronucleus, TE – tentacles. Scale bars 20  $\mu$ m.



**Figures 11c–g.** *Brachyosoma brachypoda mucosa*, swarmer genesis in type population (protargol impregnation, if not stated otherwise). **c:** Late stage showing nuclear division (arrows mark divided micronucleus) and swarmer shaping in birth ventricle. **d–f:** Live (d) and prepared (e, f) swarmers have two contractile vacuoles (arrowheads), tentacle anlagen, 5 1/2 ciliary rows, and a posterior ciliary tuft (arrow). **g:** A swarmer transforming into an adult. Arrowheads mark excretory pores. E – excretory pores, MA – macronucleus, MI – micronucleus, TE – tentacle anlagen. Scale bar division 10  $\mu$ m.

**Table 8.** Morphometric data from adults (A) and swimmers (S) of *Brachyosoma brachypoda mucosa* (Hungarian type population)

Character <sup>a</sup>	Stage	$\bar{x}$	M	SD	CV	Min	Max	n
Body, length	A	28.4	28.0	7.3	25.8	20.0	45.0	14
	S	25.6	25.0	2.9	11.3	21.0	30.0	14
Body, width	A	26.9	24.5	7.8	28.9	20.0	48.0	14
	S	14.2	13.0	1.9	13.3	12.0	18.0	14
Holdfast, length	A	3.5	3.0	1.1	32.5	2.0	6.0	13
Holdfast, width	A	3.9	4.0	0.8	19.4	3.0	5.0	13
Macronucleus, length	A	13.4	12.0	5.6	41.6	7.0	28.0	14
	S	10.2	10.0	1.4	13.9	8.0	12.0	14
Macronucleus, width	A	9.6	9.0	2.8	28.9	6.0	17.0	14
	S	5.9	6.0	0.7	12.3	5.0	7.0	14
Micronucleus, length	A	2.0	2.0	0.5	24.6	1.2	3.0	14
	S	1.9	2.0	0.2	9.6	1.5	2.0	14
Micronucleus, width	A	2.0	2.0	0.5	24.6	1.2	3.0	14
	S	1.7	1.5	0.2	13.8	1.5	2.0	14
Tentacle fascicles, number	A	2.3	2.0	0.7	28.3	1.0	4.0	30
Tentacles, number in a fascicle	A	12.5	11.0	5.1	41.1	5.0	25.0	30
Macronucleus, number	A	1.0	1.0	0.0	0.0	1.0	1.0	14
Micronucleus, number	A	1.0	1.0	0.0	0.0	1.0	1.0	14
Excretory pores, number	A	3.3	3.0	1.3	39.2	2.0	6.0	15
Somatic kinetics, number	S	5.5	5.5	0.0	0.0	5.5	5.5	14
Number of cilia in posterior row	S	5.6	5.0	1.2	20.8	4.0	8.0	14

<sup>a</sup> Data based on protargol-impregnated, mounted specimens from field (protocol A in Foissner, 1991). Measurements in  $\mu\text{m}$ . CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation,  $\bar{x}$  – arithmetic mean.

*Classification and comparison with related species:* *Podophrya brachypoda* is type of the genus *Brachyosoma* Batisse, 1975 and has not been found since 1920, when Penard described it as a new species, *Trichophrya melo*. Thus, its correct classification remained doubtful. The present investigation shows that *B. brachypoda* lacks a lorica and produces a typical tokophryid swarmer by circum-invaginative, endogenous budding (Fig. 11a–g). Thus, it belongs to the family Tokophryidae Jankowski, as defined by Batisse (1994).

The generic classification depends on the characters used, respectively, the interpretation of the holdfast. *Brachyosoma* differs from *Tokophrya* solely by the absence/presence of a stalk (Curds, 1985). The present investigation shows that *B. brachypoda mucosa* has a stalk-like structure, albeit very inconspicuous and frequently looking like a basal plate (Fig. 10a, c, e–k, s, u, v). Accordingly, the differences to *Tokophrya* are more gradual than basic, suggesting that subgeneric rank would be more appropriate. Matthes (1988) combined *Podophrya brachypoda* with the genus *Trichophrya*, using the presence/absence of a stalk as sole distinguishing character. However, trichophryids have flattened, discoidal swimmers and were thus classified in a separate family, Trichophryidae Fraipont, by Batisse (1994).

*Brachyosoma brachypoda mucosa* is very similar to *B. brachypoda brachypoda*, except for the mucilaginous envelope, which might be an adaptation to the terrestrial mode of



life, that is, some protection for short periods of drought. There is virtually no significant difference to the original description by Stokes (1885): “Body subspherical or broadly pyriform, commonly rounded posteriorly, subsessile, the pedicle being very short and inconspicuous; tentacles distinctly capitate, often twice as long as the diameter of the body, arranged in two, three, or four fascicles; contractile vesicles two; nucleus ovate, coarsely granulate, subcentral or near the posterior extremity; endoplasm granular. Diameter of the body 1/600 to 1/750 inch. In standing water with dead leaves; attached to fragments and debris; Fig. 10t”. Likewise, the description of the synonym, *Trichophrya melo*, by Penard (1920) matches my observations: “Corps subsphérique, plus large que long, non ou à peine déformable, en général fortement aplati à sa face antérieure; parfois prolongé temporairement à son pôle inférieur en un bouton adhésif, ou bien à convexité basale simplement visqueuse. La face apicale porte sur ses bords 4 faisceaux de tentacules serrés, droits, longs, capités, chaque faisceau partant le plus souvent d’une protubérance plus ou moins nettement marquée. Noyau sphérique, central. Deux vésicules contractiles, l’une à la partie antérieure, l’autre, plus petite, dans la moitié postérieure du corps. Diamètre 45 à 60 µm; hauteur 30 à 40 µm (Fig. 10o–r)”. Thus, I separate my populations not at species, but at subspecies level.

#### ***Gigantothrix* nov. gen.**

*Diagnosis:* Oxytrichoidea (?) with rigid body and many oblique ventral cirral rows, leaving blank small area between midline and left marginal row. Right half of ventral rows and cirral rows left of left marginal row morphogenetically inactive because composed of remnants from previous generations. Frontoventral cirri numerous, the uppermost distinctly enlarged forming conspicuous corona along frontal portion of adoral zone of membranelles. Dorsal cilia in numerous rather irregular rows, very likely due to multiple fragmentation during ontogenesis and/or retention of parental kinetids. Transverse and caudal cirri lacking.

*Type species:* *Gigantothrix herzogi* nov. spec.

*Etymology:* Composite of the Greek words *gigantos* (gigantic) and *thrix* (hair = ciliate s.l.), referring to the conspicuousness of the type species. Feminine gender.

*Systematic position and comparison with related genera:* *Gigantothrix herzogi* shows extensive retention of parental ciliature (Fig. 12o, q), which is successively replaced by neokinetal waves in the sense of Eigner (1995), who united all hypotrichs with neokinetal anlagen (waves) in the family Kahliellidae. However, the general morphology and, especially, the morphogenesis of the dorsal infraciliature of, for instance, *Deviata* and *Kahliella*, respectively, *Gigantothrix herzogi* and *Onychodromus quadricornutus*, are so different that a monophyletic origin is unlikely [see Eigner (1995), Foissner *et al.* (1987) and Kamra and Sapra (1993) for a detailed description of the morphology and morphogenesis of the genera and species mentioned]. In my opinion, the retention of parental ciliature is a rather simple trait, which very likely evolved independently in several hypotrichs. Thus, I prefer to place *G. herzogi* in the superfamily Oxytrichoidea Jankowski, 1979, as I did with *Onychodromus quadricornutus*, another very large hypotrich, which is doubtlessly rather closely related to *G. herzogi* (cp. Fig. 12g, k). The rigid body indicates that *G. herzogi* belongs or is closely related to the stylonychid oxytrichids, as defined by Berger and Foissner (1997).

*Gigantothrix* is a very distinct genus because it lacks transverse and caudal cirri, in spite of its huge size. This distinguishes it clearly from other oxytrichids with multiple ventral

rows and rigid body, namely *Onychodromus* (Fig. 12k), *Laurentiella* (Fig. 12f) and *Coniculostomum* (Kamra *et al.*, 1994). In the lack of transverse and caudal cirri, *Gigantothrix* resembles *Hemicycliostyla* Stokes, 1886 (Fig. 12e) and *Pseudokahliella* Berger, Foissner and Adam, 1985. However, *Hemicycliostyla* has a “soft, flexible and elastic body” (Stokes, 1886), indicating that it belongs to a different group of hypotrichs, possibly the urostylids. Unfortunately, details of the infraciliature of *Hemicycliostyla* are not known. Borror and Wicklow (1983) even rejected the genus and synonymized both species described by Stokes (1886) with *Urostyla grandis*. However, *Hemicycliostyla lacustris*, described by Gellért and Tamás (1958), also lacks transverse and caudal cirri. Thus, such a type of hypotrichs may exist. *Pseudokahliella marina* (Foissner, Adam and Foissner, 1982) has a very simple dorsal infraciliature (3 rows) and all ventral cirral rows are morphogenetically active, indicating that it belongs to the Kahliellidae (Eigner, 1995; Foissner *et al.*, 1982).

***Gigantothrix herzogi* nov. spec.** (Fig. 12a–d, g–j, l–s; Table 9)

**Diagnosis:** Size in vivo about  $300 \times 160 \mu\text{m}$ . Broadly elliptical. On average 33 macronuclear nodules, 11 micronuclei, 76 adoral membranelles, 15 ventral cirral rows, 52 cirri each in right and left marginal row, 6 buccal cirri, and 7 cirri in upper frontal cirral row.

**Type location:** Upper soil layer of the forest surrounding the Sheldrick waterfalls in the Shimba Hills Nature Reserve, Kenya, equatorial Africa ( $39^{\circ}25'E$ ,  $5^{\circ}S$ ).

