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Soil Ciliates from Saudi Arabia, Including Descriptions of Two New Genera and Six New Species

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Summary. Six soil samples from natural and cultivated sites of Saudi Arabia were investigated for ciliate diversity, using the non-flooded Petri dish culture method, live observation, and silver impregnation. We identified 135 species, all new for the fauna of Saudi Arabia, of which seven were undescribed: *Spathidium alqasabi* nov. spec.; *Enchelyodon alqasabi* nov. spec.; *Metauroleptus arabicus* nov. gen., nov. spec.; *Pseudohemisincirra arabica* nov. gen., nov. spec.; *Saudithrix terricola* Berger, Al-Rasheid and Foissner, 2006; *Oxytricha arabica* nov. spec.; and *Erimophrya monostyla* nov. spec. Based *on Spathidium alqasabi*, *S. seppelti foissneri* Vďačný *et al*., 2006 and *S. seppelti etoschense* Foissner *et al*., 2002 are raised to species rank; for the latter, a new name is required to avoid homonymy: *Spathidium fraterculum* nov. nom. The new genus *Metauroleptus*, which possesses two long and two to three short ventral cirral rows, generates all dorsal kineties intrakinetally and produces caudal cirri exclusively in dorsal kinety 1. *Metauroleptus* belongs to the hypotrichs, while family classification remains doubtful. The same applies to the new hypotrich genus *Pseudohemisincirra*, which has frontoventral and transverse cirri, while buccal cirri and caudal cirri are absent. The number of species contained in Saudi Arabian soils, including sand dunes, is in the range reported from other regions of the earth, suggesting that ciliates are well adapted to dry habitats, possibly mainly by their ability to produce very resistant resting cysts, most surviving for a long time due to reduced metazoan predation.

Key words: Adaptation, biodiversity, *Metauroleptus* nov. gen., protozoa, *Pseudohemisincirra* nov. gen., resting cysts, sand dunes, Tenerife.

INTRODUCTION

While the marine and brackish ciliate faunas of the Saudi Arabian Gulf have been investigated in some detail (for reviews, see Al-Rasheid 1999, 2001), the soil protists of Arabia remained unknown, although some early studies are available from Palestine (Bodenheimer 1935) and the Algerian Sahara (Varga 1936). More recently, Foissner (1993) and Foissner *et al.* (2002) described two new species from Tunisia (*Pseudocyrtolophosis terricola*) and Egypt (*Paragonostomum binucleatum*). Thus, we performed a study on the diversity of soil ciliates in some representative natural and cultivated habitats of Saudi Arabia. Such data are important also in the current biogeographical discussion (Foissner 2006) because Saudi Arabia is in the transition zone of two main biogeographical regions (Müller 1981): the Holarctis and the Palaeotropis.

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MATERIAL AND METHODS

The material is from Saudi Arabia, *i.e.*, from the surroundings of the capital (Riyadh) and from sites along the main road from Riyadh to the Arab Gulf. Six samples were taken in February 1998, air-dried

for one month, sealed in plastic bags, and investigated during June to December 1999. Sampling, taxonomic methods, and identification of species follow Foissner (1991) and Foissner *et al.* (2002); for details on terminology, see Foissner and Al-Rasheid (2006) and Foissner and Xu (2007). The samples were processed with the non-flooded Petri dish method, as described by Foissner *et al.* (2002), and species were identified *in vivo* and in silver preparations. Briefly, this method involves placing 50–500 g litter and mineral soil in a Petri dish (13–18 cm wide, 2–3 cm high) and saturating, but not flooding it, with distilled water. Such culture is analysed for ciliates by inspecting about 2 ml of the run-off on days 2, 7, 14, 21, and 28.

Site 1: About 40 km north of Riyadh, surroundings of the village of Al-Jubailah (Al-Dschubaila), 47° E 25° N. A vegetable field irrigated with hard ground water. Soil greyish when dry, pH 6.4 in water; not saline, but enriched with minerals. The upper 0–2 cm litter and soil layer under a weed bush was collected.

Site 2: About 150 km northwest of Riyadh, surroundings of the village of Al-Qasab (Al-Kasab), 45°30'E 26° N. Pasture land in a semi-desert with many flowers and bushes. Soil very sandy, yellowred, pH 6.7, not saline, grass roots covered with a thick layer of mycorrhiza (?). The very sandy soil was sieved with a kitchen sieve to a depth of 15 cm to enrich the sample with fine roots and partially decomposed organic matter, mainly plant remnants.

Site 3: About 200 m distant from site 2. Soil saline (21‰) and covered with halophilous vegetation, pH 6.7 in water. The sample was collected as described for site 2.

Site 4: About 150 km east of Riyadh, a shifting, hardly vegetated sand dune in the surroundings of the village of Khurays, 48°10'E 25°15'N. In a small depression, where plant litter has accumulated, the sand was sieved to a depth of 20 cm to enrich the sample with fine roots and incompletely decomposed organic material; pH 6.2 in water, slightly saline (<5‰).

Site 5: Near site 4, but another, well-vegetated sand dune. Sampling as described at site 4, *i.e.*, in a small depression where sand grains and organic debris were bound to crumbles by a massive growth of fungal hyphae; grass roots covered with a thick layer of mycorrhiza (?), similar as at site 2. Soil (sand) not saline, pH 6.0 in water.

Site 6: A leguminosae field in the Al-Hassa oasis, a few km east of the town Al-Hofuf (Al-Hufuf), 49°31'E 25°20'N. Soil very sandy, stongly penetrated by leguminosae roots, pH 6.0 in water. The upper 0–5 cm litter and soil (sand) layer was collected and enriched with litter from the surroundings.

RESULTS AND DISCUSSION

Faunistics

The six samples contained 135 identified ciliate species, all new for the fauna of Saudi Arabia. At least seven species were undescribed (Table 1): *Spathidium alqasabi*, *Enchelyodon alqasabi*, *Saudithrix terricola* Berger *et al.* (2006), *Metauroleptus arabicus*, *Pseudohemisincirra arabica*, *Oxytricha arabica* and *Erimophyra monostyla*. About 20 further species, half of which is likely undescribed, were noted in the protargol slides, but could not be described because of lack of live observations and/or sufficient specimens (Table 1). 135 (+20) species is a considerable number compared to the about 100 species found in 150 (!) samples of 1 ha of upland grassland in Southern Scotland (Esteban *et al*. 2006), the about 100 species reported from several sites of The Netherlands, Belgium and Denmark (Foissner and Al-Rasheid 2007), and the 87 species found in six samples from Singapore (Foissner 2008b). On the other hand, 80 to 140 species may be found in single samples (Foissner 1995; Foissner *et al.* 2002, 2005), showing that the Arabian sites are in the mid-range.

The richest samples were from a vegetable field and pasture land (samples 1, 2, 6; 80, 45, 42 species), while the natural sites 3, 4, and 5 contained only 22–40 species (Table 1). This is not surprising. Agriculture and pastures are set up on fertile soils, while the dry and/or saline sites are rather extreme (for details, see Foissner 1987b).

Sites 4 and 5 are from sand dunes and can be compared with similar sites globally (Table 2). Species richness in the Arabian dunes matches the general pattern, *i.e.*, single samples provide 20–50 ciliate species (but see below). Further, ciliate abundances are usually high, *i.e.*, a few days after rewetting the samples masses of ciliates appear, most possibly originating from resting cysts. The high species diversity is surprising because such numbers are widely found in various soils, for instance, in Central European meadows (Foissner 1987b) and natural forest stands (Foissner *et al.* 2005). Obviously, ciliates are adapted to desert conditions, mainly by their ability to form quickly a highly resistant dormant stage, the resting cyst, when the environmental conditions become detrimental. Further, a large group of soil ciliates, the Colpodea, contains mainly *r*-selected species adapted to extreme conditions (Foissner 1993, Lüftenegger *et al.* 1985). Last but not least, part of the rich diversity and high individual numbers might be caused by reduced metazoan competition and cyst predation in such extreme habitats.

Foissner (1987b) and Foissner *et al.* (2002) showed that, due to methodological shortcomings, a single sample from a certain site provides only about one third of the species actually present, *i.e.*, when the same site is investigated 10 or more times in the course of one or two years. This is supported by a recent study on 12 Austrian forest stands, which were investigated in spring and autumn (Foissner *et al.* 2005): 68 species (first sample)/ 75 (second sample)/ 92 (total), 73/ 58/ 87, 65/ 64 / 83, 39/ 34/ 52, 67/ 61/ 90, 36/ 33/ 45, 38/ 55/ 69, 28/ 49/ 54, 72/ 101/ 120, 55/ 60/ 86, 75/ 77/ 99, 60/ 63/ 81.

Table 1. Ciliate species found in six soil samples from Saudi Arabia. For authors and dates of species, see Foissner (1998) and Foissner *et al.* (2002).

Species	Sites					
	1	2	3	4	5	6
Acaryophrya collaris	+	–	–	–	–	–
Acropisthium mutabile	+	–	–	–	–	–
Amphisiella australis	–	+	–	–	+	–
Amphisiella elegans	–	–	+	–	–	–
Amphisiella magnigranulosa	–	–	–	+	–	–
Apertospathula verruculifera	+	–	–	–	–	–
Apocyclidium obliquum	+	–	–	+	–	+
Apospathidium longicaudatum	+	–	+	–	+	–
Arcuospathidium lionotiforme	–	–	–	–	–	+
Arcuospathidium muscorum muscorum	+	–	–	–	+	–
Arcuospathidium namibiense tristicha	–	–	+	–	–	–
Armatospathula periarmata	–	–	–	–	+	–
Blepharisma hyalinum	–	–	–	+	–	–
Blepharisma steinii	+	–	–	+	–	–
Cinetochilum margaritaceum	–	–	–	+	–	–
Circinella filiformis	–	+	+	–	–	–
Clavoplites edaphicus	+	–	–	–	–	–
Colpoda aspera	+	+	–	+	+	+
Colpoda cucullus	+	+	+	+	+	+
Colpoda edaphoni	–	–	–	+	–	–
Colpoda formisanoi	–	–	–	+	–	–
Colpoda henneguyi	–	–	–	–	–	+
Colpoda inflata	+	+	+	+	+	+
Colpoda magna	+	–	–	–	–	–
Colpoda maupasi	+	+	+	+	+	+
Colpoda steinii	+	+	+	+	+	+
Colpodidium (Colpodidium) trichocystiferum	+	+	–	–	–	–
Condylostomides trinucleatus	+	–	–	–	–	–
Cyrtohymena citrina	+	–	–	–	–	+
Cyrtolophosis muscicola	+	–	–	–	–	–
Dileptus mucronatus	–	–	–	–	–	+
Dileptus visscheri	+	–	–	–	–	–
Drepanomonas pauciciliata	–	–	–	+	–	–
Drepanomonas sphagni	+	–	–	–	–	–
Enchelyodon alqasabi nov. spec.	–	–	+	–	–	–
Enchelyodon armatides	–	–	–	+	–	–
Enchelyodon nodosus	+	–	–	–	–	–
Enchelys geleii	–	+	–	–	–	–
Enchelys polynucleata	–	–	–	+	–	–
Epispathidium ascendens	+	–	–	–	–	–
Epispathidium polynucleatum	+	–	–	–	–	–
Erimophyra monostyla nov. spec.	+	+	–	–	–	+
Euplotopsis incisa	–	–	–	–	–	+
Euplotopsis muscicola	+	+	–	–	–	–
Exocolpoda augustini	–	+	+	+	+	–

(continued)

Species	Sites					
	1	2	3	4	5	6
Fuscheria nodosa	+	–	–	–	–	–
Fuscheria terricola	+	+	+	–	+	+
Gastrostyla steinii	+	–	–	–	–	–
Gonostomum affine	+	+	+	+	+	+
Grossglockneria acuta	–	+	–	+	–	–
Halteria grandinella	+	+	–	–	–	–
Hausmanniella patella	–	–	–	–	–	+
Hemiamphisiella terricola	–	–	–	–	–	+
Hemisincirra inquieta	+	–	–	+	–	+
Hemisincirra rariseta	–	+	–	–	–	–
Hemiurosoma terricola	+	–	–	–	–	–
Holostichides chardezi	–	–	–	–	–	+
Holostichides terricola	–	–	+	+	+	–
Homalogastra setosa	+	+	+	+	–	+
Keronopsis dieckmanni	–	–	–	–	–	+
Kuklikophrya ougandae	+	–	–	–	–	–
Lamtostyla halophila	–	–	+	–	–	–
Lamtostyla islandica	–	–	–	+	–	+
Leptopharynx costatus	+	+	–	+	+	+
Metauroleptus arabicus nov. spec.	–	+	–	–	–	–
Metopus gibbus	+	–	–	–	–	–
Metopus hasei	+	+	–	–	–	–
Metopus minor	+	–	–	–	–	–
Metopus ovalis	+	–	–	–	–	–
Metopus palaeformis	+	–	–	–	–	–
Monodinium perrieri	+	+	–	–	–	–
Mykophagophrys terricola	+	–	–	+	–	–
Nassula tuberculata	–	–	+	–	–	+
Nassulides pictus	+	–	–	–	–	–
Nivaliella plana	+	+	–	+	+	+
Odontochlamys alpestris biciliata	–	–	–	–	–	+
Odontochlamys convexa	+	+	+	–	–	–
Oxytricha arabica nov. spec.	–	+	–	–	+	–
Oxytricha elegans	+	–	–	–	–	–
Oxytricha granulifera	+	–	–	–	–	–
Oxytricha longa	+	+	–	–	–	–
Oxytricha setigera	+	–	–	–	–	–
Paraenchelys terricola	–	–	–	–	–	+
Parafurgasonia sorex	–	–	–	–	–	+
Paragonostomum binucleatum	–	+	–	–	–	–
Paragonostomum caudatum	+	–	–	+	–	+
Paragonostomum multinucleatum	–	–	+	–	–	–
Periholosticha paucicirrata	+	+	–	–	–	–
Plagiocampa difficilis	–	+	+	+	–	+
Plagiocampa ovata	+	–	–	–	–	–
Plagiocampa pentadactyla	+	–	–	–	–	–
Plagioicampa rouxi	+	–	–	–	–	–

Species	Sites					
	1	2	3	4	5	6
Platyophrya macrostoma	–	+	–	+	–	+
Platyophrya spumacola spumacola	–	+	–	+	+	+
Platyophrya vorax	–	+	–	+	+	+
Plesiocaryon elongatum	+	–	+	+	+	+
Pleuroplites australis	–	–	–	–	–	+
Podophrya halophila	–	+	–	–	–	–
Protocyclidium muscicola	+	–	+	+	–	–
Protocyclidium terricola	+	+	–	+	–	–
Pseudochilodonopsis mutabilis	+	+	–	–	–	–
Pseudocohnilembus persalinus hexakineta	–	–	+	–	–	–
Pseudocyrtolophosis alpestris	+	–	–	+	–	–
Pseudohemisincirra arabica nov. spec.	–	+	–	–	–	–
Pseudoholophrya terricola	–	–	–	–	–	+
Pseudoplatyophrya nana	+	+	–	+	+	–
Pseudoplatyophrya saltans	+	–	–	–	–	–
Pseudourostyla franzi	–	–	–	+	–	–
Pseudovorticella sphagni	+	–	–	–	–	–
Rigidocortex octonucleatus	+	–	–	–	–	–
Rostrophrya fenestrata	–	–	+	–	–	–
Sagittaria hyalina	+	–	+	–	–	–
Sathrophilus muscorum	–	+	+	–	+	+
Saudithrix terricola nov. gen., nov. spec.	+	–	–	–	–	–
Semiplatyophrya foissneri	–	–	+	–	–	–
Spathidium alqasabi nov. spec.	–	–	+	–	–	–
Spathidium claviforme	+	+	+	+	–	–
Spathidium etoschense	–	–	–	–	–	+
Spathidium procerum	+	+	–	–	–	–
Spathidium spathula	+	–	–	–	–	–
Sterkiella histriomuscorum-complex	+	–	–	–	–	+
Stylonychia bifaria	+	–	–	–	–	–
Tachysoma humicola humicola	+	–	–	+	–	–
Terricirra matsusakai	+	–	–	–	+	–
Tetrahymena rostrata	+	–	–	–	–	+
Uroleptus notabilis	–	+	+	+	–	+
Urosoma emarginata	+	–	–	–	–	–
Urosomoida agiliformis	+	–	+	+	–	–
Urosomoida agilis	–	+	–	–	–	+
Urostyla grandis	+	–	–	–	–	–
Vorticella astyliformis	+	+	+	–	–	–
Vorticella infusionum	+	–	–	–	–	–
Wolfkosia loeffleri	+	–	–	–	–	–
Woodruffia rostrata	–	–	–	–	–	+
Woodruffides terricola	+	+	–	–	–	–
Number of species identified	80	45	31	40	22	42
New species	2	4	3	0	1	1
Number of unidentified taxa	13	7	4	0	0	0
Number of unidentified, likely undescribed taxa	7	3	1	0	0	0
Total number of taxa	93	51	35	40	22	42

Table 2. Comparison of ciliate diversity in sand dunes of Arabia, Namibia, Australia, the USA, and Europe.

Regions/sites	Identified species	Number of unidentified species	Number of new species[a]	Total	References
Saudi Arabia, site 4	40	0	0	40	this paper
Saudi Arabia, site 5	23	0	1	23	this paper
Namibia, site 26	31	3	3	34	Foissner *et al.* (2002)
Namibia, site 33	47	2	7	49	Foissner *et al.* (2002)
Australia, site 5	36	0	3	36	both from Blatterer and Foissner (1988)
Australia, site 9	34	8	2	42	
USA, Utah	26	0	1	26	Foissner (1994)
The Netherlands, site 1, Europe	41	0	3	41	both from Foissner and Al-Rasheid (2007)
Norderney, Germany, Europe	29	~10	?	39	

[a] Saudi Arabia, site 5: *Oxytricha arabica*; Namibia, site 26: *Paragonostomum caudatum*, *Plesiocaryon terricola*, *Spathidium namibicola*; Namibia, site 33: *Diplites arenicola*, *Metacineta namibiensis*, *Paragonostomum binucleatum*, *Paragonostomum rarisetum*, *Protospathidium namibicola*, *Spathidium lanceoplites*, *Urosomoida deserticola*; Australia, site 5: *Coriplites australis*, *Phialinides australis*, *Pseudoplatyophrya saltans*; Australia, site 9: *Oxytricha granulifera quadricirrata*, *Rostrophryides australis*; USA: *Circinella arenicola*; The Netherlands, site 1: *Apobryophyllum schmidingeri*, *Dileptus* n. sp., *Keronopsis schminkei*.

Thus, the gain of species by the second sample ranges between 16% and 48%, on average 30%, *i.e.*, only one third because the sites were investigated only two times. These values must be taken into account when interpreting the data from single samples. If we apply the "⅓ rule" to the richest site 1 (93 species) and to the poorest site 5 (22 species), 280 and 66 species can be expected, respectively. If we apply only 30%, still 133 and 31 species might be present. Likely, the true numbers lie between these extremes. Unfortunately, such extrapolations cannot be applied to the total number of species found in six or more samples because multiple samples from a certain, small area represent some sort of replication of a single site (Foissner *et al*. 2002). Nonetheless, the extrapolated values match literature data (Foissner 1987b, Foissner *et al.* 2002), showing that the Arabian samples are in the ordinary range.