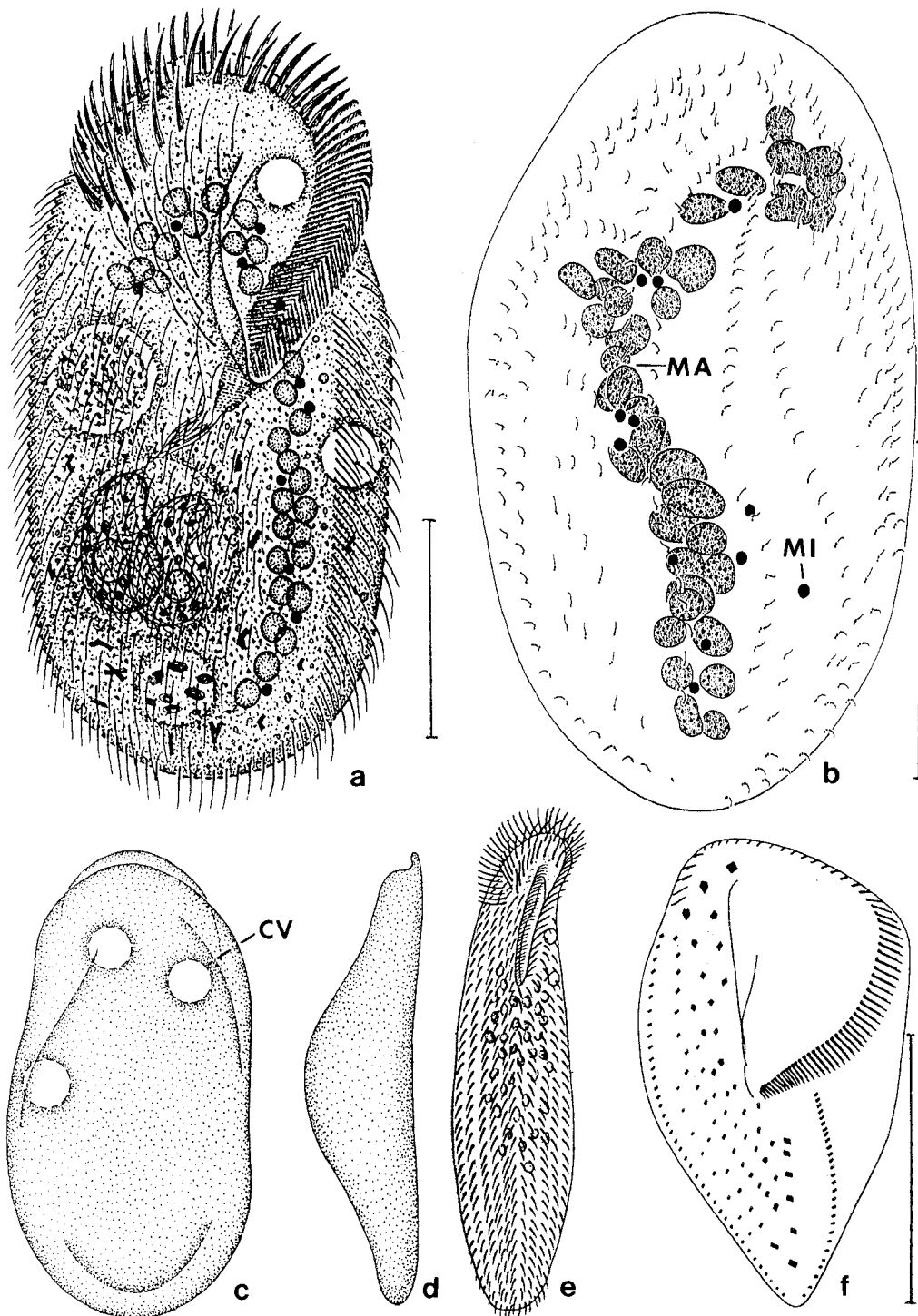
**Type slides:** Six slides (1 holotype and 5 paratypes) with protargol-impregnated morphostatic and dividing specimens have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria. The slides contain several specimens, with relevant cells marked by a black ink circle on the cover glass.

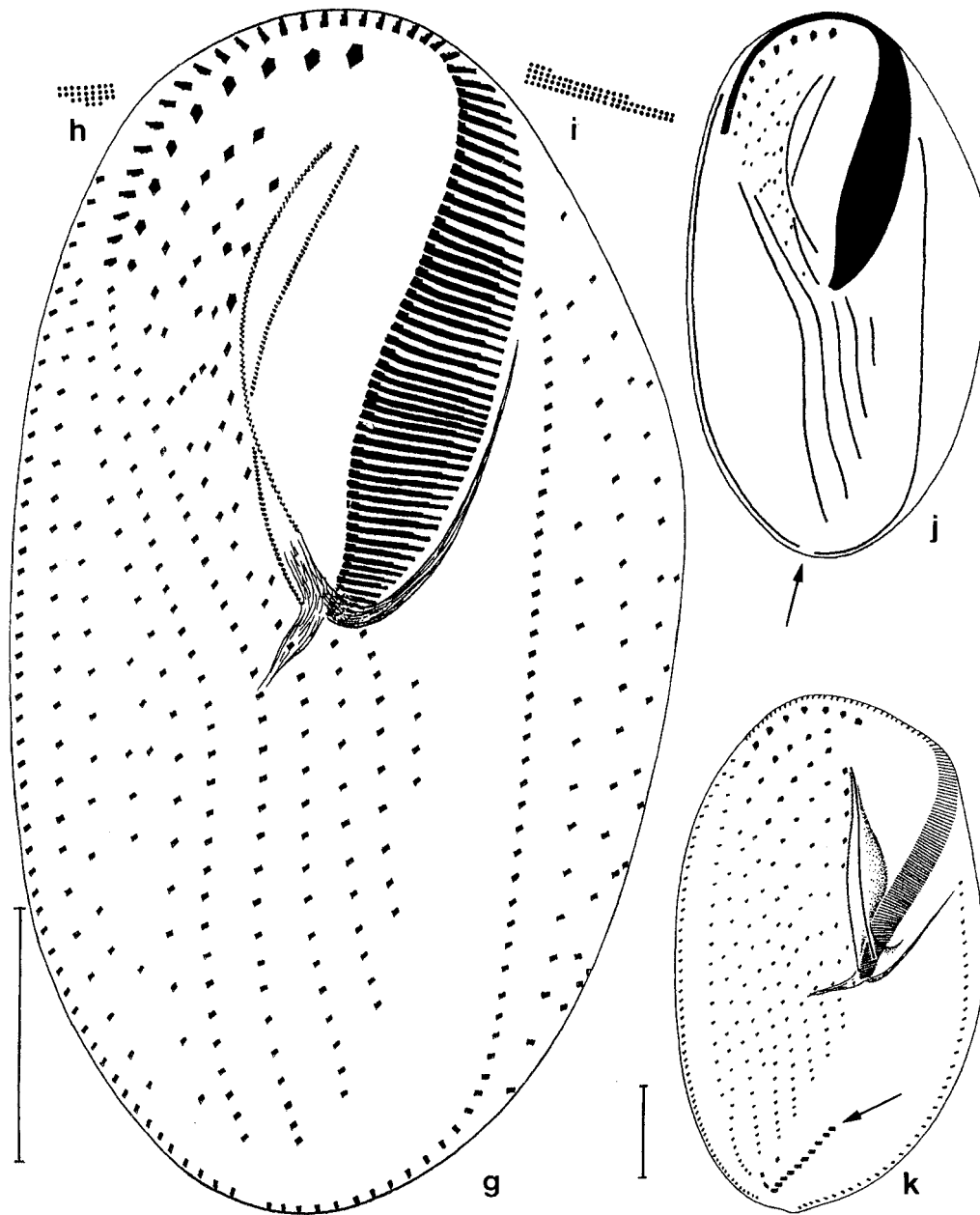
**Dedication:** I dedicate this new species to Dr. Eva Herzog for her technical help over many years.

**Description:** Size in vivo  $250\text{--}400 \times 120\text{--}200 \mu\text{m}$ , dorsoventrally flattened 2–3:1, with distinct bulge in mid-body (Fig. 12d); inflexible and acontractile. Body outline elliptical to almost rectangular (Fig. 12a, c), both ends very broadly rounded. Brownish at low magnification ( $\leq \times 100$ ) due to dense cytoplasmic granulation and large, opaque food vacuoles. Macronuclear nodules spherical to ellipsoidal, arranged left of midline in narrow strand curving to right margin of cell anteriorly forming roughly C-shaped figure; nucleoli numerous and tiny. Micronuclei globular, most near or attached to macronuclear nodules, some rather distant (Fig. 12a, b, n). Two to three contractile vacuoles along left and anterior margin of cell, possibly connected by lacunar collecting canal (Fig. 12c). Cortex without special granules, rigid and inflexible like, for instance, in *Stylonychia mytilus*. Cytoplasm very viscous and densely granulated, contains some colourless crystals, mainly in posterior half, and up to  $80 \mu\text{m}$  sized food vacuoles with heterotrophic

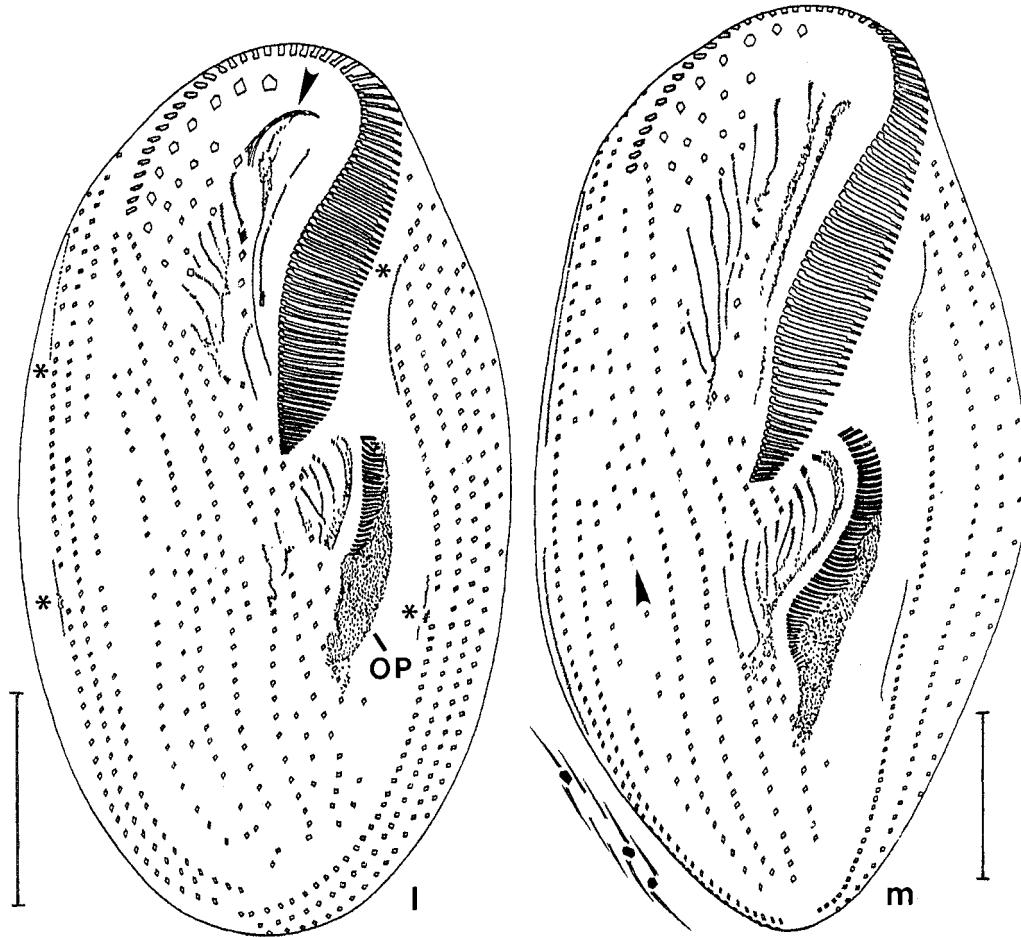
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**Figures 12a–f.** *Gigantothrix herzogi* (a–d) and other large hypotrichs (e, f) from life (a, c–e) and after protargol impregnation (b, f). **a:** Ventral view of a representative specimen with large food vacuoles. **b:** Infraciliature of dorsal side and nuclear apparatus of specimen shown in Figure 12g. **c:** Dorsal view of shape variant showing contractile vacuoles. **d:** Narrow side view. **e:** Ventral view of *Hemicycliostyla sphagni*, length  $420\text{--}500 \mu\text{m}$  (from Stokes, 1886). **f:** Infraciliature of ventral side of *Laurentiella strenua* (from Berger and Foissner, 1989). CV – contractile vacuole, MA – macronuclear nodule, MI – micronucleus. Scale bars  $100 \mu\text{m}$ .