Biogeographic aspects

Most of the new species discovered would not have been recognized 30–40 years ago, when ciliate alpha-taxonomy was much coarser and protargol impregnation and morphometry were not as widely used as today. But are these details really of significance at species level? As an example, we choose *Oxytricha arabica* and the cosmopolitan (?) *O. lanceolata*. Their size, cytology, cirral pattern, and morphometrics are highly similar, and thus the *Oxytricha* key of Berger (1999) guides to *O. lanceolata*. However, the dorsal kinetid (bristle) pattern is quite different. Of the three different features, the split of kinety 3 greatly influences the bristle pattern: while *O. lanceolata* belongs to the oxytrichids with four dorsal ciliary rows, *O. arabica* and the type species of *Oxytricha* belong to the group with five rows. As far as we know, this pattern is hardly variable and ontogenetically fixed (Berger 1999). Classifying the Arabian population as a distinct species is also supported by recent sequence data which show that *Oxytricha* is polyphyletic, and thus likely consists of much more species than recognized presently (Schmidt *et al*. 2007); many of these will be cryptic species like *O. arabica*. For instance, the study of Schmidt *et al.* (2007) shows that two populations of *Oxytricha granulifera*, virtually differing only in the shape of the cortical granules (globular *vs.* oblong), have rather different rRNA gene sequences, supporting the classification as distinct species, viz., *O. granulifera* and *O. longigranulosa* (for a review, see Berger 1999). A similar case has been reported in *Glaucoma* by Fried and Foissner (2007). Thus, inconspicuous differences in important features might be indicative of cryptic speciation.

Lumping and splitting of species greatly influences their perceived geographical range, one of the main problems in the distribution controversy of protists (for reviews, see Foissner 2006, 2008a). Most of the seven new species found in the six Arabian samples have been recorded only from their type locality, suggesting that some might have restricted distribution. A good candidate was *Saudithrix terricola* Berger *et al*., 2006, a flagship species with a size of about 270 × 100 µm. However, recently this species has been rediscovered in soil from the floodplain of the Yangtze River in Wuhan, China (Foissner 2007). This does not mean that

S. terricola is a cosmopolitan, but the range is larger than originally expected. Two further species, previously known only from Venezuela, have been observed in the Arabian samples, viz., *Armatospathula periarmata* and *Apertospathula verruculifera*, both described in Foissner and Xu (2007). We rediscovered also some species as yet known only from Namibia, Southwest Africa (Foissner *et al.* 2002): *Spathidium etoschense*, *Pseudocohnilembus persalinus hexakineta*, *Hemisincirra rariseta*, and *Rostrophrya fenestrata*.

Obviously, investigations like the present one broaden the known geographical range of some species or of even supposed endemic flagships. However, usually the loss is less than the gain, that is, more undescribed species are found than described "endemics" are rediscovered (see this study and Foissner *et al.* 2005, Foissner and Al-Rasheid 2007, Foissner 2008b).

There is also a hot debate on the number of free-living ciliate species. While Finlay (2001) suggests 3,000–4,000 species, Foissner *et al.* (2008a) estimate 30,000 species. We believe that the later number is supported by, *e.g.*, our data on the genus *Erimophrya*. Foissner *et al.* (2002) founded the genus with two species, *E. glatzeli* (type) and *E. arenicola*, both occurring in the dunes of the Namib Desert. Later, Foissner *et al.* (2005) described two further species from a *Pinus nigra* forest near Vienna, Austria: *E. sylvatica* and *E. quadrinucleata*. Now, a fifth species has been discovered, showing our ignorance on soil ciliate diversity: five new species were discovered in a single genus during the short period 2002–2008! All species obviously prefer meagre, extreme habitats, such as sand dunes, coniferous litter, and saline coastal soil.

Interestingly, the five species belong to three biogeographical regions: the Palaeotropis (*E. glatzeli*, *E. arenicola*), the Holarctis (*E. sylvatica*, *E. quadrinucleata*), and the transition zone of both (*E. monostyla*). Unfortunately, *Erimophrya* species are difficult to identify *in vivo*; further, they resemble several *Urosomoida* and *Hemisincirra* species. Thus, a definite conclusion about their biogeography is not yet possible. However, it is remarkable that, as yet, none of the species has been reported from outside its region.

Description of species

Spathidium alqasabi nov. spec. (Fig. 1a-s; Tables 3, 4)

Diagnosis: Size about 200 × 35 µm *in vivo*. Shape typically spathidiid. Oral bulge with obconical depression and of about same length as body width. On average 34 ellipsoidal, scattered macronucleus nodules and several micronuclei. Extrusomes very slenderly ellipsoidal, about 5 µm long. On average 15 ciliary rows. Dorsal brush heterostichad occupying about 24% of body length; brush row 1 composed of 21 dikinetids, row 2 of 32, and row 3 of 21 dikinetids on average.

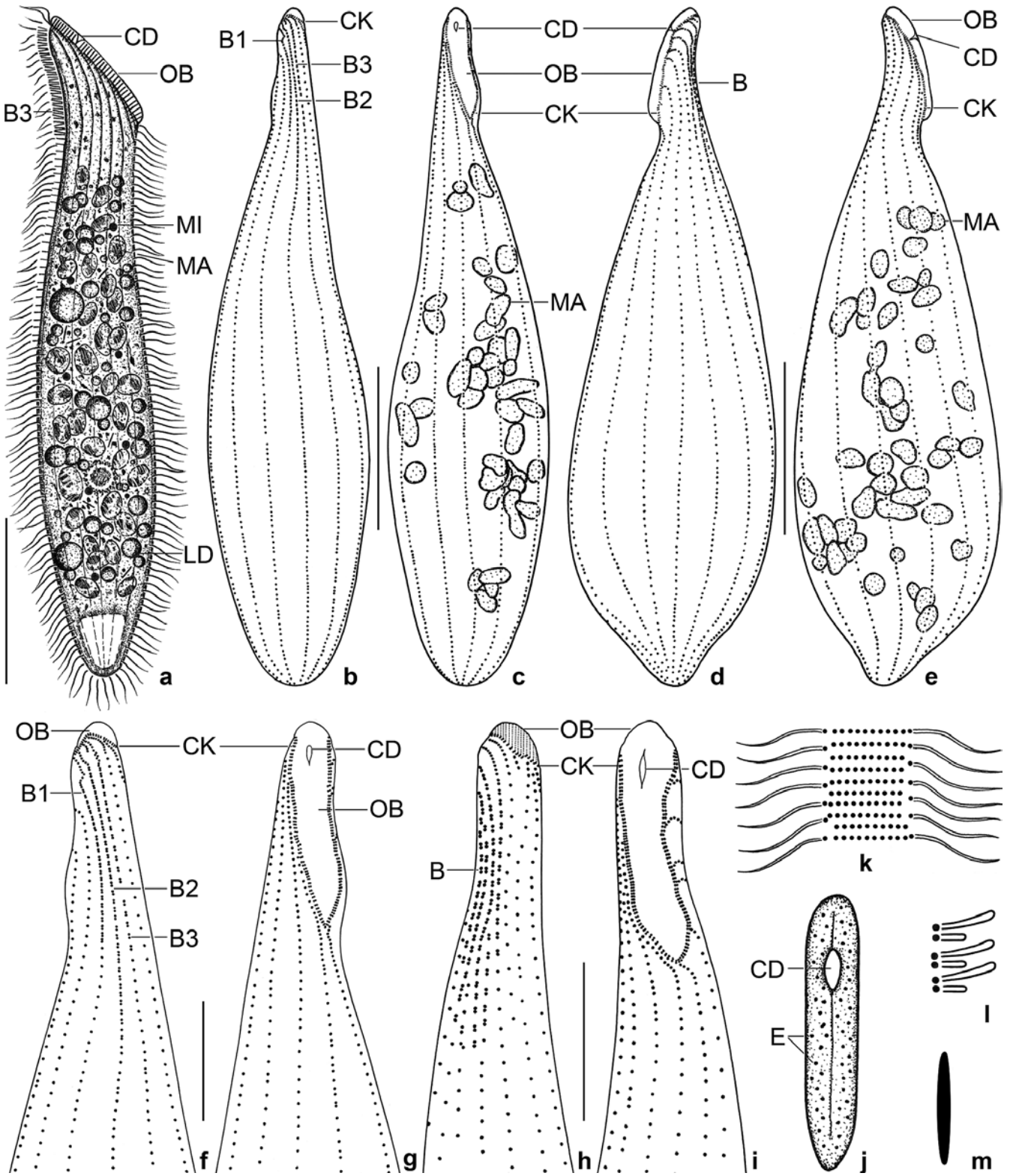
Type locality: Highly saline (21‰) sand soil in the surroundings of the village of Al-Qasab, about 150 km NW of the town of Riyadh, Saudi Arabia, 45°30'E 26° N.

Type material: 1 holotype and 5 paratype slides with protargol-impregnated specimens have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

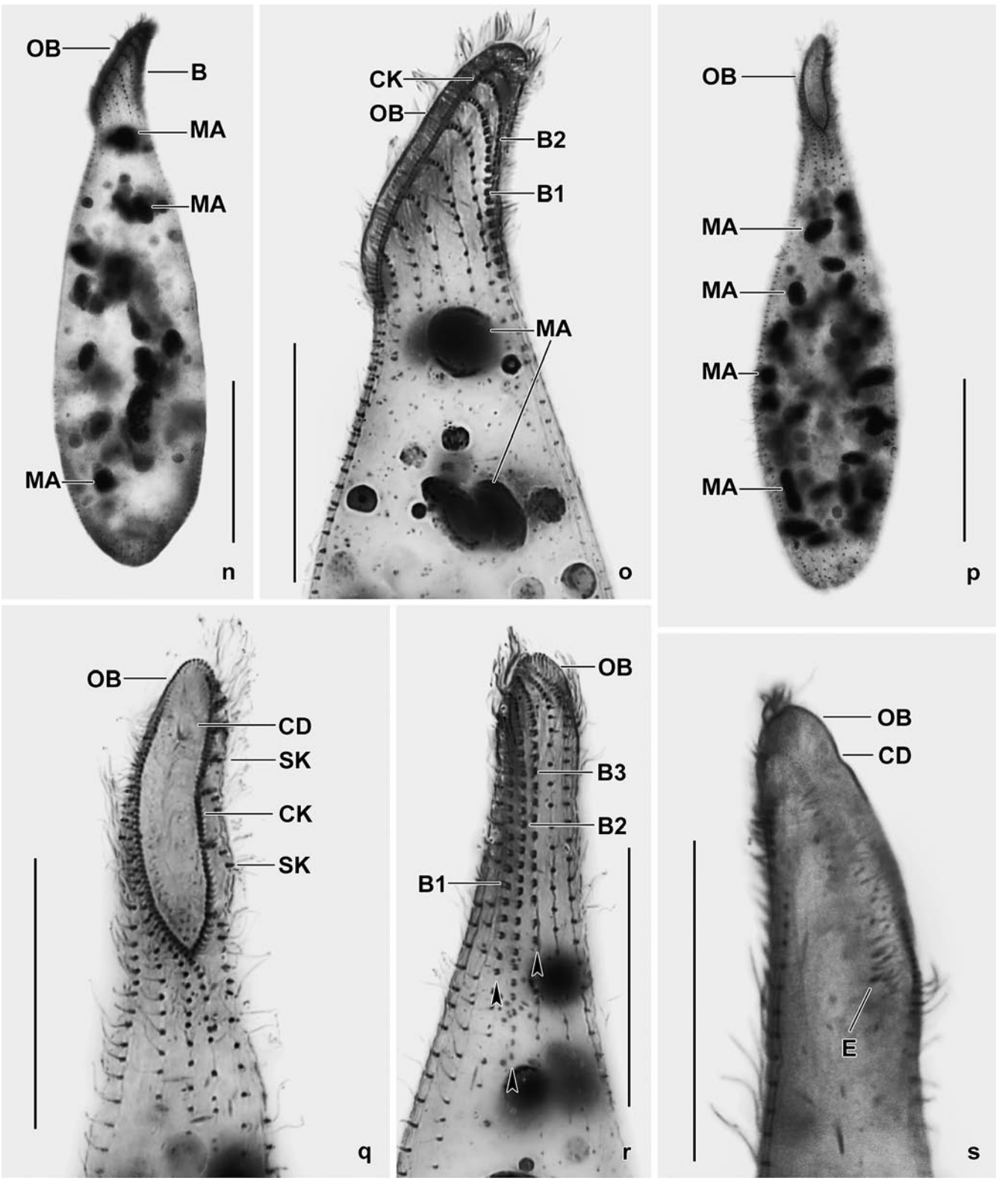
Etymology: Named after the village the species was discovered.

Description: Size 140–240 × 25–50 µm, usually about 200 × 35 µm *in vivo*, while 171 × 46 µm in protargol preparations; length:width ratio also highly different, *i.e.*, about 6:1 *in vivo* and 3.8:1 in protargol preparations, where specimens are heavily inflated due to insufficient fixation (Figs 1a, d, n; Table 3). Shape elongate spatulate, mid-body circular in cross-section, anterior region laterally flattened, hyaline, and with slightly convex oral bulge; posterior body portion slightly tapering (Figs 1a–e). On average 34 globular to broadly ellipsoidal macronucleus nodules scattered throughout cytoplasm (Figs 1a, c, e, n–p; Table 3). Micronuclei 1.5–2 µm across, scattered between macronucleus nodules, exact number difficult to determine because hardly distinguishable from similar-sized and impregnated cytoplasmic inclusions. Contractile vacuole in posterior body end, with several excretory pores in pole centre. Extrusomes attached to oral bulge, basically rod-shaped, but on detailed analysis very slenderly ellipsoidal, 4–5 µm long, impregnate faintly with the protargol method used (Figs 1m, s); developing extrusomes scattered in cytoplasm and heavily impregnated with protargol. Cortex very flexible, contains *ca* 10 rows of minute, about 0.5 × 0.2 µm-sized granules between each two ciliary rows (Fig. 1k). Cytoplasm colourless, more or less densely packed with lipid droplets 1–10 µm across and food vacuoles with granular contents, except for hyaline anterior portion. Likely feeds on ciliates.

Cilia about 10 µm long *in vivo*, densely spaced (≤2 µm) and arranged in an average of 15 ordinarily spaced (~7.3 µm), equidistant rows; widely spaced, *i.e.*,



Figs 1a–m. *Spathidium alqasabi* from life (a, j–m) and after protargol impregnation (b–i). **a** – right side view of a representative specimen, length 200 µm; **b**, **c**, **f**, **g** – ciliary pattern of dorsal and ventral side and macronucleus of holotype specimen, length 210 µm; **d**, **e** – infraciliature of left and right side of a strongly inflated specimen; **h**, **i** – dorsal and ventral view of a specimen with four dorsal brush rows; **j** – frontal view of oral bulge showing the conical depression; **k** – surface view showing cortical granulation; **l** – bristles of brush row 1; **m** – extrusome, length 4 µm. B (1–3) – dorsal brush (rows), CD – conical depression, CK – circumoral kinety, E – extrusomes, LD – lipid droplets, MA – macronucleus nodules, MI – micronucleus, OB – oral bulge. Scale bars: 50 µm (a–e) and 20 µm (f–i).



Figs 1n–s. *Spathidium alqasabi*, morphology and ciliary pattern after protargol impregnation. **n**, **o** – left side views showing the scattered macronucleus nodules, the steep oral bulge, and part of the dorsal brush; **p**, **q**, **s** – ventral and lateral views showing the shape of the circumoral kinety, the scattered macronucleus nodules and, specifically, the conical depression near the dorsal end of the oral bulge; **r** – dorsal view with ends of dorsal brush rows marked by arrowheads. Rows 1 and 3 have a similar length, an unusual feature. B (1–3) – dorsal brush (rows), CD – conical depression in oral bulge, CK – circumoral kinety, E – extrusomes, MA – macronucleus nodules, OB – oral bulge, SK – somatic kineties. Scale bars: 50 µm (n, p) and 30 µm (o, q–s).

Table 3. Morphometric data on *Spathidium alqasabi*. Data based on mounted, protargol-impregnated (Foissner 1991, protocol A), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Characteristics	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	171.3	174.0	20.8	4.3	12.2	122.0	205.0	23
Body, width	46.2	45.0	7.6	1.6	16.5	33.0	62.0	23
Body length:width, ratio	3.8	3.6	0.8	0.2	21.3	2.5	5.6	23
Oral bulge, length	30.2	30.0	3.7	0.8	12.3	24.0	40.0	22
Oral bulge, height	2.8	3.0	–	–	–	2.0	3.0	13
Body length:length of oral bulge, ratio	5.7	5.6	0.7	0.2	12.8	4.5	7.3	21
Brush kinety 1, length[a]	29.7	29.0	8.2	1.9	27.6	20.0	47.0	19
Brush kinety 2, length[a]	42.2	42.0	6.8	1.6	16.0	31.0	57.0	18
Brush kinety 3, length[a]	32.0	31.5	8.6	2.0	27.0	16.0	49.0	18
Anterior body end to first macronucleus nodule, distance	40.9	41.0	8.9	1.9	–	26.0	58.0	23
Macronucleus nodules, length	8.1	8.0	1.2	0.3	15.0	5.0	10.0	23
Macronucleus nodules, width	5.5	5.0	0.9	0.2	16.4	4.0	8.0	23
Macronucleus nodules, number	34.1	35.0	5.9	1.2	17.4	24.0	48.0	23
Somatic kineties, number	14.5	15.0	1.5	0.3	10.1	10.0	18.0	23
Ciliated kinetids in a right side kinety, number	93.4	93.0	11.9	2.9	12.7	72.0	115.0	17
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Dikinetids in brush row 1, number	20.7	21.0	3.7	0.9	17.9	15.0	29.0	19
Dikinetids in brush row 2, number	32.5	32.5	5.4	1.3	16.7	24.0	45.0	18
Dikinetids in brush row 3, number	21.2	22.0	5.6	1.3	26.6	11.0	32.0	18

[a] Distance between circumoral kinety and last dikinetid of row.

~9.5 µm in protargol preparations due to insufficient fixation; those of right side abutting to circumoral kinety at acute angles, while those of left side attached to circumoral kinety at right angles and with anterior end composed of 2–8 closely spaced cilia (Figs 1d, g, o, r). Dorsal brush three-rowed, a fourth row occurs in a few specimens (Fig. 1h); rather short because occupying on average only 24% of body length; heterostichad because row 1 about 30% shorter than longest row 2; inconspicuous because bristles merely up to 4 µm long and only slightly inflated distally. Rows 1 and 3 similar both in average length (~30 µm *vs.* 32 µm) and number of dikinetids (21 and 22), brush row 2 about 42 µm long and composed of an average of 32 dikinetids; row 3 continues to mid-body with a monokinetidal tail of about 2.5 µm long bristles. Anterior bristle of pairs of brush row 1 about 4 µm long, posterior bristle shortened by about 50% (Fig. 1l), length decreases to 2 µm posteriorly; bristles of rows 2 and 3 similar to those of row 1, but only 3 µm long (Figs 1b, d, f, n, o, r; Table 3).

Oral bulge of about same length as body width *in vivo*, whilst about one third shorter than average body width in protargol preparations because specimens became heavily inflated by the preparation procedures (Table 3); slightly convex when viewed laterally, oblong with bluntly pointed ventral end in frontal view (Figs 1a, c, g, i, q). A conical depression near dorsal end of bulge, recognizable both *in vivo* and after protargol impregnation (Figs 1a, c–e, g, i, j, q, s), seen in all appropriately oriented specimens (>30). Circumoral kinety elongate elliptical with acute proximal end, composed of closely spaced dikinetids associated with nematodesmata forming the oral basket (Figs 1c, g, i, p, q).

Occurrence and ecology: See *Enchelyodon alqasabi*.

Comparison with related species: Originally, we classified *Spathidium alqasabi* as a fourth subspecies of *S. seppelti*. However, there is no correlation of specific features between these taxa, suggesting that all represent distinct species (Table 4). For instance, *S. alqasabi* and *S. seppelti* both have a conical oral bulge depression, but differ considerably in body length (170 µm *vs.* 100 µm), the relative length of the oral bulge (5.7 *vs.* 3.1), the number of ciliary rows (15 *vs.* 21) and, especially, in the dorsal brush pattern (rows 1 and 3 of same length, a very unusual feature *vs.* of distinctly different length, as usual). A further example: the curious dorsal brush pattern (rows 1 and 3

Table 4. Comparison of main features in four *Spathidium seppelti*-like species. SA – *Spathidium alqasabi* (Saudi Arabia), SFR – *S. fraterculum*[c] (from Foissner *et al*. 2002), SF – *S. foissneri* (from Vďačný *et al.* 2006), SS – *Spathidium seppelti* (from Petz and Foissner 1997).

Characteristics[a]	SA	SFR[c]	SF	SS
Body, length	171.3	133.5	149.6	99.3
Body, width	46.2	25.1	25.7	24.8
Body length:width, ratio	3.8	5.4	5.9	4.0
Oral bulge, length	30.2	40.9	38.5	31.5
Body length:length of oral bulge, ratio	5.7	3.3	3.9	3.1
Brush kinety 1, length[b]	29.7	34.0	31.9	18.1
Brush kinety 2, length[b]	42.2	38.1	36.9	22.3
Brush kinety 3, length[b]	32.0	35.5	10.7	9.6
Macronucleus nodules, number[d]	35	67	25	>100
Somatic kineties, number[d]	15.0	28.0	23.0	21.0
Dikinetids in brush row 1, number[d]	21.0	27.0	30.0	13.0
Dikinetids in brush row 2, number[d]	32.0	40.0	35.0	18.0
Dikinetids in brush row 3, number[d]	22.0	27.0	10.0	8.0
Extrusomes, shape and size	very slenderly ellipsoidal; 4–5 µm long	rod-shaped; type I: 5–6 µm long, type II: 3 µm long	rod-shaped to slightly ellipsoidal; 5 µm long	rod-shaped; 3–4 µm long
Conical depression in oral bulge	present	absent	absent	present
Ecology	highly saline sand soil	slightly saline soil from Etosha Pan	terrestrial moss from xero-thermic meadow	algal ornithogenic soil
Type locality	Saudi Arabia	Namibia	Slovakia	Antarctica

[a] Data based on protargol-impregnated (Foissner's method for *S. alqasabi*, *S. foissneri*, *S. fraterculum*; Wilbert's method for *S. seppelti*) specimens from non-flooded Petri dish cultures. Except where noted, based on arithmetic means. Measurements in µm.
[b] Distance between circumoral kinety and last dikinetid of row.
[c] *Spathidium seppelti etoschense* in Foissner *et al.* (2002). The new name is required to avoid homonymy (see description of *S. alqasabi*).
[d] Median values.

of same length) is found in *S. alqasabi* and *S. etoschense*, but only *S. alqasabi* has an oral bulge depression.

Obviously, the four taxa represent cryptic species rather similar at first glance, but distinctly different on more detailed analysis. This is emphasized by the different geographic regions they originate (Table 4). Thus, we raise *S. seppelti foissneri* and *S. seppelti etoschense* to species rank – *Spathidium foissneri* Vďačný *et al*., 2006 nov. stat. and *Spathidium fraterculum* nov. nom. (for *S. seppelti etoschense* Foissner *et al*., 2002). The new name is required to avoid homonymy with *Spathidium etoschense* Foissner *et al.*, 2002.

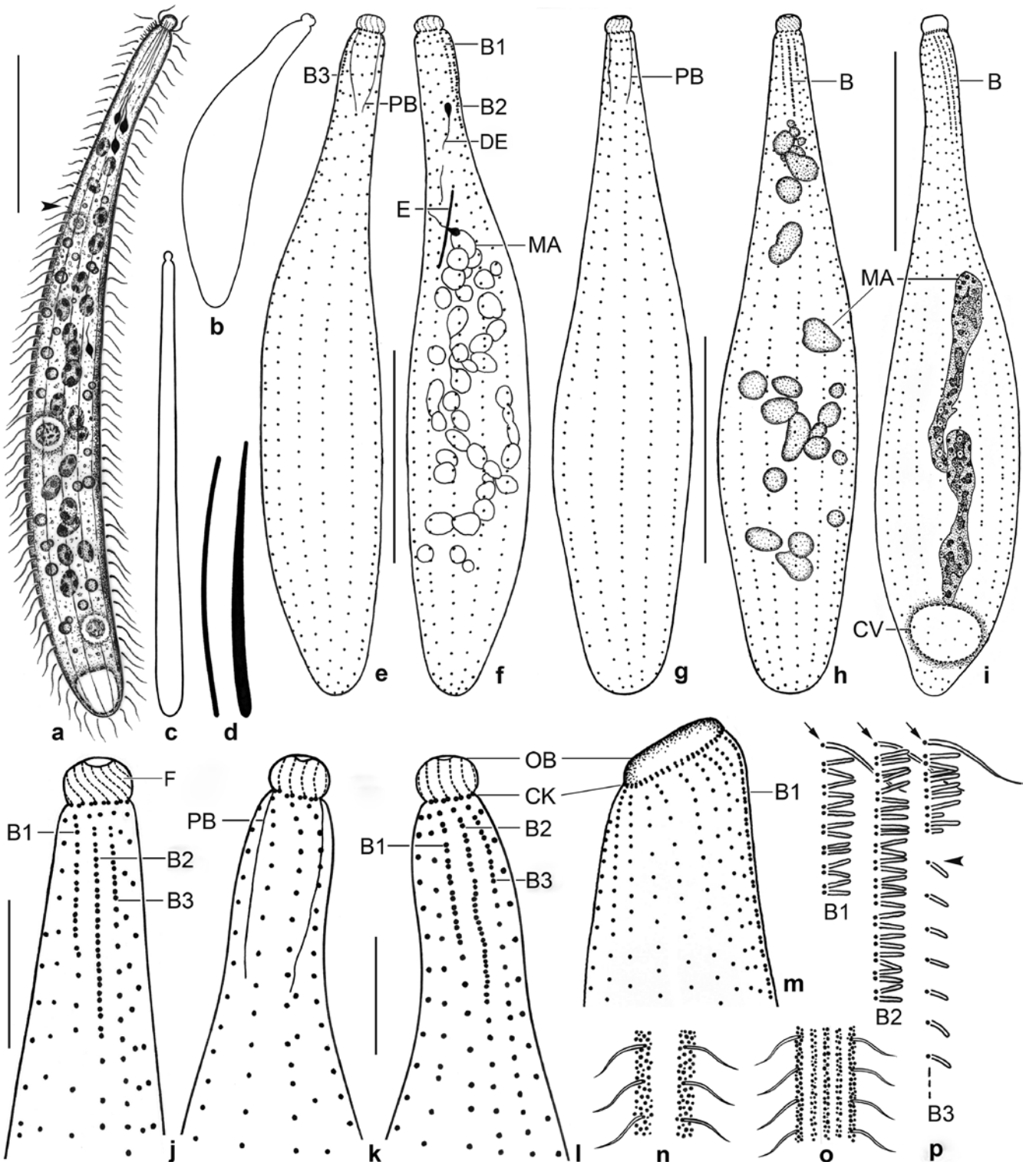
There are some similarities between *S. alqasabi* and *Arcuospathidium multinucleatum* Foissner, 1999, viz., body shape, scattered macronucleus nodules, conical depression in oral bulge, and a monokinetidal bristle tail of brush row 3 extending to mid-body. However, the ciliary pattern (spathidiid *vs.* arcuospathidiid) and the oral bulge (elliptical *vs.* narrowly cuneate) are completely different. Further, the dorsal brush of *A. multinucleatum* is isostichad, whilst that of *S. alqasabi* is heterostichad.

Enchelyodon alqasabi nov. spec. (Figs 2a–p, 3a–p; Table 5)

Diagnosis: Size about 180 × 20 µm *in vivo*, contractile up to one third of body length. Very slenderly clavate with conspicuous, hemispherical to slightly discoidal oral bulge about 5 µm across. On average 21 macronucleus nodules. Extrusomes rod-shaped, about 17 × 0.4 µm. On average 11 ciliary rows, three anteriorly differentiated to a heterostichad dorsal brush occupying about 10% of body length; brush row 1 composed of an average of 7 dikinetids, longest row 2 of 14, and row 3 of 5 dikinetids.

Type locality: Highly saline (21‰) sand soil in the surroundings of the village of Al-Qasab, about 150 km NW of the town of Riyadh, Saudi Arabia, 45°30'E 26°N.

Type material: 1 holotype and 5 paratype slides with protargol-impregnated specimens have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.



Etymology: Named after the village the species was discovered.

Description: Size of extended specimens 130–230 × × 5–30 µm *in vivo*, usually about 180 × 20 µm, contracts slowly and about one third of body length under weak coverslip pressure or when taken up with the pipette; in protargol preparations on average only 120 × 25 µm and with a high width variability (CV 19%, Table 5), indicating about 35% length loss due to contraction, fixation and 15% preparation shrinkage. Shape *in vivo*

Table 5. Morphometric data on *Enchelyodon alqasabi*. Data based on mounted, protargol-impregnated (Foissner 1991, protocol A), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

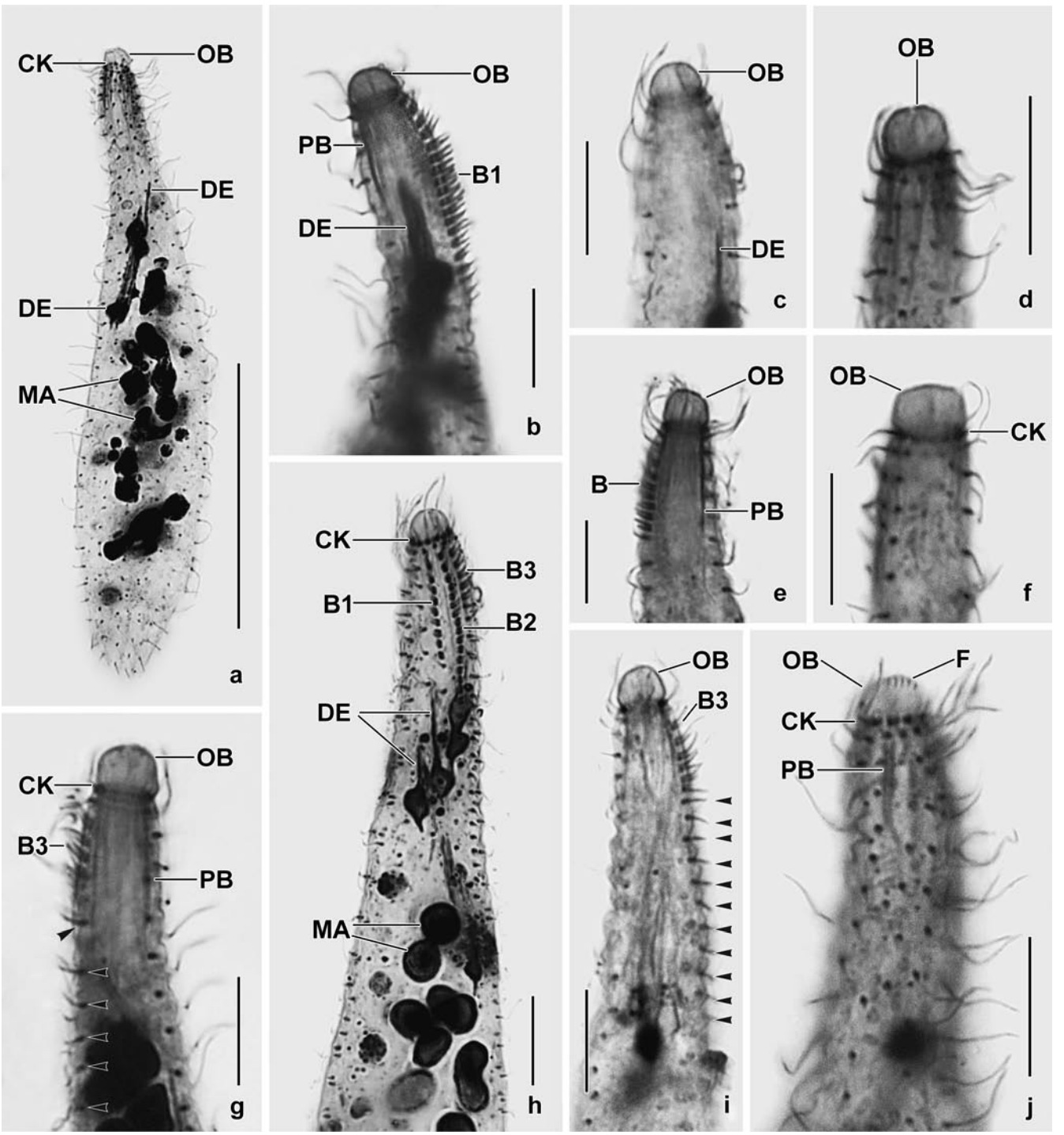
Characteristics	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	118.9	120.0	13.2	2.4	11.1	91.0	141.0	31
Body, width[a]	24.4	24.5	4.7	0.9	19.3	18.0	35.0	30
Body length:width, ratio	5.0	4.8	1.1	0.2	22.4	2.7	7.3	31
Oral bulge, width	4.5	5.0	–	–	–	3.5	6.0	31
Oral bulge, heigth	3.1	3.0	–	–	–	2.5	4.5	31
Anterior body to first macronucleus nodule, distance	25.9	23.0	7.1	1.3	27.2	14.0	40.0	31
Macronucleus nodules, length	5.8	6.0	1.1	0.2	19.3	4.0	9.0	31
Macronucleus nodules, width	4.1	4.0	0.6	0.1	14.1	3.0	5.0	31
Macronucleus nodules, number	20.6	21.0	2.8	0.5	13.7	15.0	26.0	31
Brush row 1, length[b]	9.8	9.0	1.6	0.3	16.9	6.0	14.0	31
Brush row 1, number of dikinetids	7.2	7.0	1.0	0.2	14.2	5.0	9.0	31
Brush row 2, length[b]	15.9	16.0	2.5	0.4	15.5	11.0	20.0	30
Brush row 2, number of dikinetids	13.8	14.0	2.2	0.4	15.8	10.0	19.0	30
Brush row 3, length[b]	6.1	6.0	1.0	0.2	15.6	5.0	9.0	31
Brush row 3, number of dikinetids	4.7	5.0	0.8	0.1	16.3	4.0	7.0	31
Number of ciliary rows (including brush)	10.6	11.0	1.1	0.2	10.2	8.0	12.0	31
Number of brush rows	3.0	3.0	0.0	0.0	0.0	3.0	3.0	31
Kinetids in a ventral kinety, number[c]	52.3	54.0	7.7	2.0	14.7	37.0	64.0	15

[a] One specimen with 41 µm excluded because caused by a big food vacuole.
[b] Distance between circumoral kinety and last dikinetid of row.
[c] Ciliated and unciliated kinetids (granules) were counted.

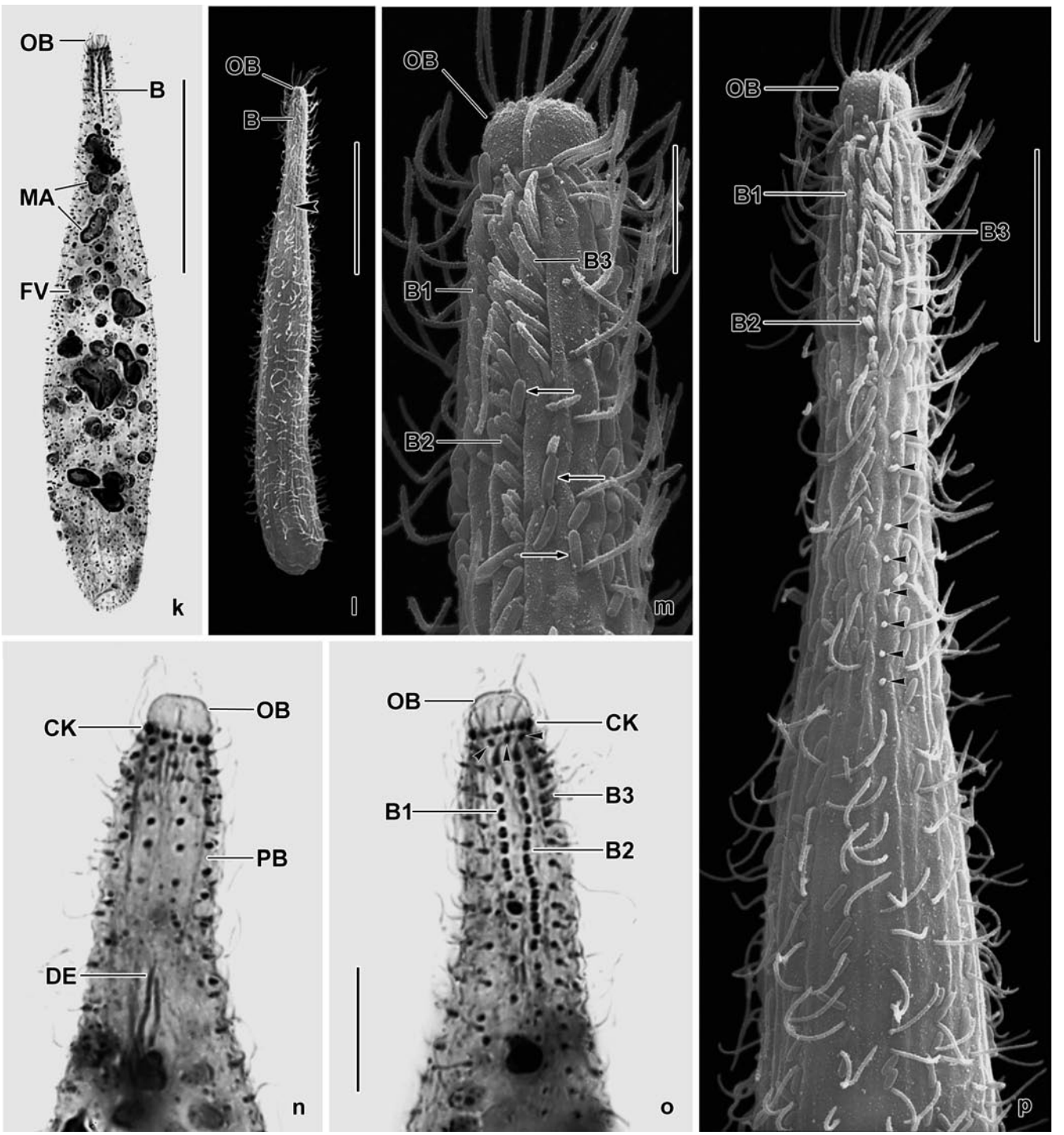
and SEM preparations very slenderly clavate to almost cylindroidal (~9:1), unflattened (Figs 2a, c, 3l); in protargol preparations slenderly clavate or, when strongly contracted, bluntly fusiform (Figs 2b, e–h, 3a, k); narrow anterior third more or less distinctly curved and slightly inflated subapically, both *in vivo* and protargol preparations. On average 21 scattered macronucleus nodules; individual nodules globular to ellipsoidal, about 6 × 4 µm in size (Figs 2a, f, h, 3a, h, k; Table 5); number of micronuclei not known because indistinguishable from cytoplasmic inclusions. Contractile vacuole in posterior body end. Extrusomes attached to oral bulge, rod-shaped and slightly curved, about 17 × 0.4 µm in size and thus rather conspicuous *in vivo* (Fig. 2d), do not impregnate with the protargol method used; several fusiform developmental stages scattered in cytoplasm and heavily impregnated (Figs 2a, f, 3a, b, h, n). Cortex colourless and very flexible, definitely without scales (lepidosomes); cortical granules minute, *i.e.*, about 0.3 µm across, but distinct *in vivo* because highly refractive, arranged in several rows between kineties in main body portion and scattered around kineties in anterior third (Figs 2n, o). Cytoplasm colourless, usually studded with lipid droplets 1–5 µm across and up to 40 µm-sized food vacuoles with granular or compact contents (Figs 2a, 3k); likely feeds on ciliates