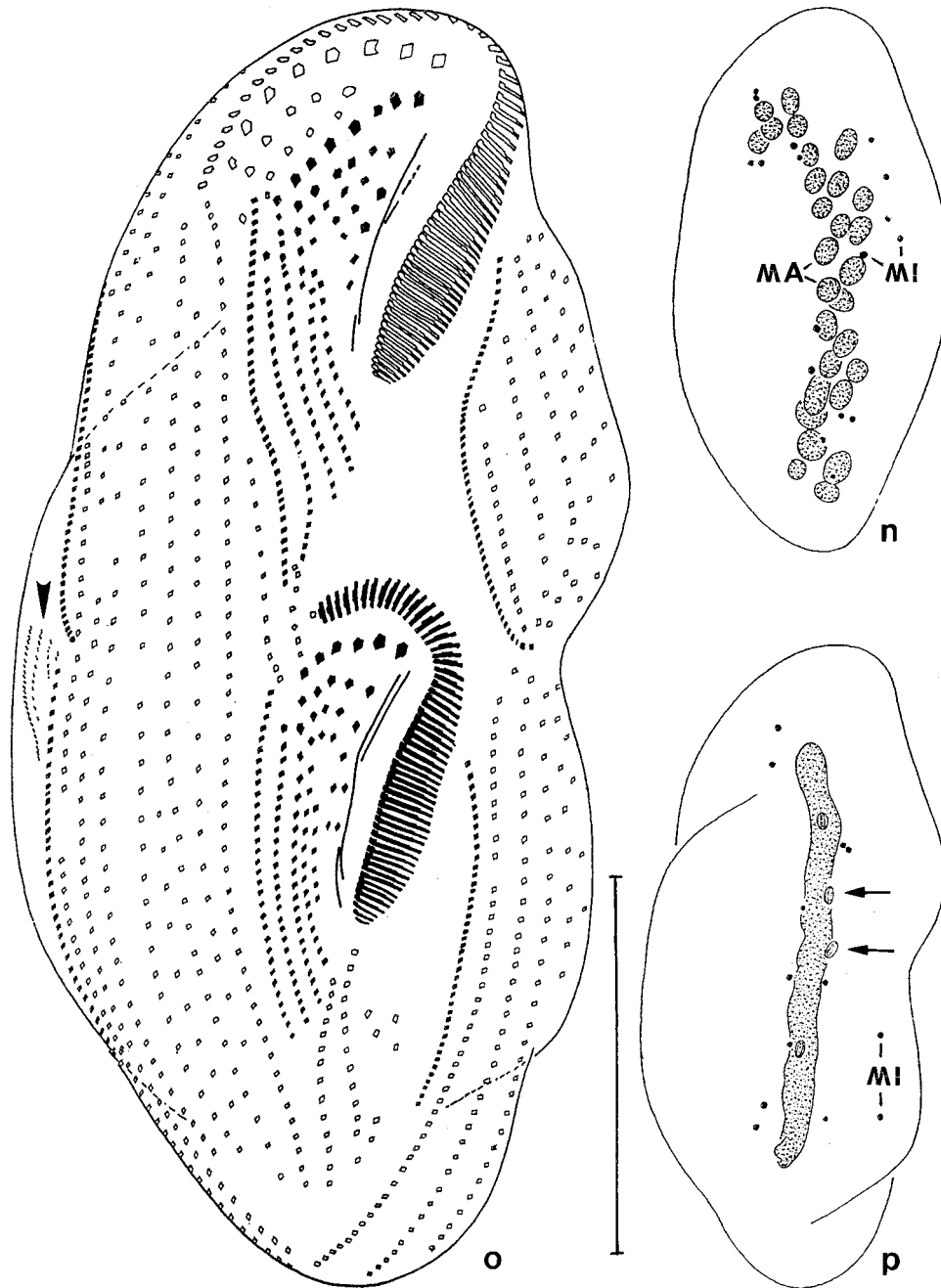
**Figures 12g–k.** *Gigantothrix herzogi* (g–j) and *Onychodromus quadricornutus* (k) after protargol impregnation. **g:** Infraciliature of ventral side (that of dorsal side is shown in Figure 12b). **h, i:** Fine structure of frontal and ventral adoral membranelles. **j:** Same specimen as shown in Figure 12g, but morphogenetically inactive ventral rows removed. Arrow marks narrow gap between posterior ends of marginal rows. **k:** *O. quadricornutus* has a similar cirral pattern as *G. herzogi*, but possesses distinct transverse (arrow) and caudal cirri, and all ventral rows are morphogenetically active. Scale bars 50  $\mu$ m.



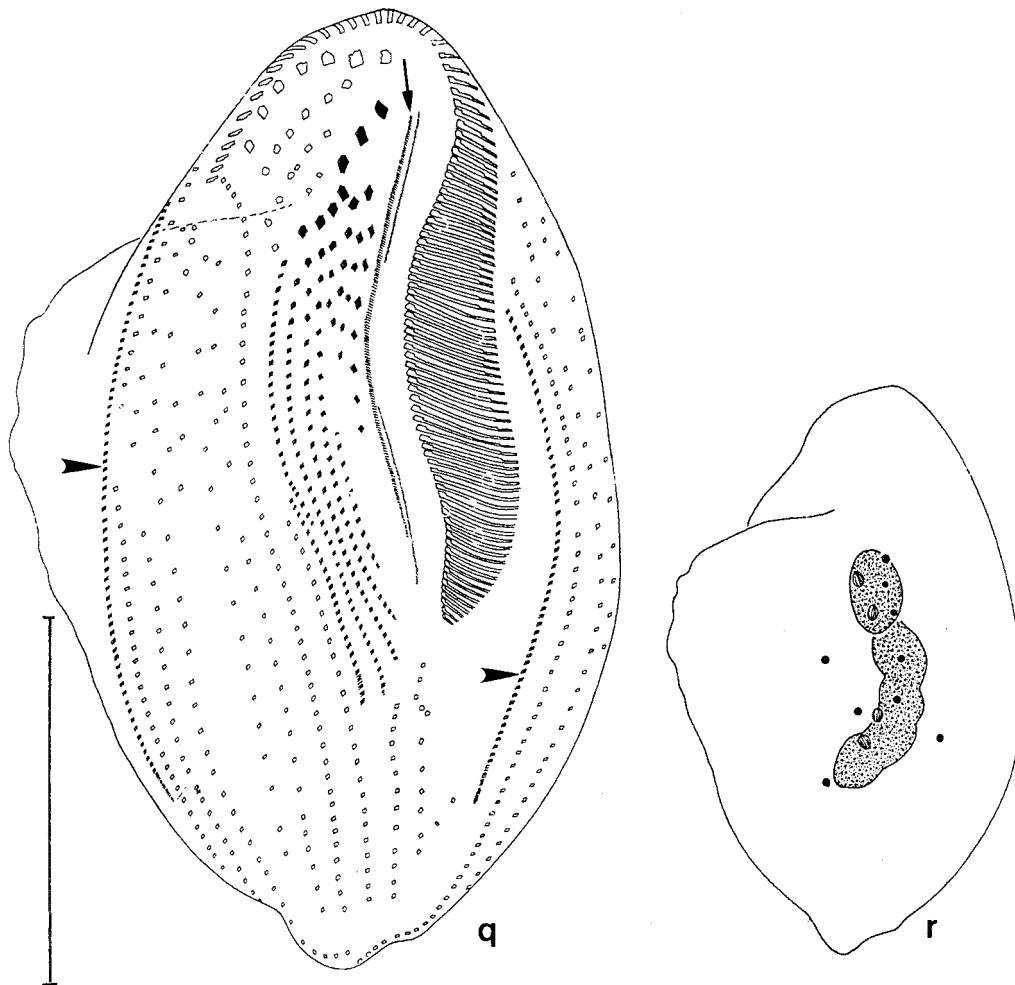
**Figures 12l,m.** *Gigantothrix herzogi*, ventral infraciliature of dividing specimens after protargol impregnation. **l:** Early divider showing origin of oral primordium (OP), ventral cirral streaks, and marginal rows (asterisks). Arrowhead marks disaggregating fibre bundle of paroral membrane. **m:** Middle divider showing about eight cirral anlagen each in the proter and opisthe. Arrowhead marks resorbing cirral row shown at higher magnification in left corner. The nuclear apparatus is still unchanged (Fig. 12n). Scale bars 50 µm.

flagellates, testate amoebae (*Trinema complanatum*, *Euglypha laevis*), ciliates (*Colpoda maupasi*, *Colpodidium caudatum*, *Drepanomonas muscicola*, *Gonostomum affine*, *Vorticella astyliforme*), and even rotifers (Fig. 12a).

Cirri rather fine compared to size of cell, in vivo about 20 µm long, similar size throughout, except those in frontal corona, which are distinctly enlarged and have a particular, pentagonal base (Fig. 12g). Marginal cirral rows almost confluent posteriorly. Frontoventral cirri numerous, form triangular field between paroral membrane, distal end of adoral zone of membranelles, and buccal vertex. Ventral cirral rows cover almost entire somatic surface, leaving blank small postoral area right of left marginal row, those in



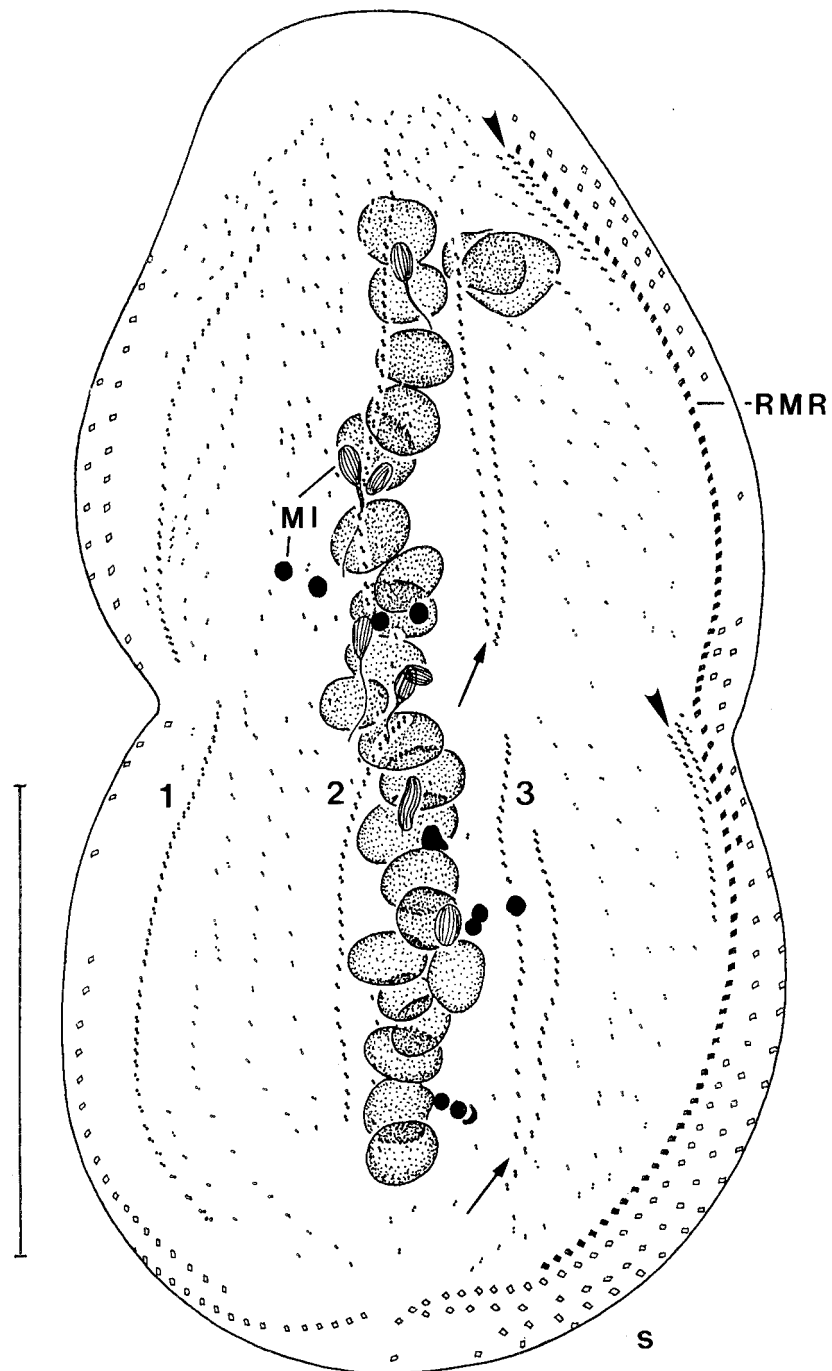
**Figures 12n–p.** *Gigantothrix herzogii*, ventral infraciliature and nuclear apparatus of dividing specimens after protargol impregnation. **n:** Nuclear apparatus of specimen shown in Figure 12m. **o, p:** Ventral cirral pattern and nuclear apparatus of a late divider. New cirri (shaded black) have formed in the anlagen and the oral apparatus is almost complete in both filial products. Arrowhead denotes dorsomarginal bristle rows, arrows mark dividing micronuclei. MA – macronuclear nodules, MI – micronuclei. Scale bar 100  $\mu$ m.



**Figures 12q,r.** *Gigantothrix herzogi*, ventral infraciliature (q) and nuclear apparatus (r) of a young post-divider after protargol impregnation. Note newly formed (shaded black) and parental (unshaded) cirral rows, most of which are retained, producing the typical cirral pattern of *G. herzogi*. Arrowheads mark new marginal rows. Arrow denotes the new paroral membrane, which is composed of many short kineties each made up of about four basal bodies; later, these kineties are reduced to dikinetids. Scale bar 100  $\mu$ m.

midline area slightly obliquely arranged and more densely and regularly ciliated than those right of midline and left of left marginal row, which are more or less distinctly shortened anteriorly and/or posteriorly (Fig. 12g); leftmost ventral cirral rows commence underneath buccal vertex and extend near posterior body end, becoming increasingly shortened from right to left.

Dorsal bristles about 4  $\mu$ m long, rather irregularly arranged in many short and long rows (Fig. 12b). A single, well-prepared and oriented late divider showed two or three dorsomarginal bristle rows and three bristle anlagen, of which the leftmost fragments



**Figure 12s.** *Gigantothrix herzogi*, dorsal infraciliature of a late divider after protargol impregnation. Three anlagen (numbers 1–3) are formed, of which anlage 3 splits posteriorly (arrows). Arrowheads mark newly formed dorsomarginal kineties. MI – dividing and non-dividing micronuclei, RMR – newly formed right marginal cirral row. Scale bar 100  $\mu$ m.



**Table 9.** Morphometric data from *Gigantothrix herzogii*

Character <sup>a</sup>	$\bar{x}$	M	SD	CV	Min	Max	n
Body, length	275.3	280	40.5	14.7	224.0	355.0	13
Body, width	144.2	148	21.4	14.8	112.0	175.0	13
Anterior somatic end to proximal end of adoral zone, distance	129.1	130	18.0	14.0	112.0	175.0	13
Macronuclear nodules, length	14.4	13	3.3	23.0	10.0	22.0	13
Macronuclear nodules, width	12.4	12	2.4	19.1	9.0	18.0	13
Macronuclear nodules, number	37.0	33	8.4	22.8	25.0	58.0	13
Micronuclei, length	4.7	5	0.6	13.2	3.8	5.6	13
Micronuclei, width	4.2	4	0.4	10.2	3.5	5.0	13
Micronuclei, number	12.4	11	4.8	38.8	5.0	21.0	13
Adoral membranelles, number	76.2	76	14.1	18.5	55.0	108.0	13
Cirral rows, total number in mid-body	15.5	15	1.7	10.8	14.0	20.0	13
Right marginal cirri, number	54.2	52	8.7	16.1	40.0	73.0	13
Left marginal cirri, number	52.5	51	4.6	8.8	47.0	61.0	13
Upper frontal cirral row, number of cirri	7.2	7	1.2	16.1	5.0	9.0	13
Lower frontal cirral row, number of cirri	4.5	5	1.3	29.3	2.0	6.0	13
Buccal cirri, number	6.4	6	1.0	16.4	5.0	8.0	13

<sup>a</sup> Data based on protargol-impregnated, mounted specimens from field (protocol A in Foissner, 1991). Measurements in  $\mu\text{m}$ . CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation,  $\bar{x}$  – arithmetic mean.

posteriorly (Fig. 12s), like in *Oxytricha* and *Stylonychia* (Berger and Foissner, 1997). Possibly, the rightmost anlage performs multiple fragmentation in very late dividers and much of the parental dorsal ciliature is retained, considering the irregular interphase pattern. No caudal cirri are formed.

Oral apparatus and adoral zone of membranelles very large and thus conspicuous, occupy about 46% of body length, that is, extend to body centre (Fig. 12a, g). Adoral zone of membranelles curves around broad anterior body end and extends back at right margin of cell for a considerable distance, accompanying frontal cirral corona; middle portion of zone distinctly broadened with bases of largest membranelles about 30  $\mu\text{m}$  wide and of conventional fine structure (Fig. 12g–i); proximal portion of zone covered by inconspicuous buccal lip. Buccal cavity large and rather deep. Undulating membranes fairly close together and distinctly curved, both very likely composed of closely spaced dikinetids; endoral optically intersects paroral in posterior half of buccal cavity. Pharyngeal fibres short, inconspicuous (Fig. 12g).

**Morphogenesis:** The slides contain some excellently prepared dividers, which show the following details: (1) The oral primordium of the opisthe develops at the posterior end of the ventral rows, whose cirri, however, remain intact (Fig. 12l); (2) The cirral pattern of the proter originates from about 8–10 anlagen formed by the frontoventral cirri right of the paroral membrane; the opisthe's cirri develop from the oral primordium and about 6–8 anlagen within the 4–5 leftmost cirral rows. Furthermore, the rightmost cirral row and the innermost left marginal row develop anlagen from which the new marginal cirral rows

originate (Fig. 12m); (3) All other cirral rows are morphogenetically inactive and gradually resorbed during the next 6 generations, as charged from the maximum number of left marginal cirral rows found (Fig. 12j, o, q); (4) The frontal cirral corona is formed from cirri at the anterior end of the anlagen for the new frontoventral cirri and the ventral cirral rows (Fig. 12o, q); (5) The parental undulating membranes are completely renewed (Fig. 12m, o, q); (6) Resorption of parental cirri occurs mainly in post-dividers (Fig. 12m, o, q); (7) The macronuclear nodules fuse (Fig. 12n, p, r).

**Occurrence and ecology:** Among about 1000 soil samples collected world-wide, including 200 samples from Africa, *G. herzogi* occurred only in three samples from the Shimba Hills (Tab. 1), suggesting that it is a very rare species with a limited geographic distribution. The large, flattened body indicates that it inhabits the litter.