◀◀

Figs 2a–p. *Enchelyodon alqasabi* (a–h, j–l, n–p), *E. armatides* (d, i; from Foissner *et al*. 2002), and *Semispathidium armatum* (m; from Foissner *et al*. 2002) from life (a, c, d, n–p) and after protargol impregnation (b, e–m). **a** – right side view of a representative specimen, length 180 µm. Arrowhead marks end of bristle tail of brush row 3; **b** – strongly contracted specimen; **c** – extreme shape variant; **d** – comparison of extrusomes of *E. alqasabi* (left; length 17 µm) and *E. armatides* (right; length 18 µm); **e**, **f** – ciliary pattern of right and left side and macronucleus of a paratype specimen; **g**, **h**, **j** – ciliary pattern of ventral and dorsal side and macronucleus of holotype specimen, length 120 µm; **i** – dorsolateral view of *E. armatides*, which has a tortuous macronucleus strand; **k**–**m** – ventral and dorsal view of a specimen with slightly curved ciliary rows, thus resembling *Semispathidium* (m); **n**, **o** – surface views showing cortical granulation in anterior third (n) and in mid-body (o); **p** – fine structure of dorsal brush. All rows commence with an ordinary monokinetid (arrows), and row 3 continues to second third of body with a monokinetidal bristle tail (arrowhead). B (1–3) – dorsal brush (rows), CK – circumoral kinety, CV – contractile vacuole, DE – developing extrusome, E – extrusome, F – oral bulge fibres, MA – macronucleus or macronucleus nodules, OB – oral bulge, PB – pharyngeal basket. Scale bars: 40 µm (a, e–i) and 10 µm (j–l).



Figs 3a–j. *Enchelyodon alqasabi* after protargol impregnation. **a** – body shape, infraciliature, and macronucleus pattern of a representative specimen; **b**–**j** – details of anterior body region of various specimens. Note developing extrusomes, inconspicuous pharyngeal basket, variation of oral bulge shape, and structure of dorsal brush. The dorsal brush is heterostichad, and the dikinetids of the circumoral kinety are composed of basal bodies side by side (j). Arrowheads in Fig. 3g, i mark the monokinetidal bristle tail of brush row 3. B – dorsal brush, B (1–3) – dorsal brush (rows), CK – circumoral kinety, DE – developing extrusomes, F – oral bulge fibres, MA – macronucleus nodules, OB – oral bulge, PB – pharyngeal basket. Scale bars: 50 µm (a) and 10 µm (b–j).



Figs 3k–p. *Enchelyodon alqasabi* after protargol impregnation (k, n, o) and in the scanning electron microscope (l, m, p). **k** – dorsal view of holotype specimen showing dorsal brush and macronucleus nodules; **l** – general shape of a representative specimen. Arrowhead marks the end of the monokinetidal bristle tail of brush row 3; **m**, **p** – anterior body end of same specimen shown in (l). Note the structure of the dorsal brush and the cell surface covered by bacteria (arrows). Arrowheads mark the monokinetidal bristle tail of brush row 3; **n**, **o** – ventral and dorsal anterior body region of same specimen, showing the circumoral kinety with basal bodies of dikinetids side by side, the anteriorly slightly curved somatic kineties, and the short, slightly displaced anterior tail of the brush rows (arrowheads). B (1–3) – dorsal brush (rows), CK – circumoral kinety, DE – developing extrusomes, FV – food vacuole, MA – macronucleus nodules, OB – oral bulge, PB – pharyngeal basket. Scale bars: 40 μm (k, l), 10 μm (p, n, o), 5 μm (m).

and, especially, heterotrophic flagellates (*Polytomella*). Glides slowly on microscope slide, rotates around main body axis when swimming.

Cilia about 7 µm long *in vivo*, ordinarily spaced (average ciliary distance 2–3 µm) and arranged in an average of 11 ordinarily spaced (~7 µm), meridional kineties slightly curved anteriorly in some specimens (Figs 2e–h, j–l, 3a, n, p). Dorsal brush three-rowed and heterostichad because row 3 distinctly shorter than row 2; inconspicuous because occupying only 10% of body length and bristles merely up to 3 µm long (Figs 2a, f, h, j, l, p, 3b, g–i, k, m, o, p; Table 5). Brush rows 1 and 3 conspicuously shorter than row 2, composed of 7 and 5 dikinetids, respectively; brush row 2 about 16 µm long and composed of an average of 14 dikinetids (Figs 2h, p); all rows with an anterior tail usually comprising a single monokinetid sometimes slightly out of line (Figs 2h, j, l, 3o); rarely, the anterior tail is lacking; row 3 continues to second third of body with a monokinetidal tail of 1.5 µm long bristles (Figs 2p, 3g, i, p). Bristles of rows 1 and 2 cylindroidal and gradually shortened from about 3 µm anteriorly to 2 µm posteriorly both *in vivo* and in protargol preparations; row 3 bristles similar to those of rows 1 and 2, but posterior bristle of last dikinetids shorted by about 50% (Figs 2p, 3m, p).

Oral bulge conspicuous *in vivo*, even at low magnification (× 100), because distinctly set off from body proper and about 4–6 µm across; in protargol preparations hemispherical to slightly discoidal, *i.e.*, 5 × 3 µm on average (Figs 2a–c, e–h, j–l; 3a–p; Table 5). Circumoral kinety at base of oral bulge, composed of slightly oblique dikinetids with basal bodies side by side; left basal body with a fibre extending sigmoidally to centre of oral bulge, right one associated with a weakly impregnating nematodesma contributing to the inconspicuous, conical pharyngeal basket (Figs 2j–l, 3j, m–p).

Occurrence and ecology: As yet found only at type locality, *i.e.*, highly saline (21‰, pH 6.7), red sand soil grown with some halophilous vegetation. Sand and soil from 0–15 cm were sieved for plant residues and used to set up, together with about 50% sand, a non-flooded Petri dish culture. *Enchelyodon alqasabi* and *Spathidium alqasabi* were numerous 48 hours after rewetting the sample. The slender shape and the contents of the food vacuoles indicate that they are euedaphic, rapacious species.

Generic assignment and comparison with related species: The generic home of this species is difficult to find because there are similarities with several families. An enchelyodonid (family Enchelyodontidae Foissner *et al*., 2002; Fig. 2i) relationship is suggested by the hemispherical oral bulge, the circular circumoral kinety, the meridionally extending ciliary rows, and the three-rowed dorsal brush. However, the basal bodies of the circumoral kinety pairs are arranged side by side (Figs 2j, 3j), similar to most members of the families Fuscheriidae Foissner *et al*., 2002 and Acropisthiidae Foissner and Foissner, 1988. Thus, we checked carefully the absence of oralized somatic monokinetids, the main feature of these families. There are also similarities with the Trachelophyllidae Kent, 1881, especially in body shape and contractility and the slight subapical widening of the neck (Figs 2e, k, 3a, b, n). However, *E. alqasabi* lacks epicortical scales, the main feature of the trachelophyllids (Foissner *et al.* 2002). Last but not least, *E. alqasabi* resembles the genus *Semispathidium* Foissner *et al*., 2002 because, in some specimens, the ciliary rows are slightly curved anteriorly (Figs 2k–m, 3n). However, this curvature might be caused by the contraction of the cell during fixation. Thus, we assign the Saudi Arabian population to *Enchelyodon*, the genus to which it fits best at the present state of knowledge (Fig. 2i).

We did not find any species in the literature that could be identical with *E. alqasabi*. However, size, shape, and contractility of *E. alqasabi* resemble *E. kenyaensis* and *E. armatides*, both described in Foissner *et al.* (2002), while the macronucleus pattern is distinctly different: many nodules in the former (Figs 2h, 3a, k) and a tortuous strand in the latter (Fig. 2i); the same applies to *Trachelophyllum* s.l. species, which have a great overall similarity to *E. alqasabi*, but usually possess only two large macronucleus nodules (Foissner *et al.* 2002). *In vivo*, *E. alqasabi* is easily identified by the slender shape, the conspicuous length, the hemispherical oral bulge, and the scattered macronucleus nodules.

Enchelyodon nodosus Berger *et al.*, 1984 (Figs 4a–q; Table 6)

Voucher material: Eight slides with protargol-impregnated specimens have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Description of a Saudi Arabian population: Size 120–200 × 50–90 µm *in vivo*, usually about 150 × 70 µm; length–width ratio rather variable, on average near 2.2:1 *in vivo* and protargol preparations (Table 6). Shape elongate ovoidal with distinct oral bulge, usually slightly flattened ventrally and thus not fully symmetrical, rarely unflattened; swimming cells often distinctly curved

in anterior third; in preparations frequently ellipsoidal or nearly ellipsoidal; not contractile (Figs. 4a, b, g, i, k, n). Macronucleus in central quarters of cell, stands out as a bright strand from the more refractive cytoplasm, usually strongly curved or wrinkled, on average 10 µm width and slightly longer than cell; rarely in two parts; numerous globular to irregular nucleoli (Figs 4a, g, k, l, n). Possibly, several globular micronuclei along and near macronucleus, but not definitely recognizable due to many similar-sized cytoplasmic inclusions. Contractile vacuole in posterior body end, surrounded by smaller adventiv blisters; several excretory pores in pole centre (Figs 4a, g, n). Two size types of rod-shaped, slightly curved, fine extrusomes scattered in oral bulge, except for bulge centre; many rod-shaped developmental stages in cytoplasm. Type I extrusomes about 40 × 0.2 µm (35–50 × 0.2–0.3 µm) in size; type II like type I but only about 20 µm long, thus possibly a developmental stage of type I; both types do not impregnate with protargol, but stain deeply with silver carbonate (Figs 4a, d, l, o, p). Somatic and oral cortex very flexible, conspicuous *in vivo* because about 1.5 µm thick due to narrowly spaced rows of ellipsoidal, colourless granules about 1 × 0.4 µm in size; conspicuous also in protargol-prepared specimens because 1.5 µm thick and separated from cytoplasm by a very thin (<0.5 µm) but deeply stained sheet, likely the *lamina (tela) corticalis* (Figs 4a, f, h, j, m, q). Cytoplasm colourless, studded with lipid droplets 0.2–10 µm across, specimens thus dark at ≤×100 magnification; contains many granular food vacuoles up to 20 µm across, likely feeds on small ciliates because a *Halteria grandinella* was observed in a food vacuole (Figs 1a, m). Swims rather rapidly by rotation about main body axis.

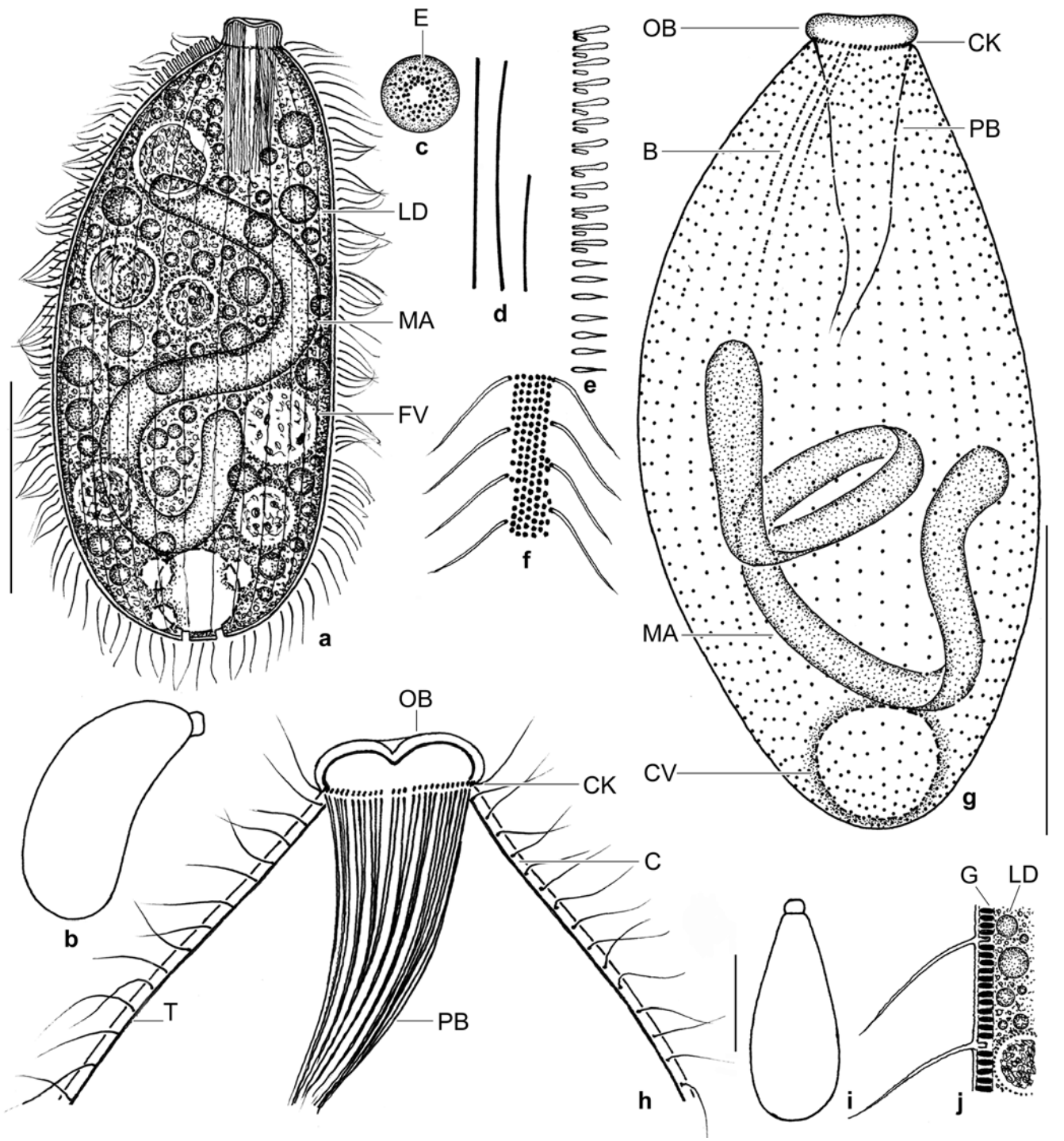
Cilia about 12 µm long *in vivo*, ordinarily spaced, *i.e.*, on average of 8 cilia in 20 µm (Table 6); arranged in an average of 43 meridional, ordinarily spaced rows abutting to circumoral kinety at right angles; rather loosely spaced underneath circumoral kinety in about half of specimens (Figs 4a, g). Dorsal brush heterostichad, inconspicuous because bristles only up to 4 µm long and largest row extending merely 24% of body length; row 1 slightly shorter than longest row 2, row 3 two thirds shorter than row 2, but with a monokinetidal bristle tail extending to last quarter of cell. Bristles similar in all rows, anterior bristle of pairs about 4 µm long and slightly inflated distally, posterior bristle stump-like because only 1.5 µm long; bristles of monokinetidal tail narrowly cuneate and about 4 µm long (Figs 4a, e, g, o; Table 6).

Oral bulge massive, on average 18 × 7 µm both *in vivo* and protargol preparations; circular in frontal view, studded with extrusomes except of concave centre. Circumoral kinety circular, dikinetids comparatively widely spaced, give rise to rods forming a conical basket 40–60 µm long (Figs 4a, c, g, h, k, n; Table 6). Oral bulge not recognizable in two specimens and minute

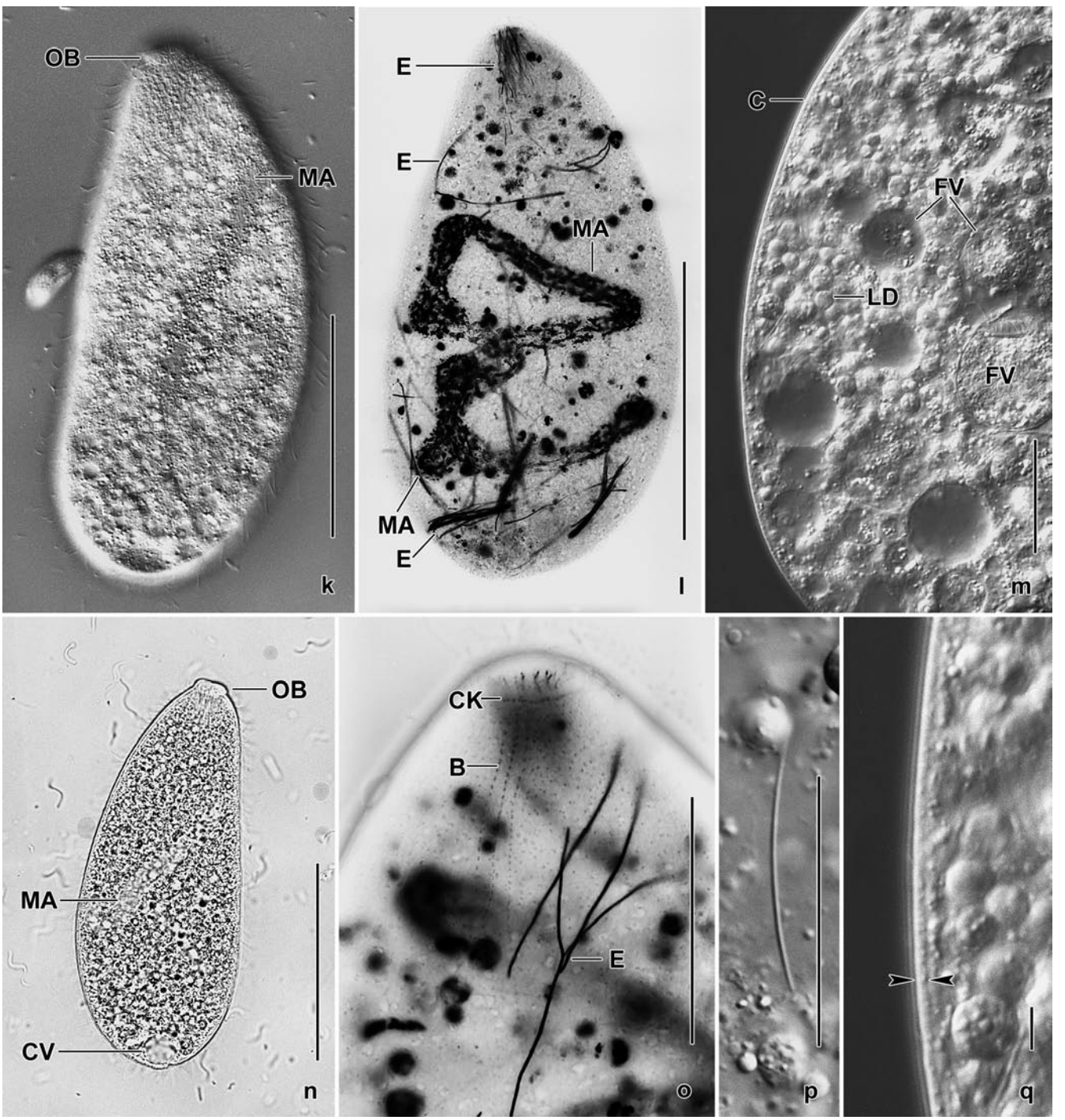
Table 6. Morphometric data from *Enchelyodon nodosus*. Data based on mounted, protargol-impregnated (Foissner 1991, protocol A), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\bar{x}$ – arithmetic mean.

Characteristics	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	131.7	130.0	16.4	4.5	12.4	103.0	172.0	13
Body, width	64.5	60.0	12.6	3.5	19.6	46.0	87.0	13
Macronucleus, length[a]	170.8	160.0	–	–	–	120.0	260.0	13
Macronucleus, width	9.8	10.0	1.2	0.3	12.6	8.0	12.0	13
Brush row 1, length[b]	24.8	25.0	6.7	3.4	27.1	18.0	31.0	4
Brush row 1, number of dikinetids	19.7	20.5	6.9	3.4	34.9	11.0	27.0	4
Brush row 2, length[b]	32.6	30.0	6.5	2.9	20.1	25.0	42.0	5
Brush row 2, number of dikinetids	29.8	29.0	7.9	3.5	26.6	19.0	38.0	5
Brush row 3, length[b]	14.4	13.0	2.9	1.3	20.0	12.0	18.0	5
Brush row 3, number of dikinetids	12.2	12.0	2.6	1.2	21.2	9.0	16.0	5
Number of ciliary rows (including brush)	42.9	43.0	1.8	0.5	4.3	40.0	45.0	12
Number of brush rows	3.0	3.0	0.0	0.0	0.0	3.0	3.0	7
Number of cilia in 20 µm[c]	8.1	7.5	2.6	0.8	32.7	6.0	15.0	12

[a] Rough values because usually strongly curved.
[b] Measured as distance from circumoral kinety to last dikinetid of row.
[c] Counted in 10 µm each in anterior and posterior third of specimens.



Figs 4a–j. *Enchelyodon nodosus* from life (a–f, i, j) and after protargol impregnation (g, h). **a** – right side view of a representative specimen, length 150 µm; **b**, **i** – swimming specimens; **c** – frontal view of oral bulge. Note lack of extrusomes in bulge centre; **d** – two size types of extrusomes (40 µm, 20 µm); **e** – part of dorsal brush row 3. Note the monokinetidal tail of flame–shaped bristles; **f**, **j** – surface view and optical section showing the conspicuous cortical granulation; **g** – ciliary pattern of dorsal side; **h** – anterior body portion showing oral structures and the thick cortex separated from the cytoplasm by the darkly impregnated *tela corticalis*. B – dorsal brush, C – cortex, CK – circumoral kinety, CV – contractile vacuole, E – extrusomes, FV – food vacuole, G – cortical granules, LD – lipid droplets, MA – macronucleus, OB – oral bulge, PB – pharyngeal basket, T – *tela corticalis*. Scale bars: 50 µm (a, g) and 10 µm (h).



Figs 4k–q. *Enchelyodon nodosus* from life (k, m, n, p, q) and after silver carbonate impregnation (l, o). **k**, **n** – freely motile specimens shown in interference contrast and bright field; **l**, **o** – overview and detail, showing the dorsal brush (B) and the long, deeply impregnated extrusomes; m, q – optical sections showing the thick cortex (opposed arrowheads) and the cytoplasm studded with food vacuoles, lipid droplets, and granules; **p** – a long extrusome. B – dorsal brush, C – cortex, CK – circumoral kinety, CV – contractile vacuole, E – extrusomes, FV – food vacuoles, LD – lipid droplets, MA – macronucleus, OB – oral bulge. Scale bars: 80 µm (k, l, n), 40 µm (m, o, p), 5 µm (q).

(~6 µm across) in a third one; possibly, these are post-dividers because two of the 13 specimens investigated commenced division.

Occurrence and ecology: Found only at site 1, where it was rare in the non-flooded Petri dish culture three days after rewetting the air-dried sample. As the sample was from an irrigated vegetable field and contained a mixture of soil and freshwater species, *e.g.*, *Monodinium perrieri* (redescribed from this locality by Foissner *et al.* 1999), *Stylonychia bifaria* and *Urostyla grandis*, we could not decide which habitat *E. nodosus* prefers. The same problem adheres to the type population, which was discovered in soil from the margin of a lake.

Comparison with other populations: This population was difficult to impregnate and few specimens were available. Thus, the morphometric data are incomplete. The same applies to the Austrian type population, where Berger *et al.* (1984) could not count the ciliary rows, but estimated their number by multiplying kinety distance with body diameter. This, of course, provides rough values. Thus, we reinvestigated the type slide series of *E. nodosus* and could count the ciliary rows in six specimens: 60, 64, 60, 62, 62, 62; this gives an average of 62, in contrast to the 76 kineties calculated by Berger *et al.* (1984). Further, Berger *et al.* (1984; their Figures 14, 15) figured a very small specimen because it showed the ciliary pattern more clearly. Obviously, this specimen has only 45–50 ciliary rows and thus looks highly similar to the Arabian population in this respect. The slides also show that the Austrian specimens have as distinct cortical granules as the Arabian ones.

Berger *et al.* (1984) studied a second population of *E. nodosus* from soil of the Austrian Central Alps. These specimens have, like the Arabian ones, 42 ciliary rows, but possess only one type of rather short (~20 µm) extrusomes. Unfortunately, the data are not very detailed, *i.e.*, no information is given on the attachment of the extrusomes and the possible occurrence of a second type of very short extrusomes. Thus, this population will not be discussed further.

The Arabian specimens of *E. nodosus* differs from the Austrian type population by three main features: extrusomes lacking in bulge centre *vs.* present; two long (40 µm and 20 µm) types of extrusomes *vs.* a long (~30 µm) and a very short (~2.5 µm) type; 43 *vs.* 62 ciliary rows. Further, the macronucleus is longer by about 60% in the Arabian than Austrian specimens. Except of the ciliary rows, these are rather sophisticated features, although we could confirm the differences by a reinvestigation of specimens from the type locality (Burgenland, eastern Austria) and from Namibia, Southwest Africa. However, little is known on the variability and key features of large *Enchelyodon* species. Thus, we prefer to assign the Arabian population to the Austrian one, waiting for detailed data from further populations.

Metauroleptus nov. gen.

Diagnosis: Slightly twisted hypotrichs with 1 right and 1 left row of marginal cirri as well as 2 long and 2–3 short ventral rows and a row of buccal cirri. With transverse and caudal cirri, the latter originating exclusively from dorsal kinety 1 and thus forming a short row. All dorsal kineties generated intrakinetally.

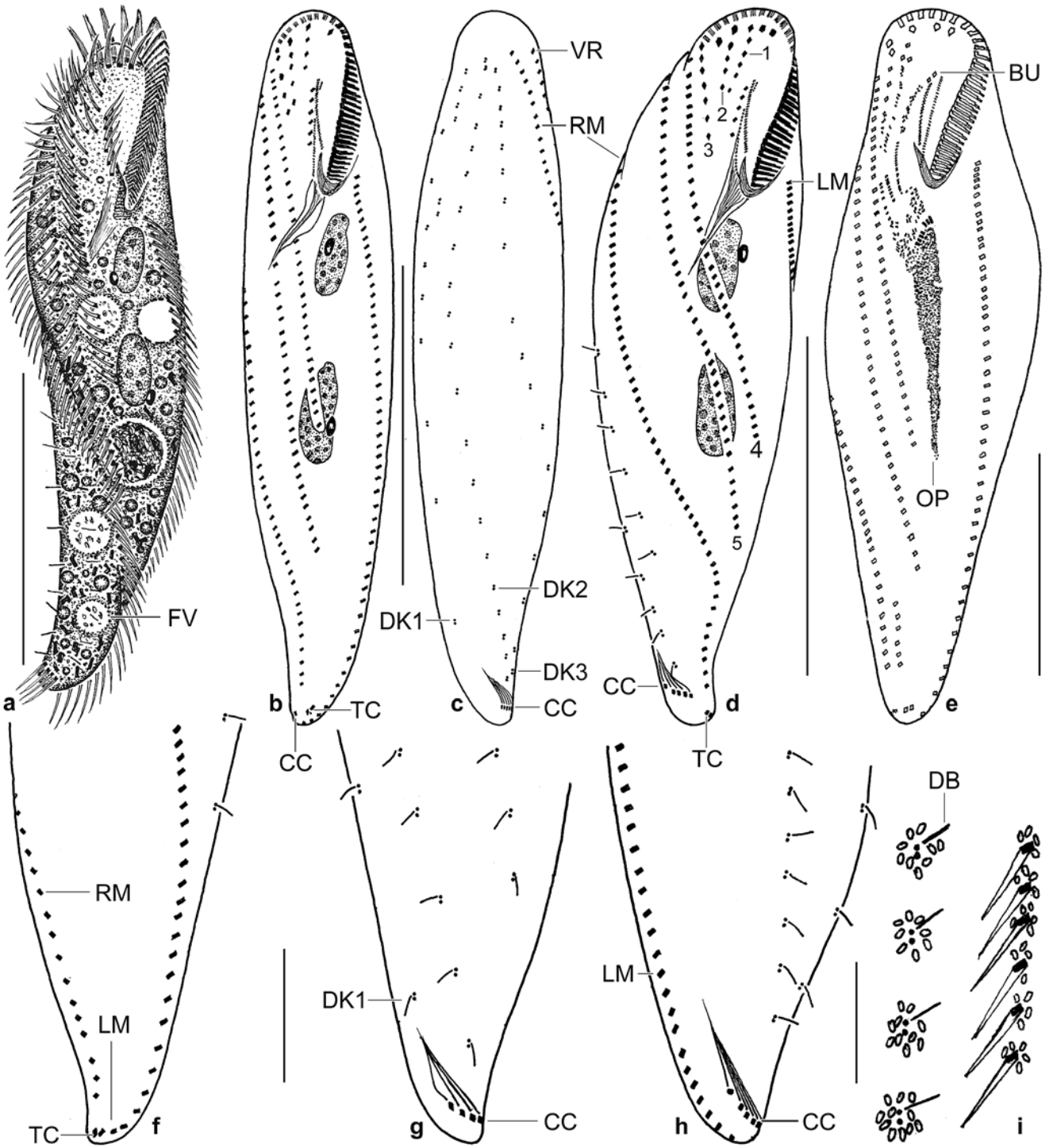
Type species: *Metauroleptus arabicus* nov. spec.

Etymology: Composite of the Greek prefix *meta* (associated with, changed, substituted for) and the generic name *Uroleptus*, referring to the supposed affinity to the Kahliellidae. Masculine gender.

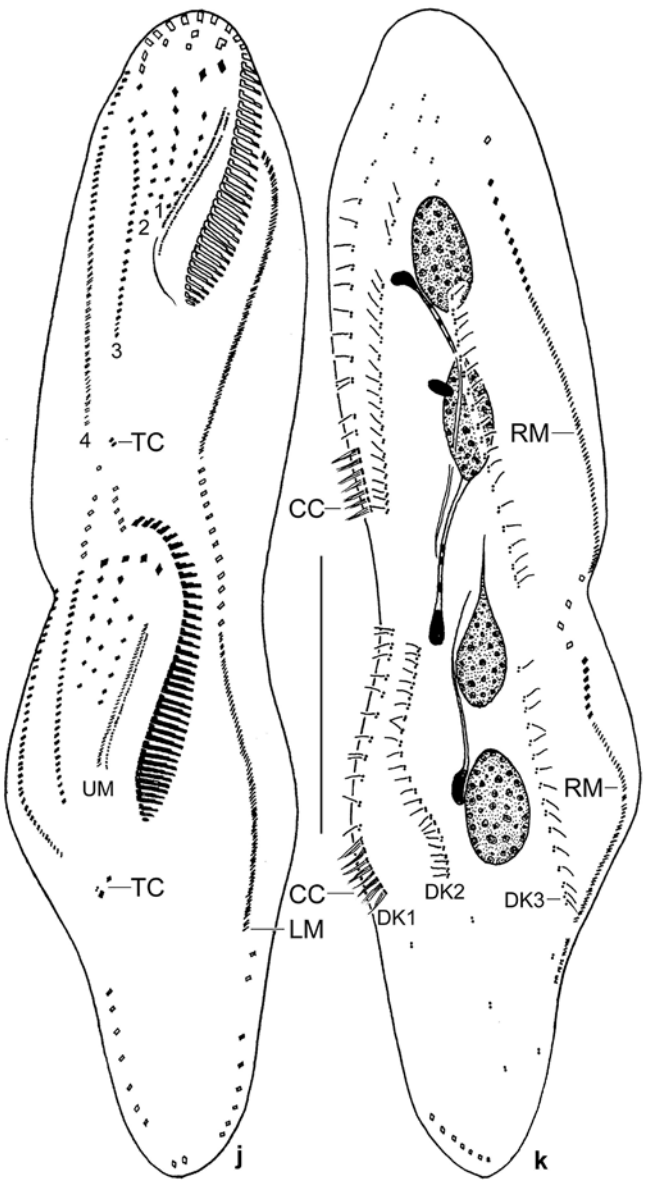
Species assignable: *Metauroleptus arabicus* nov. spec. (type); *Metauroleptus procerus* (Berger and Foissner, 1987) nov. comb. (basionym – *Pseudouroleptus procerus* Berger and Foissner, 1987); *Metauroleptus terrestris* (Hemberger, 1985) nov. comb. (basionym: *Pseudouroleptus terrestris* Hemberger, 1985). For distinguishing these species, see Table 8 and the description of *M. arabicus*.

Two other species have been assigned to *Pseudouroleptus* (Berger, 2001). They do not meet the diagnosis of *Metauroleptus: Uroleptus humicola* Géllert (transverse and caudal cirri lacking) and *Paraurostyla buitkampi* Foissner (lacks caudal cirri).

Comparison with related genera and systematic affinity: The cirral pattern of *Metauroleptus* resembles that of *Pseudouroleptus* Hemberger, 1985. However, *Pseudouroleptus* lacks the short frontal cirral rows so typical and important (see ontogenesis!) for *Metauroleptus*. On the other hand, *Metauroleptus* lacks a posteristomial cirrus which has a complex ontogenesis (Hemberger 1985, Berger 1999). Likely, ontogenesis of the ventral cirral rows is also different and should be included in the diagnosis of *Metauroleptus* when more detailed data become available: in *Metauroleptus*, the two long ventral rows are likely silent (Fig. 5j), while the left row is ontogenetically active, producing both ventral rows in *Pseudouroleptus* (Hemberger 1985, Berger 1999). Another main difference concerns the dorsal ontogenesis: in *Pseudouroleptus*, kinety 3 splits, producing a fourth row, while all dorsal kineties of *Metauroleptus* are produced intrakinetally (Fig. 5k); further, *Pseudouroleptus* produces a caudal cirrus each in



Figs 5a–i. *Metauroleptus arabicus* from life (a, i) and after protargol impregnation (b–h). **a** – ventral view of a representative, slightly twisted specimen, length 180 μm; **b**–**d** – ventral and dorsal view of holotype specimen (180 μm) and ventral view of a distinctly twisted paratype specimen. Both specimens have three (1–3) short and two (4, 5) long ventral cirral rows; **e** – ventral view of an early divider; **f**, **g** – ventral and dorsal view of posterior body region, showing the location of the transverse and caudal cirri; **h** – dorsal view of a distinctly twisted specimen with seven caudal cirri, of which five are recognizable; **i** – cortical granulation around dorsal bristles and cirri. BU – buccal cirral row, CC – caudal cirri, DB – dorsal bristles, DK 1–3 – dorsal kineties, FV – food vacuole, LM – left row of marginal cirri, OP – oral primordium, RM – right row of marginal cirri, TC – transverse cirri, VR – ventral cirral row. Scale bars: 80 μm (a–d), 50 μm (e), and 20 μm (f–h).



Figs 5j, k. *Metauroleptus arabicus*, ventral and dorsal view of a late divider after protargol impregnation. Parental structures shown by contour, newly formed structures shaded black. The four (1–4) ventral cirral rows likely originated from extensions of the oral primordium, the buccal cirral row, and the two short ventral rows (cp. Fig. 5e). Note that caudal cirri are formed only in dorsal kinety 1. CC – new caudal cirri, DK 1–3 – newly formed dorsal kineties, LM, RM – newly formed left and right row of marginal cirri, TC – newly formed transverse cirri, UM – newly formed undulating membranes. Scale bar: 50 µm.

kineties 1, 2 and 4, while *Metauroleptus* produces caudal cirri only in kinety 1, a highly unusual feature possibly occurring also in some urostylids, for instance, in *Keronella gracilis*, *Caudiholosticha sylvatica*, and *Bicoronella costaricana* (for reviews, see Berger 1999, 2006).

We cannot assign *Metauroleptus* to a certain family because family classification is highly controversial in hypotrichs (for reviews see, Berger 1999, 2006; Lynn and Small 2002; Foissner and Stoeck 2008). If Berger's system is applied, it can be excluded that *Metauroleptus* belongs to the Dorsomarginalia (Oxytrichidae s.l.) because it lacks dorsomarginal kineties. Likewise, an urostylid relationship can be excluded due to the lack of paired ventral cirri in zigzag pattern. The Amphisiellidae can also be excluded because *Metauroleptus* lacks an "amphisiellid median cirral row" (Eigner and Foissner 1994). Possibly, *Metauroleptus* belongs to the kahliellids, keronopsids (Figs 6a, c), or to a not yet defined group.