**Comparison with related species:** No ciliate has been found in the literature that might be identical with *G. herzogi*. As it has a very distinct size and morphology, *G. herzogi* can hardly be confused with any other large hypotrich, for instance, *Onychodromus quadricornutus*, which has many transverse cirri and distinct horns on the dorsal surface (Fig. 12k).

#### ***Afrothrix* nov. gen.**

**Diagnosis:** Hypotrichida with bipartited adoral zone of membranelles, one right and left marginal cirral row, two ventral rows with cirri in midventral pattern, frontoterminal cirri, and transverse cirri.

**Type species:** *Afrothrix darbyshirei* nov. spec.

**Etymology:** Composite of the Latin word *Africa* and the Greek noun *thrix* (hair = ciliate s. l.), meaning “a ciliate occurring in Africa”. Feminine gender.

**Systematic position and comparison with related genera:** *Afrothrix darbyshirei* has, like *Erniella filiformis* Foissner, 1987c, a very distinctive oral apparatus which, however, probably evolved convergently, as indicated by the different nuclear apparatus and somatic infraciliature of the two (type) species mentioned: two vs. many macronuclear nodules, ventral cirral rows with midventral pattern vs. distinctly separate, frontoterminal cirri present vs. absent, one buccal cirrus vs. many buccal cirri, three dorsal bristle rows vs. one dorsal kinety. Thus, I do not unite *Afrothrix* and *Erniella* to a distinct family, but prefer to leave them unassigned until ontogenetic data become available and probably enable a proper classification.

*Notocephalus* Petz et al. (1995) has, like *Afrothrix*, midventral and transverse cirri and a conspicuous proximal half of adoral membranelles covered almost entirely by the buccal lip. However, the adoral zone of membranelles is continuous and extends on the distinctly cephalized anterior body portion, frontoterminal cirri are lacking, and the single known species lives in marine habitats.

#### ***Afrothrix darbyshirei* nov. spec. (Fig. 13a–g; Table 10)**

**Diagnosis:** Size in vivo about  $250 \times 50 \mu\text{m}$ , contractile by about 30% of body length. Cylindroidal with ends narrowly rounded. Cortical granules colourless, about  $1 \mu\text{m}$  in diameter, mainly around bases of cirri and dorsal bristles. Midventral row usually composed of 4 cirri pairs, thus terminating close underneath adoral zone of membranelles. On average 2 macronuclear nodules, 5 micronuclei, 9 frontal and 23 ventral adoral membranelles, about 52 cirri each in right and left marginal row, 3 frontal cirri, 2 frontoterminal cirri, 1 buccal cirrus, 9 transverse cirri, and 3 dorsal kineties.

*Type location:* Grassland soil near the Sheldrick waterfalls in the Shimba Hills Nature Reserve, Kenya, equatorial Africa (39°25'E, 5°S).

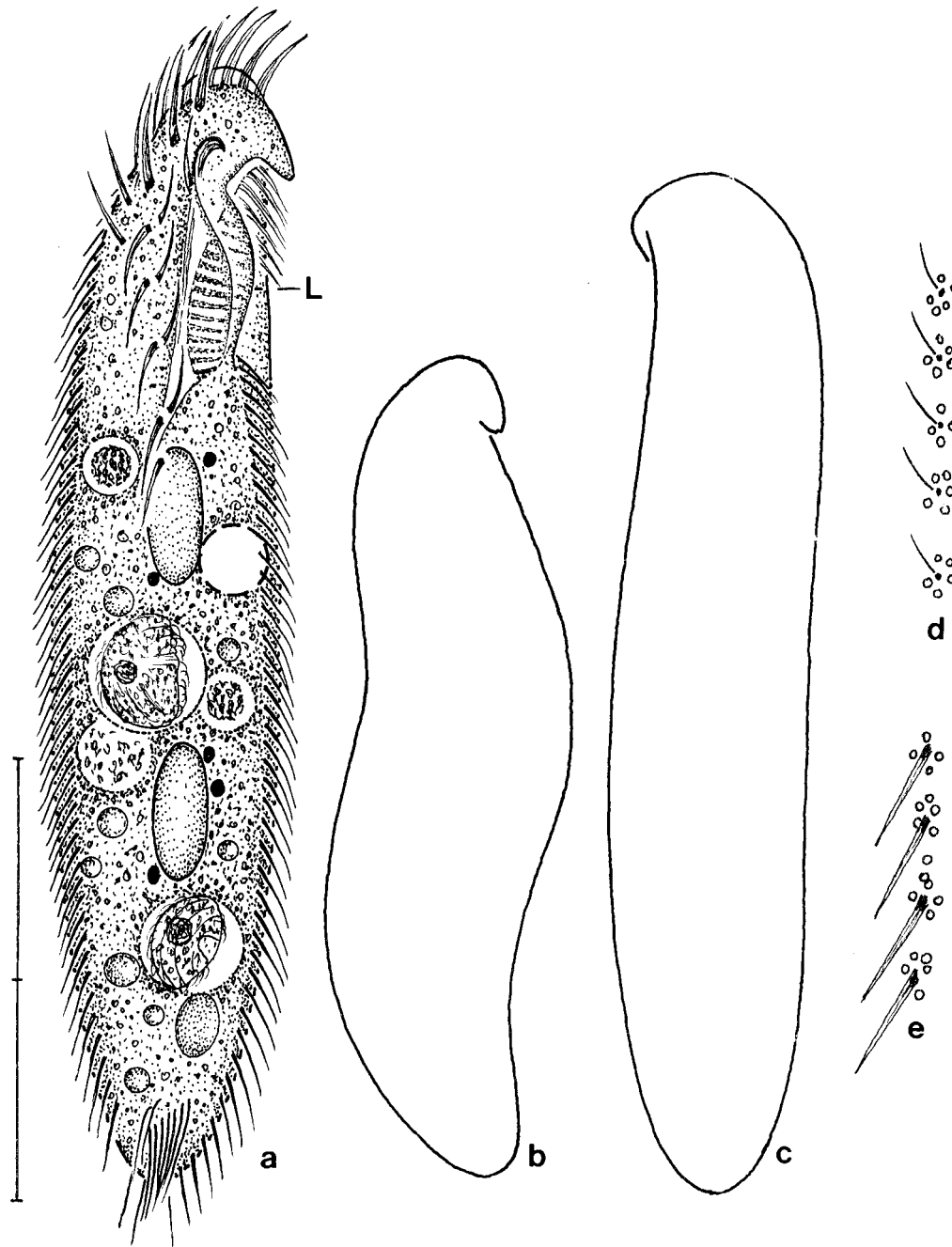
*Type slides:* Two slides (1 holotype and 1 paratype) with protargol-impregnated specimens have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria. The slides contain several specimens, with relevant cells marked by a black ink circle on the cover glass. The species is difficult to preserve with conventional fixatives, that is, most specimens burst or become distorted. Thus, the type slides are of mediocre quality.

*Dedication:* I dedicate this new species to Dr. John F. Darbyshire, eminent Scottish soil protozoan ecologist, for his continuous interest in my work.

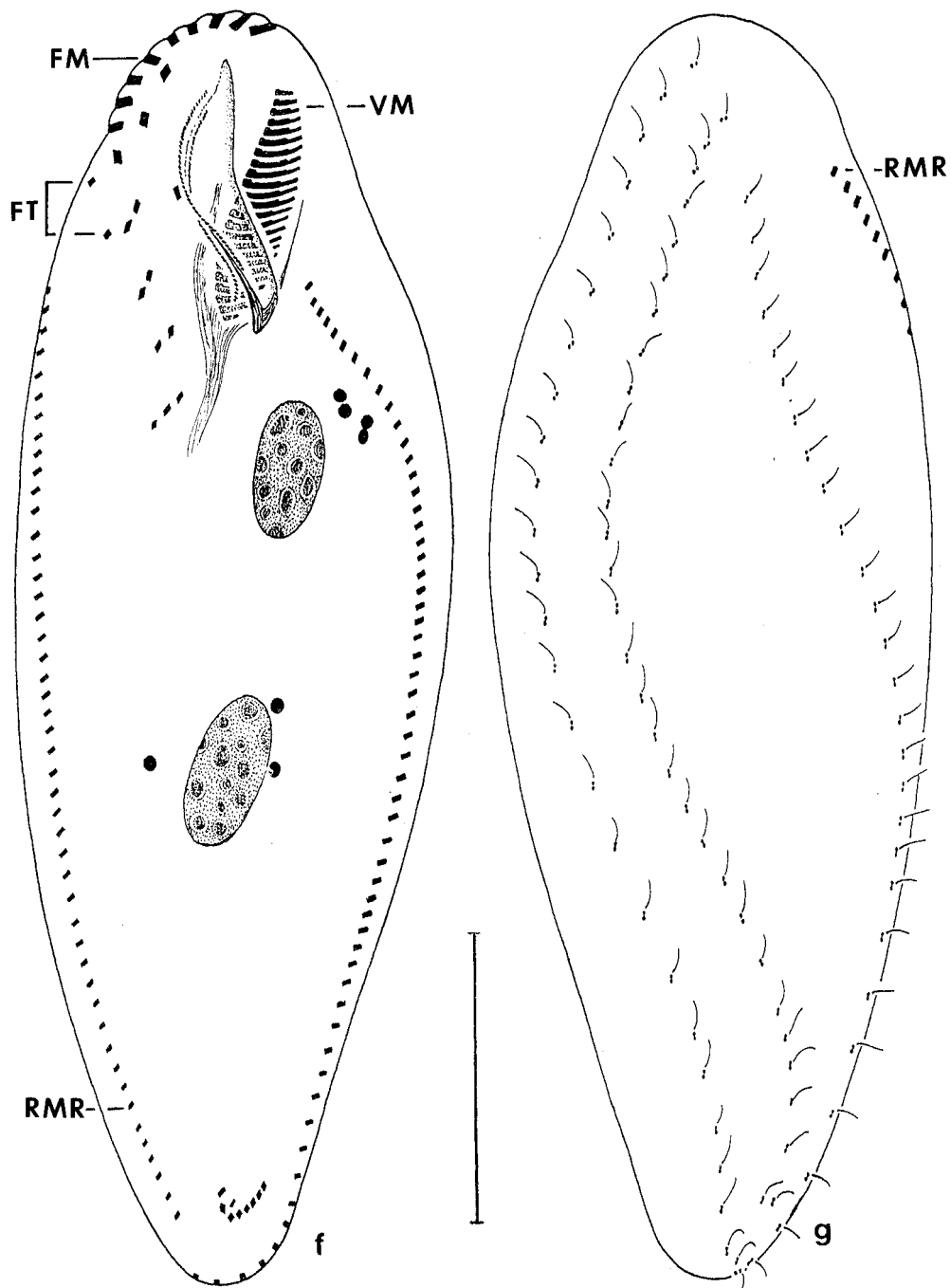
*Description:* Size in vivo 230–330 × 40–60 µm, very flexible and contractile by about 30% of body length, especially in anterior half; prepared specimens on average thus considerably smaller and broader than live cells (Table 10; Fig. 13a, f). Cylindroidal to elongate fusiform, both ends narrowly rounded, middle portion slightly widened, with small but distinct subapical process at anterior end of ventral portion of adoral zone of membranelles (Fig. 13a); dorsoventrally flattened up to 2:1. Macronuclear nodules in middle third of cell, distinctly apart and ellipsoidal (on average 2.5:1; Table 10), contain large, globular nucleoli. Micronuclei slightly ellipsoidal, near to or rather distant from macronuclear nodules, compact and thus easy to recognise in vivo (Fig. 13a, f). Contractile vacuole in mid-body at left margin of cell. Cortical granules inconspicuous because minute (about 1 µm in diameter) and colourless, located around bases of cirri and dorsal bristles and on inner surface of buccal cavity; do not stain with protargol (Fig. 13d, e). Cytoplasm colourless, usually packed with some yellowish globules up to 13 µm across and food vacuoles containing various small ciliates (*Cyclidium muscicola*, *Drepanomonas pauciciliata*, *Leptopharynx costatus*, *Pseudochilodonopsis mutabilis*). Swims and glides hastily to and fro, contracting spasmodically and becoming sigmoidal when touching an obstacle (Fig. 13b).