Metauroleptus arabicus nov. spec. (Figs 5a–k, 6a, b; Table 7)

Diagnosis: Differs from the congeners in having 3 complete dorsal kineties.

Type locality: Very sandy pasture soil in the surroundings of the village of Al-Qasab, about 150 km NW of the town of Riyadh, Saudi Arabia, 45°30'E 26°N.

Etymology: Named after the region the species was discovered.

Type material: 1 holotype and 4 paratype slides with protargol-impregnated specimens have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Description: Size 150–220 × 35–50 µm *in vivo*, usually near 180 × 40 µm; length–width ratio fairly constant, *i.e.*, 3–5:1, on average 4.5:1 both *in vivo* and protargol preparations (Table 7); flattened up to 2:1 dorsoventrally; not contractile. Outline pisciform with posterior half gradually narrowed; slightly to distinctly sigmoidal and usually more or less twisted about main body axis, especially when just collected from soil; anterior end broadly rounded, posterior narrowly rounded, never acute, directed to the right or to the left when cells are distinctly twisted (Figs 5a, b, d, f, h, 6a). Nuclear apparatus slightly above mid-body left of midline. Macronucleus nodules on average only 12 µm apart, broadly to slenderly ellipsoidal, on average near 2.5:1, contain many small, globular nucleoli. A micronucleus each attached in variable positions to macronucleus nodules; individual micronuclei globular to ellipsoidal, on average 5 × 3 µm in protargol preparations (Figs 5a, b, d, k, 6a; Table 7). Contractile vacuole slightly above mid-body near left margin of cell. Cortex thin and flexible. Cortical granules difficult to recognize because colourless and only 0.5 × 0.25 µm in size, form small clusters

Table 7. Morphometric data on *Pseudohemisincirra arabica* (PA) and *Metauroleptus arabicus* (MA). Data based on mounted, protargol-impregnated (Foissner 1991, protocol A), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. AZM – adoral zone of membranelles, CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, VR – ventral cirral row, $\overline{x}$ – arithmetic mean.

Characteristics	Species	$\overline{x}$	M	SD	SE	CV	Min	Max	n
Body, length	PA	86.7	82.0	13.4	3.1	15.4	68.0	110.0	19
	MA	159.6	160.0	18.2	4.2	11.4	135.0	194.0	19
Body, width	PA	15.4	16.0	2.7	0.6	17.3	11.0	19.0	19
	MA	40.6	41.0	5.3	1.2	13.1	32.0	50.0	19
Body length: width, ratio	PA	5.7	5.7	1.0	0.2	17.9	4.0	8.4	19
	MA	4.0	4.0	0.5	0.1	12.0	3.0	4.9	19
Anterior body end to proximal end of adoral zone of membranelles (AZM), distance	PA	19.1	19.0	1.9	0.4	10.0	14.0	22.0	19
	MA	42.1	42.0	3.0	0.7	7.1	37.0	48.0	19
Body length: AZM length, ratio	PA	4.6	4.7	0.6	0.1	13.4	3.5	5.4	19
	MA	3.8	3.7	0.5	0.1	11.9	3.2	5.1	19
Anterior body end to right marginal row, distance	PA	13.7	14.0	2.2	0.5	15.7	10.0	17.0	19
	MA	11.5	11.0	4.1	1.0	36.0	5.0	19.0	19
Anterior body end to paroral membrane, distance	PA	7.0	7.0	1.2	0.3	17.6	5.0	9.0	19
	MA	12.0	12.0	1.4	0.3	11.8	9.0	15.0	19
Anterior body end to frontoventral row/buccal row, distance	PA	6.6	6.0	1.0	0.2	15.5	5.0	9.0	19
	MA	14.5	15.0	1.9	0.4	13.1	11.0	18.0	19
Anterior body end to end of frontoventral row/ventral row 1, distance	PA	20.3	20.0	3.4	0.8	16.6	15.0	27.0	19
	MA	16.8	18.0	4.6	1.1	27.4	6.0	24.0	19
Anterior body end to first macronucleus nodule, distance	PA	17.3	17.0	2.7	0.6	15.8	10.0	21.0	19
	MA	44.1	43.0	4.2	1.0	9.6	38.0	52.0	19
Anterior body end to end of VR 2, distance	MA	27.0	27.0	4.6	1.1	17.3	19.0	36.0	19
Anterior body end to end of VR 3, distance	MA	82.5	82.0	14.6	3.3	17.7	60.0	111.0	19
Anterior body end to end of VR 4, distance	MA	110.7	110.0	14.8	3.4	13.4	87.0	138.0	19
Posterior body end to lowermost transverse cirrus, distance	PA	1.6	2.0	–	–	–	1.0	2.0	19
	MA	2.1	2.0	1.0	0.2	47.2	1.0	5.0	19
Posterior body end to right marginal row, distance	PA	7.4	7.0	3.0	0.7	40.0	4.0	16.0	19
Posterior body end to left marginal row, distance	PA	6.8	6.0	4.1	0.9	60.3	2.0	17.0	19
Length of nuclear figure/distance between macronucleus nodules	PA	52.6	51.0	10.2	2.3	19.3	37.0	73.0	19
	MA	12.4	10.0	6.5	1.5	51.9	5.0	26.0	19
Macronucleus nodules/anterior nodule, length	PA	6.2	6.0	1.2	0.3	19.7	4.0	8.0	19
	MA	20.1	20.0	1.9	0.4	9.4	16.0	24.0	19
Macronucleus nodules/anterior nodule, width	PA	3.2	3.0	0.7	0.2	20.2	2.0	4.0	19
	MA	8.3	8.0	1.2	0.3	13.9	6.0	10.0	19
Posterior macronucleus nodule, length	MA	21.2	21.0	2.5	0.6	11.6	16.0	26.0	19
Posterior macronucleus nodule, width	MA	8.8	9.0	1.0	0.2	11.1	7.0	10.0	19
Macronucleus nodules, number	PA	15.6	16.0	0.9	0.2	5.7	14.0	17.0	19
	MA	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
Micronuclei, length	PA	2.8	3.0	0.5	0.1	17.0	2.0	4.0	19
	MA	4.7	5.0	0.6	0.1	11.9	4.0	6.0	19
Micronuclei, width	PA	1.7	1.5	–	–	–	1.0	2.0	19
	MA	3.1	3.0	–	–	–	3.0	4.0	19

(continued)

Characteristics	Species	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Micronuclei, number	PA	2.2	2.0	–	–	–	2.0	3.0	19
	MA	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
Adoral membranelles, number	PA	15.1	15.0	1.2	0.3	7.8	12.0	17.0	19
	MA	38.5	38.0	2.2	0.5	5.6	34.0	43.0	19
Longest membranellar base, length	PA	4.4	4.0	0.6	0.1	13.7	3.0	5.0	19
	MA	6.4	6.0	0.8	0.2	13.0	5.0	8.0	19
Cirri in right marginal row, number	PA	17.8	17.0	2.7	0.6	15.0	13.0	23.0	19
	MA	53.4	54.0	6.5	1.5	12.1	41.0	63.0	19
Cirri in left marginal row, number	PA	19.1	19.0	2.6	0.6	13.4	15.0	26.0	19
	MA	50.9	51.0	6.8	1.6	13.4	41.0	65.0	19
Frontoventral cirral rows, number	PA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
	MA	4.2	4.0	–	–	–	4.0	5.0	19
Frontoventral cirral row/ventral row 1, number of cirri	PA	7.1	7.0	1.7	0.4	23.9	5.0	11.0	19
	MA	4.1	4.0	1.2	0.3	30.2	2.0	6.0	19
Ventral row 2, number of cirri	MA	5.1	5.0	1.1	0.3	21.4	3.0	7.0	19
Ventral row 3, number of cirri	MA	30.0	31.0	4.4	1.0	14.8	22.0	36.0	19
Ventral row 4, number of cirri	MA	39.6	41.0	5.3	1.2	13.3	30.0	52.0	19
Frontoterminal cirri, number	PA	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
	MA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	19
Frontal cirri, number	PA	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
	MA	4.1	4.0	–	–	–	3.0	5.0	19
Buccal cirri, number	PA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	19
	MA	6.2	6.0	0.8	0.2	12.7	5.0	8.0	19
Transverse cirri, number	PA	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
	MA	1.8	2.0	–	–	–	1.0	2.0	19
Caudal cirri, number	PA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	19
	MA	4.6	4.0	1.3	0.3	27.5	3.0	7.0	19
Dorsal kineties, number	PA	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
	MA	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
Dorsal kinety 1, number of kinetids	MA	11.8	12.0	2.4	0.5	20.1	8.0	18.0	19
Dorsal kinety 2, number of kinetids	MA	21.0	22.0	3.1	0.7	14.6	15.0	29.0	19

around bases of cirri and dorsal bristles, do not impregnate with protargol (Fig. 5i). Cytoplasm colourless, usually studded with lipid droplets up to 7 µm across, ordinary crystals in posterior third, and food vacuoles up to 30 µm across. Feeds on filamentous bacteria, flagellates (*Polytomella*) and middle-sized ciliates, such as *Colpoda inflata* and *Halteria grandinella* (Fig. 5a). Glides slowly on microscope slide and between soil particles, showing great flexibility.

Cirri short (12–15 µm *in vivo*) and fine compared to body size; cirral pattern of usual variability, rows extend more or less obliquely, depending on body twist (Figs 5a, b, d, e, 6a, b; Table 7). Marginal rows almost as long as body, both rows extend onto dorsal side in anterior (right row) or posterior (left row) third of cell. Two to three, usually two short ventral cirral rows (rows 1 and 2) in oral area right of buccal row and two long ventral rows extending slightly (row 3) to distinctly (row 4) above mid-body. One or two minute transverse cirri near posterior body end. Frontoterminal and postperistomial cirri lacking. Dorsal bristles about 4 µm long, arranged in three rows slightly shortened anteriorly and posteriorly. Row 1 consisting of an average of 12 kinetids with kinetid distances gradually increasing posteriorly (Figs 5c, g; Table 7). Three to seven, on average four caudal cirri in an oblique row originating from dorsal kinety 1 (see ontogenesis) and associated with rather conspicuous fibres (Figs 5c, d, g, h, 6a, b; Table 7).

Table 8. Comparison of main characteristics in *Metauroleptus arabicus* (present paper), *M. procerus* (from Berger and Foissner 1987), and *M. terrestris* (from Hemberger 1985). Data are arithmetic means based on protargol-impregnated specimens.

Characteristics	*M. arabicus*	*M. procerus*	*M. terrestris*
Body length: width, ratio	4:1	4.3:1 (4–6:1)	3 or 4:1
Body length: AZM length, ratio	3.8:1	3.8:1	4–5:1
Geographic location	Arabia	Austria	Germany
Adoral membranelles, number	38	33	30–33
Ventral cirral rows, number	4 (rarely 5)	4	4
Buccal cirri, number	6	4	4
Transverse cirri, number	2	2	2–3
Right marginal cirri, number	53	48	31–35
Left marginal cirri, number	51	46	32–37
Dorsal kineties, number	3 ordinary rows	3 rows with row 1 reduced to a few kinetids	4 ordinary rows

Table 9. Comparison of *Pseudohemisincirra* nov. gen. with similar genera[a].

Characteristics	*Pseudo-hemisincirra*	*Hemisincirra*	*Circinella*	*Periholosticha*	*Paragastrostyla*	*Holostichides*	*Holostichides terricola*
Body acut posteriorly	no	most species	yes	yes	yes	no	yes
Buccal cirri	absent	present	present	absent	absent	present	absent
Transverse cirri	present	present	absent	absent	absent	absent	absent
Caudal cirri	absent	absent	absent	present	present	present	present
Midventral pattern in anterior half of ventral row	absent	present	absent	present	absent	present	present

[a] Based on data from Hemberger 1982, 1985 (*Hemisincirra*, *Periholosticha*, *Paragastrostyla*); Foissner 1982, 1987a, 1988, 1994 (*Hemisincirra*, *Circinella*, *Holostichides*, *H. terricola*), and Foissner *et al*. 2002 (*Hemisincirra*, *Periholosticha*).

Oral apparatus of ordinary structure. Adoral zone short, occupies only 26% of body length, composed of an average of 38 membranelles with largest bases about 8 µm wide *in vivo* (Table 7). Buccal cavity rather narrow and flat, buccal lip inconspicuous. Undulating membranes short, almost straight, optically intersect in anterior third; paroral cilia about 7 µm long *in vivo*. Pharyngeal fibres of ordinary distinctness (Figs 5a, b, d, 6a; Table 7).

Ontogenesis: Some key ontogenetic stages are contained in the slides deposited. They show: (i) the oral primordium develops apokinetally and forms a long streak of disordered basal bodies between the left long ventral row and the left marginal row (not shown); (ii) cirral row anlagen originate from the anterior end of the oral primordium, the buccal cirral row, and from the short ventral rows 1 and 2, *i.e.*, the long ventral rows are likely not involved (Figs 5e, j); (iii) two transverse cirri are generated (Fig. 5j); and (iv) caudal cirri are produced only by dorsal kinety 1 (Fig. 5k).

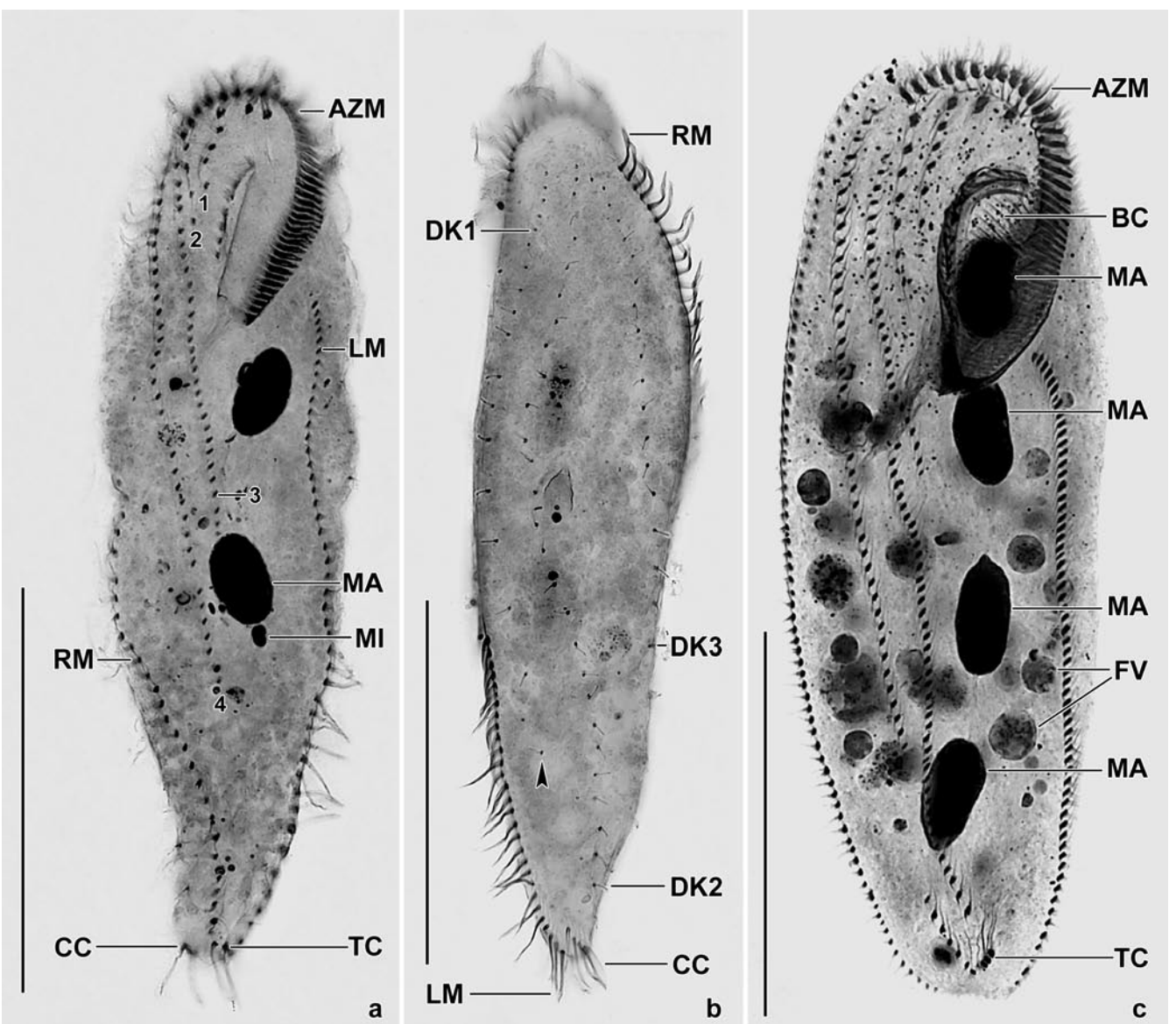
Occurrence and ecology: As yet found only at type locality, *i.e.*, a rather fertile site in a semi-desert. The European *P. procerus* and *P. terrestris* were discovered also in fertile soils, viz., a pasture in Salzburg and a forest near Bonn, Germany, respectively.

Comparison with congeners: The data compiled in Table 8 show that the three *Metauroleptus* species differ only in one reliable feature, viz., the number of dorsal kineties: 4 ordinary rows in *M. terrestris*, 3 ordinary rows in *M. arabicus*, and 3 rows in *M. procerus* with row 1 reduced to a single kinetid. Further, *M. arabicus* is slightly larger in many features, *e.g.*, has more adoral membranelles and buccal cirri on average (Table 8). The number of dorsal kineties is considered a "strong" species feature (Berger 1999, 2006). None the less, subspecies rank would be probably more appropriate for these three species because the number of dorsal kineties is a sophisticated feature well recognizable only in protargol preparations.

No cortical granules have been mentioned in the original descriptions of *M. procerus* and *M. terrestris*. However, a Namibian population of *M. procerus* has cortical granules like *M. arabicus*, but 1 × 0.5 µm in size, indicating that they were overlooked in the type population. Further, the Namibian specimens have composed dorsal kinety 1 of 2–3 widely spaced kinetids.

***Keronopsis dieckmanni* Foissner, 1998 (Figs 6c, 7g, h)**

The Saudi Arabian specimens of this species, which is probably restricted to the African continent, match the original description, both in morphology (Fig. 6c) and habitat (saline oasis soil; saline soil from shore of Lake Baringo, Kenya). Thus, a redescription is not necessary but three voucher slides have been deposited and some *in vivo* observations are added: (i) specimens more slender (about 230 × 50 µm *vs.* 220 × 70 µm) and frequently rather distinctly narrowed posteriorly (Figs 7g, h); (ii) cortex without specific granules, confirming the original description; (iii) paroral and endoral membrane optically intersecting in mid-buccal cavity; (iv) feeds an *Colpoda maupasi* ingested whole (Fig. 7h).



Figs 6a–c. *Metauroleptus arabicus* (a, b) and *Keronopsis dieckmanni* (c) after protargol impregnation. **a**, **b** – ventral and dorsal view showing main features, such as the four ventral cirral rows (1–4), the transverse and caudal cirri, and the two macronucleus nodules. The arrowhead marks the last kinetid in dorsal kinety 1; **c** – ventral view showing a main feature of *K. dieckmanni*, viz., the four macronucleus nodules. The cirral pattern is highly similar to that of *M. arabicus*, but caudal cirri are absent from *K. dieckmanni*. AZM – adoral zone of membranelles, BC – buccal cavity, CC – caudal cirri, DK 1–3 – dorsal bristle rows, FV – food vacuoles, LM – left row of marginal cirri, MA – macronucleus nodules, MI – micronucleus, RM – right row of marginal cirri, TC – transverse cirri. Scale bars: 80 µm.

***Pseudohemisincirra* nov. gen.**

Diagnosis: Oblong hypotrichs with 1 right and left row of marginal cirri, a short row of frontoventral cirri, and transverse cirri. Buccal cirri and caudal cirri absent.

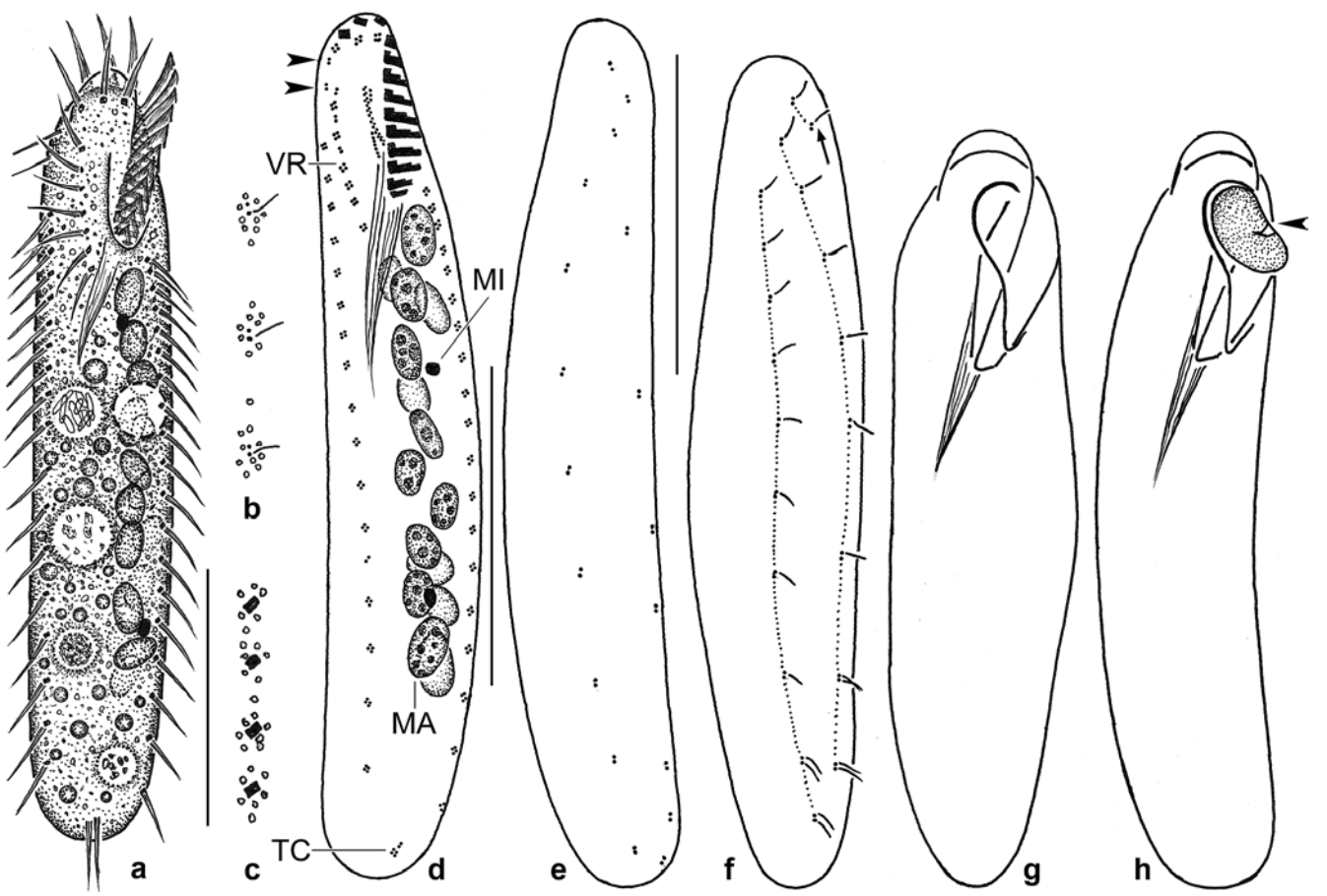
Type species: *Pseudohemisincirra arabica* nov. spec.

Etymology: The name is a composite of *pseudo* (false, *i.e.*, resembling but not equalling) and the generic name *Hemisincirra*.

Comparison with similar genera: Hypotrichs of this type are difficult to classify. Thus, we compiled main characteristics of similar genera in Table 9, showing the unique combination of features in *Pseudohemisincirra*. *Holostichides terricola* Foissner, 1988 likely belongs to *Periholosticha* which, however, lacks frontoterminal cirri according to the ontogenetic data of Hemberger (1982); however, the investigations of Foissner *et al.* (2002) indicate the presence of such cirri. Generally, the frontoterminal cirri are insufficiently defined and thus a difficult feature. This is why we did not include them in Table 9. Likewise, several *Hemisincirra* species have been described that likely belong to other or new genera.

***Pseudohemisincirra arabica* nov. spec.**
(Figs 7a–f; Tables 7, 9)

Diagnosis: Size about 90 × 15 µm *in vivo*; narrowly oblong. Cortical granules <1 µm in size, colourless, form clusters around bases of cirri and dorsal kinetids. On average 16 macronucleus nodules and 2 micronuclei in a series left of midline, 15 adoral membranelles, 17 cirri in right and 19 cirri in left marginal row, 7 cirri in frontoventral row, 2 frontoterminal cirri, 2 transverse cirri, and 3 dorsal kineties with kinety 3 composed of only two kinetids. All cirri comprising 2–4 cilia.



Figs 7a–h. *Pseudohemisincirra arabica* (a–f) and *Keronopsis dieckmanni* (g, h) from life (a, g, h) and after protargol impregnation (b–f). **a** – ventral view of a representative specimen, length 90 µm; **b**, **c** – cortical granulation around dorsal bristles and cirri; **d**, **e** – infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen, length 80 µm. Note lack of buccal and caudal cirri as well as the minute cirri each composed of only 2–4 cilia. Arrowheads mark frontoterminal cirri; **f** – dorsal view of a paratype specimen with kinetids connected by dotted lines. Arrow marks row 3 consisting of only two kinetids; **g** – outline of an ordinary specimen, length 250 µm; **h** – outline of a slender specimen just ingesting a *Colpoda maupasi* (arrowhead), length 220 µm. MA – macronucleus nodules in two rows one upon the other, MI – micronucleus, VR – ventral cirral row. Scale bars: 30 µm (a, d–f).

Type locality: Very sandy pasture soil in the surroundings of the village of Al-Qasab, about 150 km NW of the town of Riyadh, Saudi Arabia, 45°30'E 26°N.

Etymology: Named after the region the species was discovered.

Type material: 1 holotype and 2 paratype slides with protargol-impregnated specimens have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Description: Size *in vivo* 70–120 × 10–20 µm, usually near 90 × 15 µm; length–width ratio 4–8:1, on average about 6:1 both *in vivo* and protargol preparations (Tab. 7); flattened about 2:1 dorsoventrally. Outline oblong (elongate rectangular) because both ends broadly rounded and margins straight or only slightly convex (Figs 7a, d, f). Macronucleus nodules invariably in two rows on top of each other between adoral zone of membranelles and posterior body end left of cell's midline; individual nodules globular to ellipsoidal, on average about 6 × 3 µm, contain many small nucleoli. Usually a broadly ellipsoidal, compact micronucleus each near ends of macronucleus row (Figs 7a, d). Contractile vacuole slightly above mid-body near left margin of cell. Cortex thin and very flexible. Cortical granules about 0.5 µm across, colourless to yellowish, form small clusters around bases of cirri and dorsal kinetids, impregnate faintly with protargol (Figs 7b, c). Cytoplasm colourless, contains some lipid droplets 1–3 µm across and food vacuoles with bacterial remnants. Glides rather fast on slide surface and between soil particles showing great flexibility.

All cirri about 10 µm long *in vivo* and composed of 2–4 cilia only; pattern of usual variability (Figs 7a, d; Table 7). Frontal cirri in transverse row subapically; frontoterminal cirri in gap between frontal cirri and ventral cirral row at right margin of cell, each consisting of only two cilia; buccal cirrus lacking. Ventral cirral row usually ends at or underneath buccal vertex, slightly oblique, cirri not zigzagging and composed of 2–4 cilia. Transverse cirri near posterior margin of cell and thus distinctly projecting from body proper, one cirrus usually composed of four cilia, the other of only two. Both marginal rows end subterminally, right row commences far subapically, *i.e.*, at level of mid-buccal cavity, most cirri composed of four cilia. Dorsal bristles about 3 µm long, widely spaced, arranged in three rows in and right of cell's midline, row 3 consists only of two kinetids (Figs 7e, f). Caudal cirri absent.

Adoral zone composed of an average of 15 membranelles, occupies about 22% of body length, longest bases *ca* 5 µm wide *in vivo*; three, rarely four frontal membranelles separated from ventral membranelles by an indistinct gap at left anterior body end. Buccal cavity narrow and flat. Paroral and endoral membrane inconspicuous, slightly curved, optically intersect at level of mid-buccal cavity, paroral composed of oblique dikinetids. Pharyngeal fibres conspicuous, compared to size of oral apparatus (Figs 7a, d; Table 7).

Ontogenesis commences at proximal end of ventral cirral row.

Comparison with similar species: Small, slender hypotrichs are numerous in soil habitats and difficult to identify. *In vivo*, *P. arabica* highly resembles *Hemisincirra gellerti verrucosa* Foissner and Schade, 2000 in Foissner (2000) due to the specific arrangement of the cortical granules. The features separating these species are recognizable only on very careful live observation or in protargol preparations: the buccal cirrus (absent *vs.* present) and the number of dorsal kineties (3 *vs.* 4). There are also several other morphometric differences, for instance, the number of macronucleus nodules (16 *vs.* 8) and transverse cirri (2 *vs.* 4), but none is sufficiently distinct to make *P. arabica* easily identifiable. The same applies to several other small soil hypotrichs, especially *H. inquieta* (for a brief review, see Foissner *et al.* 2002). Thus, protargol impregnation and the character combination given in Table 9 are indispensable for a reliable identification of *P. arabica*.

Oxytricha arabica nov. spec. (Figs 8a–g; Table 10)

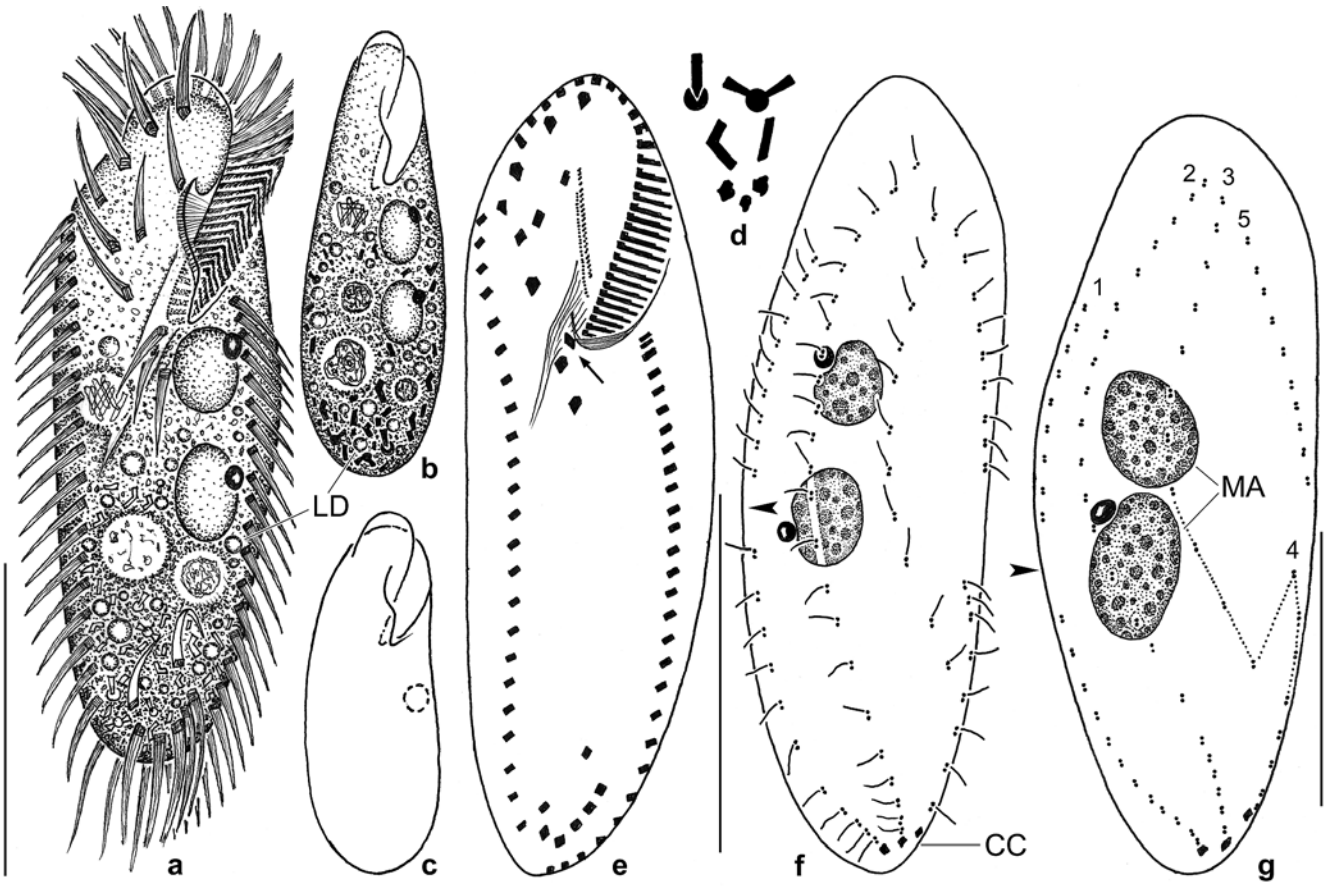
Diagnosis: Size, cytology, and ventral cirral pattern very similar to that of *O. lanceolata*. Dorsal kinety 1 with distinct gap underneath mid-body; kinety 3 split subequatorially, producing a classical *Oxytricha* pattern; kinetids very narrowly spaced in posterior region of kineties 1 and 2.

Type locality: Sand dune soil from the Khurays area, NE of the town of Riyadh, Saudi Arabia, 48°E 25°N.

Etymology: Named after the region the species was discovered.

Type material: 1 holotype and 4 paratype slides with protargol-impregnated specimens have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Description: Size 80–125 × 30–40 µm *in vivo*, usually near 110 × 35 µm, length–width ratio 2.2–3.2, on average 2.8:1 (Table 10); flattened about 2:1 dorsoventrally. Shape fairly constant, ellipsoidal to elongate ellipsoidal with both ends broadly rounded, thus appearing



Figs 8a–g. *Oxytricha arabica* from life (a–d) and after protargol impregnation (e–g). **a**, **d** – ventral view of a representative specimen, length 110 µm. The posterior half is highly refractive and thus dark due to masses of crystals (d) and lipid droplets; **b**, **c** – when touched by the coverslip, specimens become elongate ovoid (b) and contract ellipsoidally (c) when touching an obstacle. Drawn to scale; **e**, **f** – infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen, length 110 µm. Arrow marks first postoral cirrus very close to the buccal vertex, arrowhead denotes gap in dorsal kinety 1; **g** – ciliary pattern of dorsal side of a paratype specimen with only one micronucleus. The split kinety 3 is connected by a dotted line; arrowhead marks gap in kinety 1. Note condensation of kinetids in end region of kineties 1 and 2. CC – caudal cirri, LD – lipid droplets, MA – macronucleus nodules, 1–5 – kinety numbers. Scale bars: 50 µm (a, e, f) and 30 µm (g).

very similar to large-sized specimens of *O. longa* and *Urosomoida agiliformis* (Fig. 8a).Very flexible but not contractile, oral area may swing slightly right and left; shows, however, distinct contractility in anterior body half under mild coverslip pressure, *i.e.*, becomes elongate ovoidal and contracts ellipsoidally when touching an obstacle (Figs 8b, c). Nuclear apparatus in mid-body left of midline, conspicuous because nodules only 3 µm apart on average (Table 10). Macronucleus nodules globular to broadly ellipsoidal, about 15 × 12 µm *in vivo* and protargol preparations, posterior nodule longer by 2 µm than anterior one; contain many small, globular nucleoli. Usually, a globular to broadly ellipsoidal micronucleus 4 × 3 µm in size attached to each macronucleus nodule; rarely specimens with 1 or 3 micronuclei (Figs 8a, f, g). Contractile vacuole in mid-body near left margin of cell, with short collecting canals. Cortex flexible, without specific granules. Cytoplasm colourless, but specimens appear black-white-spotted in posterior half due to masses of highly refractive crystals up to 7 µm in size among the bright food vacuoles and many lipid droplets up to 5 µm across (Figs 8a, b, d). Food vacuoles up to 15 µm in size, contain bacteria, naked amoebae, flagellates (*Polytomella*), and fungal spores (Fig. 8a). Glides rather rapidly in small arcs or straight ahead when touched by the coverslip.

Cirral pattern and number of cirri constant, pattern exactly as in *Oxytricha*. Cirri conspicuous because thick and forming distinct fringe terminally (Figs 8a, e; Table 10). Marginal cirri about 15 µm long, each composed of three ciliary rows, slightly decrease in size posteriorly, right row ends subterminally, left extends to body midline and thus frequently difficult to distinguish from caudal cirri. Frontoventral cirri thick, about 15 µm long,

Table 10. Morphometric data on *Oxytricha arabica* (OA) and *Erimophrya monostyla* (EM). Data based on mounted, protargol-impregnated (Foissner 1991, protocol A), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, $\overline{x}$ – arithmetic mean.