Marginal cirri in vivo about 12 µm long, become gradually thinner posteriorly. Left marginal row conspicuous because extending around posterior body margin, the rightmost cirri thus being easily misinterpreted as caudal cirri; right marginal row commences subapically at level of buccal cirrus and terminates at level of transverse cirri, thus being separated from left row by distinct break (Fig. 13f). Frontal cirri slightly enlarged, in vivo about 15 µm long, rightmost cirrus underneath distal end of adoral zone of membranelles. Buccal cirrus at summit of curve formed by paroral membrane. Frontoterminal cirri distinctly apart from midventral row, upper cirrus right of rightmost frontal cirrus, lower right of first midventral pair (Fig. 13a, f). Midventral row inconspicuous because composed of an average of four cirri pairs only, terminates slightly beyond adoral zone of membranelles, usually one cirrus more in right than in left ventral row, occasionally forming a distinct triplet with last midventral pair (Fig. 13f; Table 10). Transverse cirri not enlarged, in vivo about 20 µm long, project slightly beyond posterior body margin, form slightly curved, oblique row left of midline; usually two minute (ventral?) cirri ahead of transverse cirri (Fig. 13a, f). Dorsal cilia (bristles) about 4 µm long, arranged in three rows almost as long as body, invariably two tightly spaced bristles each at posterior end of rows, possibly remnants of caudal cirri (Fig. 13g).

Oral apparatus, though comparatively small, that is, occupying only about 23% of body length, conspicuous because of its particular organization (Fig. 13a, f; Table 10). Adoral zone of membranelles with distinct break in upper third, dividing zone in a frontal and ventral portion: frontal portion at upper and right anterior margin of cell, composed



**Figures 13a–e.** *Afrothrix darbyshirei* from life. **a, b:** Ventral view of a representative, extended and contracted specimen. **c:** Shape variant. **d, e:** Cortical granules around dorsal bristles and marginal cirri. L – buccal lip. Scale bar division 50  $\mu\text{m}$ .



**Figures 13f, g.** *Afrothrix darbyshirei*, infraciliature of ventral and dorsal side after protargol impregnation. FM – frontal adoral membranelles, FT – frontoterminal cirri, RMR – right marginal row, VM – ventral adoral membranelles. Scale bar 50  $\mu$ m.

**Table 10.** Morphometric data from *Afrothrix darbyshirei*

Character <sup>a</sup>	$\bar{x}$	M	SD	CV	Min	Max	n
Body, length	217.8	215	22.2	10.2	185	280	13
Body, width	60.0	60	9.0	15.0	47	75	13
Anterior somatic end to proximal end of adoral zone, distance	52.6	50	7.0	13.3	45	70	13
Anterior somatic end to proximal end of midventral row, distance	72.5	70	13.6	18.7	50	100	13
Macronuclear nodules, length	28.9	27	4.8	17.0	23	40	13
Macronuclear nodules, width	11.0	11	1.2	11.1	9	13	13
Macronuclear nodules, number	2.0	2	0.0	0.0	2	2	13
Micronuclei, length	2.8	3	0.5	18.1	2	4	13
Micronuclei, width	2.6	2.5	0.4	13.9	2	3	13
Micronuclei, number	5.2	5	1.6	31.5	3	9	13
Frontal adoral membranelles, number	8.8	9	0.9	10.2	8	10	13
Ventral adoral membranelles, number	22.4	23	1.3	5.9	20	25	13
Frontal cirri, number	3.0	3	0.0	0.0	3	3	10
Buccal cirri, number	1.0	1	0.0	0.0	1	1	13
Frontoterminal cirri, number	2.0	2	0.0	0.0	2	2	11
Right midventral cirri, number	5.1	5	0.6	12.6	4	6	13
Left midventral cirri, number	4.3	4	—	—	4	5	13
Transverse cirri, number <sup>b</sup>	9.1	9	1.2	13.1	7	11	13
Right marginal cirri, number	53.1	54	5.4	10.2	46	66	13
Left marginal cirri, number	50.3	50	5.1	10.1	40	59	13
Dorsal kineties, number	3.0	3	0.0	0.0	3	3	13

<sup>a</sup> Data based on protargol-impregnated, mounted specimens from field (protocol A in Foissner, 1991). Measurements in  $\mu\text{m}$ . CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation,  $\bar{x}$  – arithmetic mean.

<sup>b</sup> Including ventral cirri possibly present ahead of transverse cirri.

of 9 short membranelles on average; ventral portion extends obliquely from left anterior end, which projects hook-like, to midline of cell, composed of 23 membranelles on average, elliptical because widest membranelles near centre of zone. Buccal cavity narrow and rather flat but with conspicuous, curved roof almost completely covering ventral portion of adoral zone of membranelles. Undulating membranes about as long as ventral portion of adoral zone of membranelles, close together and distinctly curved, both very likely composed of closely spaced dikinetids; paroral in distinct cleft on surface of buccal lip, intersects endoral optically in mid of buccal cavity. Pharyngeal fibres form distinct bundle.

*Occurrence and ecology:* As yet found only at type location.

*Comparison with related species:* There is only a single species which is rather similar to *A. darbyshirei*, namely *Erniella filiformis*, which, however, has many macronuclear nodules and two long ventral cirral rows (Foissner, 1987c). Thus, these species cannot be confused, not even in vivo.

***Oxytricha africana* nov. spec.** (Fig. 14a–e; Table 11)

**Diagnosis:** Size in vivo about  $90 \times 35 \mu\text{m}$ , ellipsoidal. 2 macronuclear nodules, each usually with 1 micronucleus. All cirri conspicuously thick and long (up to  $35 \mu\text{m}$ ). Undulating membranes in typical *Oxytricha* pattern. On average 25 adoral membranelles, 15 right and 19 left marginal cirri, and 5 transverse cirri. Dorsal bristles about  $10 \mu\text{m}$  long, arranged in 6 rows, rows 1 and 3 each with distinct break in posterior quarter.

**Type location:** Grass sward soil (pH 6.7) from a public park in the city of Nairobi, Kenya, equatorial Africa ( $36^{\circ}50'E$ ,  $1^{\circ}20'S$ ).

**Type slides:** Two slides (1 holotype and 1 paratype) with protargol-impregnated specimens have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria. The slides contain several specimens, with relevant cells marked by a black ink circle on the cover glass.

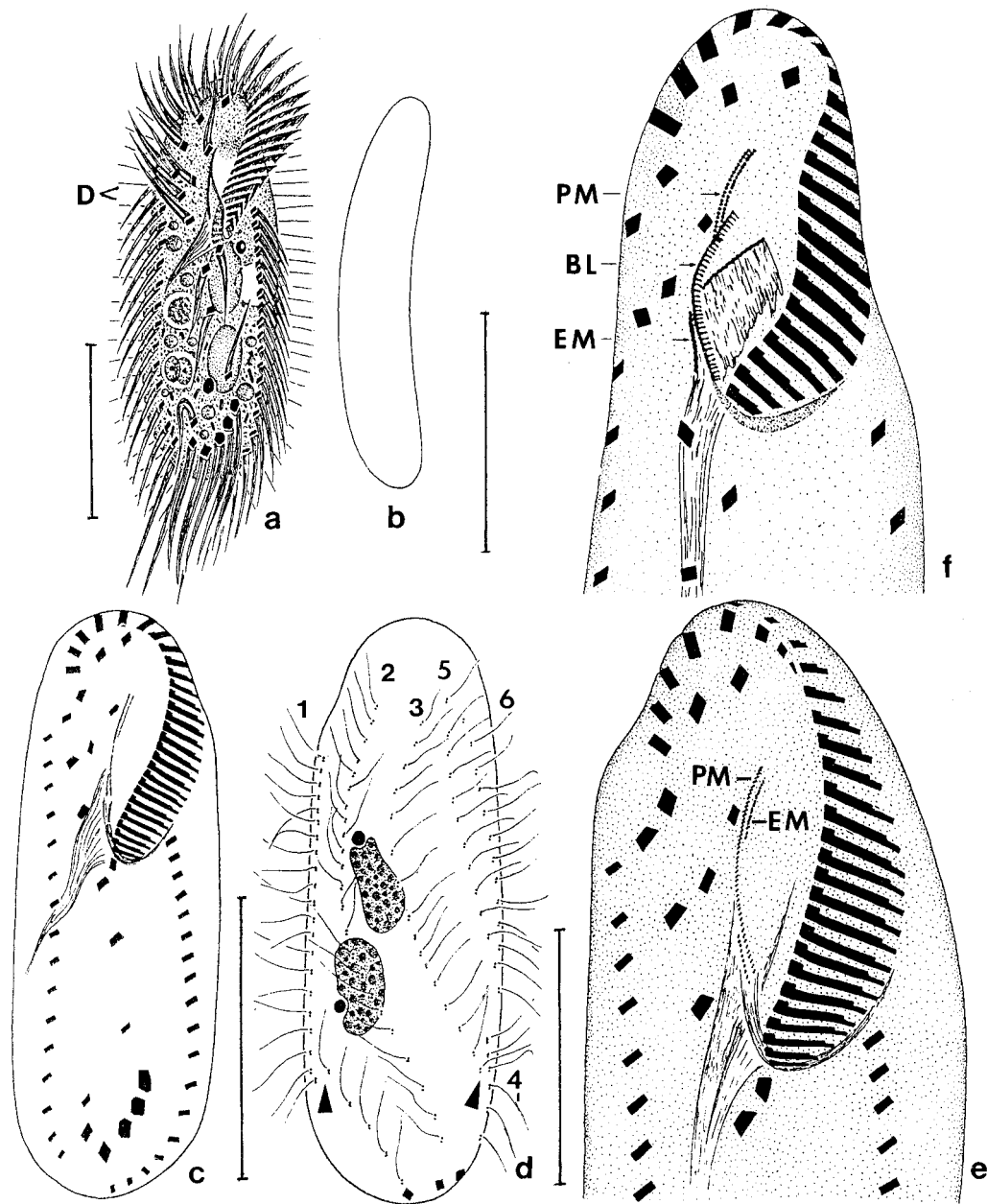
**Etymology:** “africana” (adjective of the Latin noun Africa) because discovered in Africa.