Characteristics	Species	$\overline{x}$	M	SD	SE	CV	Min	Max	n
Body, length	OA	98.1	97.0	9.2	2.0	9.4	82.0	116.0	21
	EM	60.8	60.0	8.6	2.5	14.1	50.0	74.0	12
Body, width	OA	35.4	35.0	4.7	1.0	13.3	30.0	45.0	21
	EM	10.0	10.0	0.7	0.2	7.4	9.0	11.0	12
Body length: width, ratio	OA	2.8	2.8	0.3	0.1	9.9	2.2	3.2	21
	EM	6.1	6.0	1.1	0.3	17.6	5.0	8.2	12
Adoral zone of membranelles, length[a]	EM	13.1	13.0	0.8	0.2	6.1	12.0	14.0	12
	OA	33.6	34.0	2.4	0.5	7.2	29.0	38.0	21
Anterior body end to paroral membrane, distance	OA	10.7	11.0	1.3	0.3	12.2	8.0	13.0	21
Anterior body end to endoral membrane, distance	OA	15.5	15.0	1.6	0.3	10.1	14.0	19.0	21
Anterior body end to last frontoventral cirrus, distance	OA	25.5	26.0	2.5	0.5	9.7	21.0	30.0	21
Anterior body end to first postoral cirrus, distance	OA	34.3	34.0	3.0	0.7	8.8	29.0	40.0	21
Anterior body end to third postoral cirrus, distance	OA	42.1	42.0	3.6	0.8	8.5	36.0	48.0	21
Anterior body end to right marginal row, distance	OA	16.6	17.0	2.9	0.6	17.6	10.0	20.0	21
Anterior end to first macronucleus nodule, distance	OA	32.6	33.0	3.8	0.8	11.7	21.0	38.0	21
Posterior end to uppermost transverse cirrus, distance	OA	10.5	11.0	1.3	0.3	11.9	8.0	12.0	21
Macronucleus nodules, distance in between	OA	3.2	3.0	1.7	0.4	53.7	1.0	7.0	21
	EM	2.3	2.0	1.7	0.5	73.7	0.0	5.0	12
Anterior macronucleus nodule, length	OA	14.0	14.0	2.1	0.5	14.8	11.0	19.0	21
	EM	11.0	10.0	1.9	0.6	17.4	9.0	15.0	12
Anterior macronucleus nodule, width	OA	11.1	11.0	1.3	0.3	11.5	9.0	13.0	21
	EM	4.0	4.0	0.7	0.2	18.5	3.0	5.0	12
Posterior macronucleus nodule, length	OA	15.0	16.0	1.8	0.4	11.4	13.0	20.0	21
Posterior macronucleus nodule, width	OA	10.8	10.0	1.3	0.3	11.7	9.0	14.0	21
Micronuclei, maximum length	OA	3.3	3.0	–	–	–	3.0	4.0	21
	EM	2.2	2.1	0.4	0.1	18.8	1.6	3.0	12
Micronuclei, width	EM	1.5	1.5	–	–	–	1.2	2.0	12
Largest membranellar base, length	OA	7.5	8.0	–	–	–	7.0	8.0	21
Adoral membranelles, number	OA	29.8	30.0	1.3	0.3	4.2	27.0	32.0	21
	EM	14.9	15.0	0.5	0.2	3.5	14.0	16.0	12
Macronucleus nodules, number	OA	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	EM	2.0	2.0	0.0	0.0	0.0	2.0	2.0	12
Micronuclei, number	OA	1.8	2.0	0.5	0.1	28.3	1.0	3.0	21
	EM	1.8	2.0	–	–	–	1.0	2.0	12
Right marginal cirri, number	OA	20.6	20.0	1.9	0.4	9.4	17.0	25.0	21
	EM	18.0	18.0	1.4	0.4	7.5	16.0	21.0	12
Left marginal cirri, number	OA	22.9	23.0	1.5	0.3	6.7	21.0	27.0	21
	EM	17.3	18.0	1.8	0.5	10.5	14.0	20.0	12
Frontal cirri, number	OA	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	EM	3.0	3.0	0.0	0.0	0.0	3.0	3.0	12
Frontoventral cirri, number	OA	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21
	EM	4.0	4.0	0.4	0.1	10.7	3.0	5.0	12
Buccal cirri, number	OA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	EM	1.0	1.0	0.0	0.0	0.0	1.0	1.0	12

Characteristics	Species	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Postoral ventral cirri, number	OA	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	EM	1.0	1.0	0.0	0.0	0.0	1.0	1.0	12
Pretransverse cirri, number	OA	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	EM	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12
Transverse cirri, number	OA	5.0	5.0	0.0	0.0	0.0	5.0	5.0	21
	EM	2.0	2.0	0.0	0.0	0.0	2.0	2.0	12
Caudal cirri, number	OA	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	EM	2.0	2.0	0.0	0.0	0.0	2.0	2.0	12
Dorsal ciliary rows, number	OA	5.0	5.0	0.0	0.0	0.0	5.0	5.0	21
	EM	4.0	4.0	0.0	0.0	0.0	4.0	4.0	12
Kinetids in dorsal kinety 1, number	OA	19.9	20.0	1.8	0.4	9.1	16.0	24.0	21
	EM	5.0	5.0	0.0	0.0	0.0	5.0	5.0	6
Kinetids in dorsal kinety 4, number	OA	7.4	7.0	1.3	0.3	16.8	5.0	10.0	21
	EM	4.0	4.0	0.0	0.0.	0.0	4.0	4.0	10
Kinetids in dorsal kinety 5, number	OA	11.6	12.0	1.5	0.3	12.7	9.0	14.0	21

[a] Measured as distance from anterior body end to proximal end of zone.

buccal cirrus at right anterior end of paroral membrane; postoral ventral cirri close together underneath buccal vertex. Transverse cirri slightly thinner than frontoventral cirri, proximal end frayed, about 20 µm long *in vivo*, near body end and thus distinctly projecting.

Adoral zone of ordinary shape and distinctness, occupies about 34% of body length, composed of 30 membranelles on average, largest bases about 8 µm wide *in vivo* and protargol preparations (Figs 8a, e; Table 10). Buccal cavity narrow, short, and flat; buccal lip angular (for terminology, see Foissner and Al-Rasheid 2006), narrow, proximal margin thickened. Paroral and endoral membrane short and staggered with paroral slightly projecting anteriorly; side by side, rarely optically intersecting at level of mid-buccal cavity; paroral cilia gradually decreasing in length from 10 µm anteriorly to 6 µm posteriorly. Pharyngeal fibres of ordinary location and length (Figs 8a, e; Table 10).

Dorsal kinety (bristle) pattern as in *O. granulifera*, type of the genus, that is, composed of five rows with rows 3 and 4 originating by a subequatorial split of row 3 (Figs 8f, g); bristles about 5 µm long *in vivo*. Kinety 1 usually with a distinct gap, one to three kinetids wide, underneath mid-body; kinetids more narrowly spaced posteriorly than anteriorly in kineties 1 and 2, an unusual feature hardly found in any other hypotrich. Caudal cirri in gap left by marginal rows, beat rapidly, comparatively thick and about 20 µm long *in vivo*.

Comparison with related species: The species mentioned in the following discussion have been monographed by Berger (1999). Thus, only the more recent literature is cited.

Oxytricha arabica has several distinct features fostering identification, at least to group level. These are the comparatively thick and long cirri, producing a conspicuous cirral fringe posteriorly; the narrowly spaced macronucleus nodules; the tight spacing of the postoral ventral cirri underneath the buccal vertex; the 4–5 µm long dorsal bristles (3 µm in most congeners); and the moderate size (~100 µm). However, these features are found also in the following species (main distinguishing characteristics in parentheses): *O. longa* (4 *vs.* 5 transverse cirri, 2 *vs.* 3 caudal cirri), *O. quadricirrata* (special cortical granules present *vs.* absent; 4 *vs.* 5 transverse cirri), *O. minor* (poorly described; length–width ratio 4–6:1 *vs.* about 3:1), *O. similis* (2 *vs.* 3 caudal cirri) and *O. lanceolata*. The last mentioned species matches *O. arabica* in almost all features, except for the dorsal bristle pattern (Figs 8f, g): kinety 3 continuous *vs.* split subequatorially, as in the type species of *Oxytricha*; kinety 1 continuous *vs.* with subequatorial gap; kinetids of rows 1 and 2 ordinarily *vs.* narrowly spaced in posterior region. Of these characteristics, the split of kinety 3 is the most distinct and important feature because it is ontogenetically fixed and thus used to distinguish species. To be sure, we checked the protargol slides of the three *O. lanceolata* populations described by Foissner and Berger (1987, 1989) and Foissner (1996). We confirm that the descriptions are correct, *i.e.*, that the three specific features of *O. arabica* are absent from *O. lanceolata*.

The species mentioned above are difficult to distinguish *in vivo*, and thus identifications should be checked in protargol preparations. Possibly, the biogeographic pattern might be useful: while *O. arabica* is rare and probably restricted to a certain area (North Africa?), *O. lanceolata* is a cosmopolitan occurring, inter alia, in Austria, Japan, Madeira and Antarctica (Foissner 1998, Berger 1999).

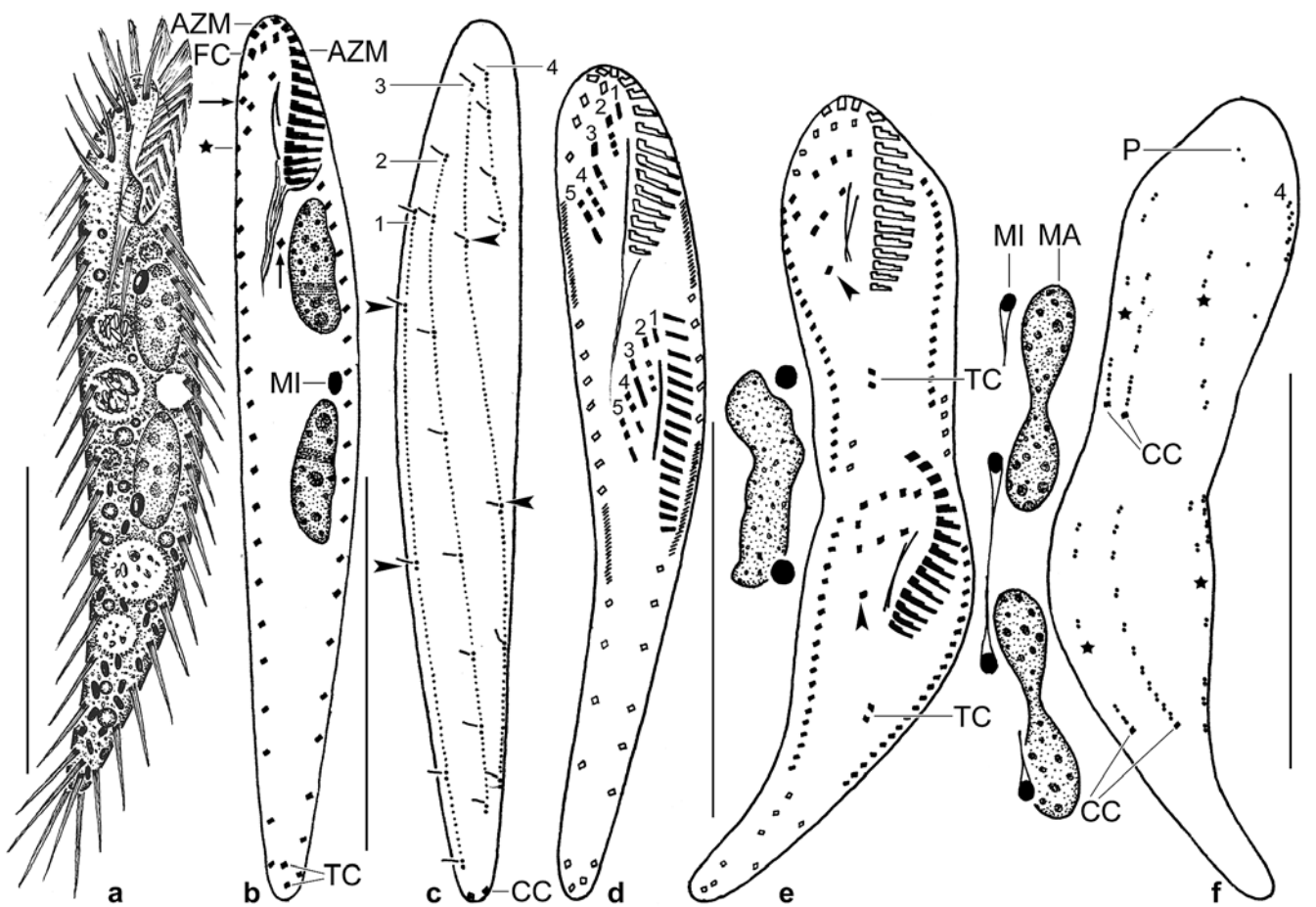
Erimophrya monostyla nov. spec. (Figs 9a–f; Table 10)

Diagnosis: Size about 70 × 12 µm *in vivo*; slenderly pisciform. On average 2 almost abutting, elongate ellipsoidal macronucleus nodules, 15 adoral membranelles, 18 cirri each in right and left marginal row, 1 postoral ventral cirrus, 2 transverse and caudal cirri, and 4 dorsal kineties with an average of 5 almost equidistantly spaced kinetids in kinety 1.

Type locality: Soil from Tenerife, southwest coast of Candelaria, 28° N 17° W.

Etymology: Composite of the Greek numeral *mono* (single) and the Latin noun *stylo* (style, process), referring to the single postoral ventral cirrus, a main feature of the species.

Type material: 1 holotype and 2 paratype slides with protargol-impregnated morphostatic and dividing specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.



Figs 9a–f. *Erimophrya monostyla* from life (a) and after protargol impregnation (b–f). **a** – ventral view of a representative specimen, length 70 µm; **b**, **c** – ventral and dorsal view of holotype specimen, length 72 µm. Arrows mark the single postoral cirrus and frontoventral cirri III/2 and IV/3, which are close together. Asterisk denotes begin of right marginal row. Arrowheads delimit gaps in dorsal bristle rows 1 and 3. Note that this specimen has only one micronucleus; **d** – cirral pattern and nuclear apparatus of an early divider, showing that only five (numerals) fronto-ventral--transverse cirral anlagen streaks are produced; **e**, **f** – ventral and dorsal view of a late divider, showing that two transverse and two caudal cirri are generated. Arrowheads mark the postoral cirrus, which is migrating posteriorly. Asterisks mark gaps in dorsal kineties 1 and 3 (cp. Fig. 9c). Dorsal bristle row 4 originates close to the right row of marginal cirri. The macronucleus nodules divide a second time. Parental structures shown by contour, newly formed shaded black. AZM – adoral zone of membranelles, CC – caudal cirri, FC – frontal cirri, MA – macronucleus nodule, MI – micronucleus, P – parental dorsal bristles, TC – transverse cirri, 1–4 – dorsal bristle rows, 1–5 – cirral anlagen streaks. Scale bars: 30 µm.

Description: Size 55–80 × 10–14 µm *in vivo*, usually near 70 × 12 µm; length–width ratio comparatively constant, *i.e.*, 5–8:1, on average 6:1 in protargol preparations; very flexible but not contractile (Table 10). Shape fairly constant, usually slenderly oblanceolate and slightly sigmoidal, that is, pisciform and widest in mid-body, gradually narrowing posteriorly with narrowly rounded or acute end; hardly flattened dorsoventrally, but sometimes slightly twisted about main body axis (Figs 9a, b). Nuclear apparatus slightly above middle body third between midline and left body margin. Macronucleus nodules ellipsoidal (2:1) to very elongate ellipsoidal (5:1), on average near 3:1 and only 2 µm apart; contain many small and some middle-sized nucleoli. On average two broadly ellipsoidal micronuclei, one each attached to macronucleus nodules in variable positions (Figs 9a, b). Contractile vacuole slightly above mid-body at left cell margin. No specific cortical granules. Cytoplasm colourless, with some lipid droplets and many 1–2 µm long, cylindroid crystals in posterior body third, which thus appears dark under low magnification (≤ × 100). Food vacuoles 4–8 µm across, contain bacteria and heterotrophic flagellates. Moves rather slowly on microscope slide and between soil particles, showing great flexibility.

Cirral pattern rather constant, number of cirri of usual variability (Figs 9a, b; Table 10). Most cirri about 8 µm long *in vivo* and rather fine; transverse and caudal cirri about 10 µm long and V-like spread *in vivo*. Right marginal row begins underneath last frontoventral cirrus and ends subterminally; distances between individual cirri increase slightly from anterior to posterior in both right and left marginal row. Frontal cirri of about same length as other cirri, form an oblique, subapical row. Buccal cirrus right of anterior end of paroral membrane. Frontoventral cirri near right body margin, first cirrus at level of buccal cirrus, cirrus IV/3 close to cirrus III/2, a special pattern found also in *E. quadrinucleata*. A single postoral cirrus far underneath buccal vertex. Two transverse cirri one after the other near body end and thus difficult to distinguish from marginal and caudal cirri, both *in vivo* and protargol preparations (Figs 9a, b). Dorsal bristles about 2 µm long *in vivo* and widely spaced, arranged in four rows (Fig. 9c; Table 10): row 1 distinctly shortened anteriorly commencing at level of buccal vertex, with conspicuous, one-kinetid-wide gap in mid-body; row 2 commences far subapically and ends subterminally; row 3 commences subapically and ends far subterminally, with conspicuous, one-kinetid-wide gap above mid-body; row 4 composed of only four kinetids extending in anterior body fifth close to right body margin. Two caudal cirri at posterior body end.

Oral apparatus inconspicuous because adoral zone occupies only 20–23% of body length, of usual shape and structure; consists of an average of 15 membranelles, bases of largest membranelles about 4 µm wide *in vivo*. Buccal cavity narrow and flat; buccal lip angularly projecting and thus prominent partially covering proximal third of adoral zone, bears paroral membrane. Both undulating membranes slightly curved and almost in parallel, paroral begins about 2 µm in front of endoral at level of buccal cirrus; exact structure of membranes not clearly recognizable. Pharyngeal fibres distinct *in vivo* and protargol preparations, of ordinary length and structure, extend obliquely backwards (Figs 9a, b; Table 10).

Ontogenesis: Some key ontogenetic stages were found, showing (i) five fronto-ventral-transverse cirral anlagen streaks (Fig. 9d); (ii) two transverse cirri (Fig. 9e); and (iii) two caudal cirri one each developing in dorsal kineties 1 and 2 (Fig. 9f).

Occurrence and ecology: At Tenerife, *E. monostyla* occurred in a sandy, greyish, meagre, non-saline coastal soil with pH 8.2 in water (sample kindly collected by Dr. B. Krassnigg, Salzburg University). In Saudi Arabia, this species was found at sites 1, 2 and 6, that is, in a wide variety of habitats, including saline oasis soil (see site descriptions). Thus, *E. monostyla* has a wide ecological range, possibly preferring sandy, meagre soils in hot areas. With its slender and flexible body, *E. monostyla* is perfectly adapted to the soil habitat.

Comparison with related species: The genus *Erimophrya* was established by Foissner *et al*. (2202) for *Urosomoida* – like oxytrichids with only five frontoventral-transverse cirral anlagen streaks. The Saudi Arabian and Tenerife populations match this specific feature (Figs 9d, e).

Of the four described *Erimophrya* species, *E. monostyla* is most similar to *E. arenicola* which has also only one postoral cirrus (Figs 9b, e). However, *E. arenicola* has only a single (*vs.* two) transverse cirrus, only 3 (*vs.* 4) dorsal kineties, and the kinetid pattern in dorsal kinety 1 and the arrangement of the frontoventral cirri are different; the latter is rather similar to that found in *E. quadrinucleata*. As mentioned above, *Erimophrya* species are difficult to identify *in vivo*; thus, identifications should be checked in protargol preparations.

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