**Description:** Size in vivo  $80\text{--}115 \times 30\text{--}40 \mu\text{m}$ , length:width ratio of prepared specimens on average 2.7:1 (Fig. 14a, c; Table 11). Shape rather constant, elongate-ellipsoidal to slightly ovoid, both ends broadly rounded, dorsoventrally flattened up to 2:1. Very flexible, especially under slight cover glass pressure. Macronuclear nodules close together in middle third of cell slightly left of midline, ellipsoidal (about 2:1), with many globular nucleoli. Micronuclei slightly ellipsoidal, location and number variable, usually (about 60% of specimens) one micronucleus attached to each macronuclear nodule in variable position, about 40% have only one micronucleus near the anterior or posterior macronuclear nodule, occasionally it is between the nodules. Contractile vacuole in mid-body at left margin of cell, without distinct collecting canals. Cortex colourless, flexible, without special granules. Cytoplasm packed with fat globules  $1\text{--}7 \mu\text{m}$  across,  $2\text{--}3 \mu\text{m}$  long crystals, and food vacuoles containing heterotrophic flagellates and, occasionally, small testate amoebae (*Euglypha laevis*). Movement moderately rapid, without peculiarities.

Number (18) and pattern of ventral cirri as in other typical members of genus, cirri, however, extraordinarily thick and long compared to size of cell (Fig. 14a, c, d), viz. about  $20 \mu\text{m}$  (marginal and frontoventral cirri) to  $30\text{--}35 \mu\text{m}$  (transverse and caudal cirri). Marginal rows open widely at posterior end, gap occupied by caudal cirri on dorsal side right of midline. Transverse cirri sigmoidally curved, project distinctly beyond posterior body margin, form conspicuous corona together with posterior marginal cirri and caudal cirri. Dorsal cilia (bristles) about  $10 \mu\text{m}$  long in vivo, arranged in 6 rows, of which rows 1 and 3 invariably have distinct break in posterior quarter; break of row 3 very likely caused by fragmentation during ontogenesis, like in other oxytrichids (Berger and Foissner, 1997); thus, the short posterior fragment has been interpreted as kinety 4. Bristle rows 5 and 6 distinctly shortened posteriorly, that is, end subequatorially (Fig. 14d).

Oral apparatus and adoral zone of membranelles conspicuous because occupying about 40% of body length (Fig. 14a, c, e; Table 11). Buccal cavity, however, rather flat and narrow and with inconspicuous hyaline lip covering proximal portion of adoral zone. Paroral and endoral membrane only slightly curved and close together, intersect optically in mid-portion of buccal cavity, both very likely composed of dikinetids. Pharyngeal fibres distinct.

**Occurrence and ecology:** As yet found at type location, in the Shimba Hills (sample 16), and in three samples from Australia (coastal soil at Darwin, Northern Territory, pH 6.7;



**Figure 14a–f.** *Oxytricha africana* (a–e) and *O. siseris* (f) from life (a, b) and after protargol impregnation (c–f). **a, b:** Ventral and narrow side view of a representative specimen. **c, d:** Infraciliature of ventral and dorsal side. Arrowheads mark break in kineties 1 and 3. If the posterior segment of kinety 3 is designated as kinety 4, then *O. africana* has 6 dorsal kineties, like many other oxytrichids. **e, f:** Oral area of *O. africana* and *O. siseris* (from Foissner, 1982) at higher magnification. BL – buccal lip, D – dorsal bristles, EM – endoral membrane, PM – paroral membrane. Scale bars 40 µm (a, b, c, d) and 20 µm (e, f).



**Table 11.** Morphometric data from *Oxytricha africana* (upper line) and *O. elegans* (lower line)

Character <sup>a</sup>	$\bar{x}$	M	SD	CV	Min	Max	n
Body, length	80.7	80.0	7.2	8.9	72.0	100.0	12
	60.6	59.0	6.7	11.0	51.0	77.0	11
Body, maximum width	29.8	28.5	2.5	8.4	28.0	35.0	12
	26.6	26.0	2.2	8.3	24.0	30.0	11
Anterior somatic end to proximal end	32.2	31.5	2.3	7.2	29.0	36.0	12
of adoral zone of membranelles, distance	17.7	18.0	0.9	5.1	17.0	20.0	11
Macronuclear nodules, length	13.1	13.0	1.2	8.9	11.0	15.0	12
	11.5	11.0	1.2	10.6	10.0	14.0	11
Macronuclear nodules, width	7.3	7.0	0.7	8.9	6.0	8.0	12
	6.0	6.0	0.6	10.5	5.0	7.0	11
Macronuclear nodules, distance in between	3.2	3.0	1.6	51.9	1.0	7.0	12
	—	—	—	—	—	—	—
Macronuclear nodules, number	2.0	2.0	0.0	0.0	2.0	2.0	12
	2.0	2.0	0.0	0.0	2.0	2.0	19
Micronuclei, length	2.7	2.8	0.1	5.1	2.5	2.8	12
	3.9	4.0	0.4	8.9	3.2	4.5	11
Micronuclei, width	2.6	2.5	0.2	9.1	2.1	2.8	12
	2.9	3.0	0.2	6.3	2.6	3.2	11
Micronuclei, number	1.6	2.0	0.5	32.5	1.0	2.0	12
	1.0	1.0	0.0	0.0	1.0	1.0	19
Adoral membranelles, number	25.2	25.5	1.8	7.0	22.0	28.0	12
	16.2	16.0	0.8	4.6	15.0	17.0	11
Right marginal cirri, number	15.2	15.0	1.0	6.8	13.0	17.0	12
	8.8	9.0	1.2	13.2	7.0	11.0	11
Left marginal cirri, number	18.6	19.0	1.7	9.3	14.0	21.0	12
	10.7	10.0	1.2	11.1	9.0	13.0	11
Frontal cirri, number	3.0	3.0	0.0	0.0	3.0	3.0	12
	3.0	3.0	0.0	0.0	3.0	3.0	11
Frontoventral cirri, number	4.0	4.0	0.0	0.0	4.0	4.0	12
	4.0	4.0	0.0	0.0	4.0	4.0	11
Buccal cirri, number	1.0	1.0	0.0	0.0	1.0	1.0	12
	1.0	1.0	0.0	0.0	1.0	1.0	11
Postoral ventral cirri, number	3.0	3.0	0.0	0.0	3.0	3.0	11
	3.0	3.0	0.0	0.0	3.0	3.0	12
Pretransverse cirri, number	2.0	2.0	0.0	0.0	2.0	2.0	12
	2.0	2.0	0.0	0.0	2.0	2.0	11
Transverse cirri, number	5.0	5.0	0.0	0.0	5.0	5.0	12
	5.0	5.0	0.0	0.0	5.0	5.0	11
Caudal cirri, number	3.0	3.0	0.0	0.0	3.0	3.0	12
	3.0	3.0	0.0	0.0	3.0	3.0	11
Dorsal kineties, number	6.0	6.0	0.0	0.0	6.0	6.0	12
	4.0	4.0	0.0	0.0	4.0	4.0	11

<sup>a</sup> Data based on protargol-impregnated, mounted specimens from field (protocol A in Foissner, 1991). Measurements in  $\mu\text{m}$ . CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation,  $\bar{x}$  – arithmetic mean.

Green Island near Cairns, about 20 m inshore, litter and upper soil layer under a *Caesalpinia* tree, pH 7.1; Green Island near Cairns, collection of litter and soil from the rain forest in the centre of the island, pH 6.5). Thus, *O. africana* is probably widely distributed, at least in Gondwanan soils.

**Comparison with related species:** This new species highly resembles *O. siseris* Vuxanovici, as redescribed by Foissner (1982), except for the oral apparatus, which is of typical oxytrichid structure, while it is very distinctive in *O. siseris*, which has been confirmed by a reinvestigation of the type slides (Fig. 14f). The same applies to *O. pseudosimilis*, for which Hemberger (1985) definitely states: "The undulating membranes are very short and do not intersect". Thus, these populations are definitely different. Minor distinguishing characters between *O. africana* and *O. siseris* concern the number of marginal cirri (15–19 vs. 11–14) and the pattern and length (10 vs. 13–20 µm) of the dorsal bristles. Unfortunately, the dorsal infraciliature of *O. pseudosimilis* has not been described in detail.

There are several other *Oxytricha* species which resemble *O. africana* [see reviews by Kahl (1932) and Berger (1999) as well as discussion by *O. elegans*, described below]. However, none possesses the character combination found in *O. africana*, which is in vivo easily confused with *O. siseris* and *O. setigera*-like hypotrichs (see *O. elegans*, described below).

***Oxytricha elegans* nov. spec.** (Fig. 15a–f; Table 11)

**Diagnosis:** Size in vivo about  $70 \times 25$  µm, elongate-ellipsoidal. 2 macronuclear nodules and 1 micronucleus in between. All cirri conspicuously thin and long (up to 30 µm). Buccal cirrus near distal end of undulating membranes. On average 16 adoral membranelles, 9 right and 10 left marginal cirri, and 5 transverse cirri. Dorsal bristles 3–5 µm long, sparse, arranged in 4 rows, rows 1 and 4 each with conspicuous break in mid-body, rows 2 and 3 distinctly shortened posteriorly.

**Type location:** Forest soil near the Sheldrick waterfalls in the Shimba Hills Nature Reserve, Kenya, equatorial Africa (39°25', 5°S).

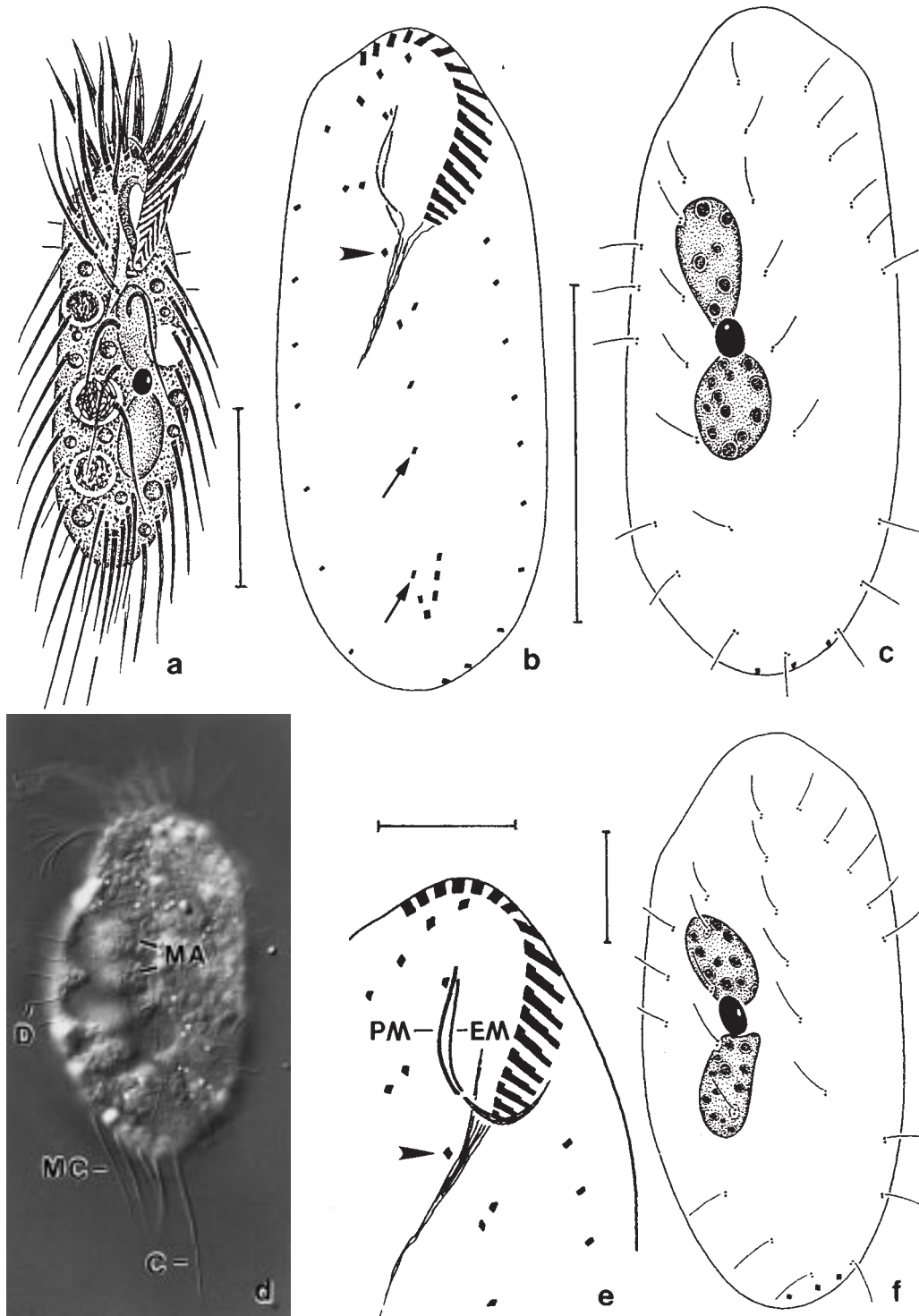
**Type slides:** Two slides (1 holotype and 1 paratype) with protargol-impregnated specimens have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria. The slides contain several specimens, with relevant cells marked by a black ink circle on the cover glass.

**Etymology:** "elegans" (Lat., elegant) because of the elegant general appearance.

**Description:** Size in vivo  $55\text{--}90 \times 20\text{--}30$  µm, length:width ratio thus about 3:1 (Fig. 15a), preserved specimens stouter (about 2.3:1; Table 11; Fig. 15b, f) because inflated by preparation procedures. Shape rather constant, elongate-ellipsoidal to almost parallel-sided, both ends narrowly rounded, dorsoventrally flattened up to 2:1, depending on

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**Figure 15a–f.** *Oxytricha elegans* from life (a, d) and after protargol impregnation (b, c, e, f). **a:** Ventral view of a representative specimen. **b, c, e, f:** Infraciliature of ventral and dorsal side. The three postoral ventral cirri are between the lowermost frontoventral cirrus (arrowhead), which is close underneath the buccal vertex, and the pretransverse cirri (arrows). Note one of the most important species characters, namely the distinct break in the centre of the marginal bristle rows (c, f). **d:** Dorsal view of a specimen from the Madagascan population. Note one of the long (30 µm) caudal cirri, some marginal cirri (20 µm) and dorsal bristles (5 µm), and the two macronuclear nodules. C – caudal cirrus, D – dorsal bristles, EM – endoral membrane, MA – macronuclear nodules, MC – marginal cirri, PM – paroral membrane. Scale bars 30 µm (a, b, c) and 10 µm (e, f).



nutrition state (Fig. 15a). Body soft and flexible. Macronuclear nodules close together in middle third of cell slightly left of midline, ellipsoidal (about 2:1), with many globular nucleoli. Micronucleus slightly ellipsoidal, invariably between macronuclear nodules (Fig. 15a, c, d, f). Contractile vacuole slightly above mid-body at left margin of cell, without distinct collecting canals. Cortex colourless, flexible, without special granules (checked with methyl green-pyronin). Cytoplasm packed with 2–7 µm sized fat globules and food vacuoles up to 10 µm across containing bacteria and heterotrophic flagellates; no cytoplasmic crystals. Movement moderately rapid, without peculiarities. Morphogenesis commences close to uppermost left transverse cirrus.

Number (18) of ventral cirri as in other typical members of genus, cirral pattern, however, with several peculiarities (Fig. 15a, b, d): (i) posterior frontoventral cirrus close underneath buccal vertex; (ii) upper pretransverse cirrus near mid-body, that is, very distant from transverse cirri; (iii) transverse cirri in narrowly V-shaped pattern, that is, almost forming a straight line, project beyond posterior body margin; (iv) marginal cirri very widely spaced, rows open at posterior end, gap occupied by caudal cirri on dorsal side right of midline. All cirri extraordinarily long and thin compared to size of cell (Fig. 15a, d): marginal and frontoventral cirri 17–20 µm long, transverse cirri 20–25 µm long, caudal cirri 30 µm long and spread rightwards. Dorsal cilia (bristles) 3–5 µm long, form very constant pattern (cp. Fig. 15c, d, f): marginal rows 1 and 4 each with distinct central break due to lack of 2–3 bristles, central rows 2 and 3 distinctly shortened posteriorly. Whether the posterior fragment of row 4 belongs to that row or originates by fragmentation of row 3, needs to be clarified by an investigation of its ontogenesis.

Oral apparatus and adoral zone of membranelles inconspicuous because occupying only about 29% of body length (Fig. 15a, b, e; Table 11); bases of largest membranelles in vivo about 5 µm wide and of conventional fine structure. Buccal cavity narrow and flat, right half covered by thick and thus distinct roof (lip). Paroral membrane composed of very closely spaced, about 5 µm long cilia, extends at base (right margin) of buccal roof, slightly curved, optically intersects endoral membrane in anterior and posterior third (Fig. 15b), occasionally both side by side (Fig. 15e). Pharyngeal fibres rather distinct and obliquely extending to mid-body.

*Occurrence and ecology:* As yet found at type location (site 16), in South Africa (Cape Peninsula, Sirkelsvlei, 18.2.1995, upper 0–10 cm grass sward and soil layer at shore of a small lake, soil sandy, pH 5.4, flooded during high water of the lake), and in Madagascar (leaf litter from a forest rivulet on Nosey-Be Island, pH 6.1; collected on 19.9.1988 by G. Steinberg, Kiel).

*Comparison with related species:* *Oxytricha elegans* resembles *O. setigera*, *O. opisthomuscorum*, *O. balladyna*, and *O. pseudofusiformis* as concerns body size and shape, nuclear apparatus, cirral pattern, and number of adoral membranelles. *Oxytricha setigera* Stokes, as redescribed by Foissner (1982) and Song and Wilbert (1989), has the buccal cirrus near the *proximal* end of the undulating membranes, and the dorsal bristles are distinctly longer (10–15 µm vs. 3–5 µm). *Oxytricha opisthomuscorum* Foissner *et al.*, 1991, as redescribed by Petz and Foissner (1997), has more adoral membranelles (18–22 vs. 15–17) and marginal cirri (11–16 vs. 7–13), and more and longer (10 µm vs. 3–5 µm) dorsal bristles, which are also differently arranged. *Oxytricha balladyna* Song and Wilbert, 1989 is similar to *O. elegans* in many respects, especially in having a distinct break in the leftmost dorsal kinety and a very similar number of adoral membranelles; it differs, however, by the lack of a break in the rightmost dorsal kinety, the length of the dorsal bristles (10 µm vs.

3–5 µm), the more densely ciliated and unshortened dorsal bristle rows 3 and 4, and the upper pretransverse cirrus, which is distinctly nearer to the transverse cirri. *Oxytricha pseudofusiformis* Dragesco and Dragesco-Kernéis, 1986 has been described very superficially, that is, without any information about the dorsal infraciliature and the living cell. Thus, a reliable comparison with *O. elegans* is impossible. However, the frontoventral cirral pattern is different, that is, the posterior cirrus is above the buccal vertex.

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