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Two new "flagship" ciliates (Protozoa, Ciliophora) from Venezuela: *Sleighophrys pustulata* and *Luporinophrys micelae*

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Abstract

Sleighophrys pustulata nov. gen., nov. spec. and *Luporinophrys micelae* nov. gen., nov. spec. were discovered in a slightly saline mud and soil sample from some flat, dry puddles in the Maracay National Park on the north coast of Venezuela. Their morphology was studied in vivo, in protargol preparations, and in the scanning electron microscope. The new genera are monotypic and belong to the trachelophyllid haptorids. They are characterized by the unique shape of the epicortical scales (lepidosomes). *Sleighophrys pustulata*, which has a size of about 180 × 23 μm, possesses type I and unique type V lepidosomes which are hat-shaped and about 7 × 7 μm in size. *Luporinophrys micelae*, which has a size of about 200 × 35 μm, possesses types I, II, and unique type VI lepidosomes which are narrow, about 10 μm high cones composed of fibrous stripes connected by polygonal meshes. The conspicuous body size and the richly structured, comparatively large lepidosomes make *S. pustulata* and *L. micelae* biogeographic flagships which may help to cast some light on the pending question whether or not microorganisms have biogeographies. The available data suggest that both species have a restricted geographic distribution, not only because they were not described previously, but mainly because they were absent in about 2000 freshwater samples from central Europe and in about 1000 soil samples collected globally.

Keywords: Haptorida; Lepidosomes; Maracay National Park; Protist biogeography; Soil ciliates; Trachelophyllina

Introduction

Endemicity is difficult to prove in microscopic organisms because (i) they are not easily recognizable; (ii) many species are dormant (encysted) most of their life; (iii) distinctive morphological features are rare, as compared to higher plants and animals; (iv) the field is distinctly undersearched, and (v) differences may remain unrecognized or misclassified as "site variations" due to the use of holarctic identification literature for species from other biogeographical regions (Foissner 2004). In this situation, eyecatching "flagships" with conspicuous size and/or morphology are the best distribution indicators. Many such species have been described (for a review, see Foissner 2004), but others remain to be discovered, showing our ignorance about even conspicuous taxa (Foissner et al. 2003). The two species described here are just other examples for this situation and support my hypothesis that we know mainly the more abundant and/or widely distributed protist species (Foissner 2004).

Sleighophrys pustulata and *Luporinophrys micelae* belong to an assemblage of free-living ciliates with a

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mucilaginous cortex cover; taxonomically, they are haptorid trachelophyllids, which are part of the time-honoured Gymnostomatea, now often called Litostomatea (Corliss 1979; Lynn 2003). Several such species were already described by Stokes (1884) and Kahl (1930), but it was only in 1984 that Nicholls and Lynn investigated a "slimy" species with the electron microscope. This showed the mucilaginous layer to be composed of minute, organic scales, which are now termed lepidosomes (Foissner et al. 2005). More recently, Foissner et al. (2002) described several new trachelophyllids, showing a considerable diversity of the lepidosomes. However, the individual lepidosomes of these species are difficult to recognize because they are $\leqslant 3\,\mu m$ in size. In contrast, the lepidosomes of *S. pustulata* and *L. micelae* have a size of $\geqslant 5\,\mu m$ and many fine details useable as biogeographic markers. Accordingly, they will be documented in great detail, allowing a meticulous comparison if they ever should be found in another biogeographic region.

Material and methods, terminology

Sleighophrys pustulata and *L. micelae* were discovered west of the Venezuelan capital Caracas, that is, in the Maracay National Park, about 13 km inshore from the north coast, where some Flamingo lakes surround the village of Chichiriviche, W67°13′N11°33′. This area, which is used as a cattle pasture and occasionally burnt, contains countless flat depressions which become small puddles after heavy rains. The sample, which was taken in May 1997, consisted of dry cyanobacterial and algal crusts, mud with plant litter, and loamy soil from the upper 2 cm of some very flat, dry puddles covered with grass and halophytes. The material, which was slightly saline (4‰) and had pH 6 in water, was air-dried for 3 weeks and then stored in a plastic bag. In the laboratory, the dry sample was rewetted in July 2000 to obtain a "non-flooded Petri dish" culture (Foissner et al. 2002).

Field material as obtained with the non-flooded Petri dish method was used for all investigations because several culture attempts failed. Living cells were studied using a high-power oil immersion objective, phase contrast, and differential interference contrast. Protargol impregnation and scanning electron microscopy (SEM) were performed as described by Foissner (1991).

Counts and measurements on silvered specimens were performed at a magnification of $\times 1000$. In vivo measurements were conducted at magnifications of $\times 40$–1000. Drawings of live specimens were based on free-hand sketches and micrographs; those of impregnated cells were made with a drawing device.

Terminology is according to Corliss (1979) and Foissner et al. (2002). The epicortical scales, now termed lepidosomes (Foissner et al. 2005), were classified into "shape types" by Foissner et al. (2002). Several types may occur in a single species, and if new types are discovered, they can be added to the "type system" without problems. All known types are shown in Fig. 82. Morphometry of the lepidosomes was performed on SEM micrographs. As the lepidosomes of these species are complex, the features measured are shown in Fig. 1. Note that cells and structures shrink by 40–60% in SEM preparations.

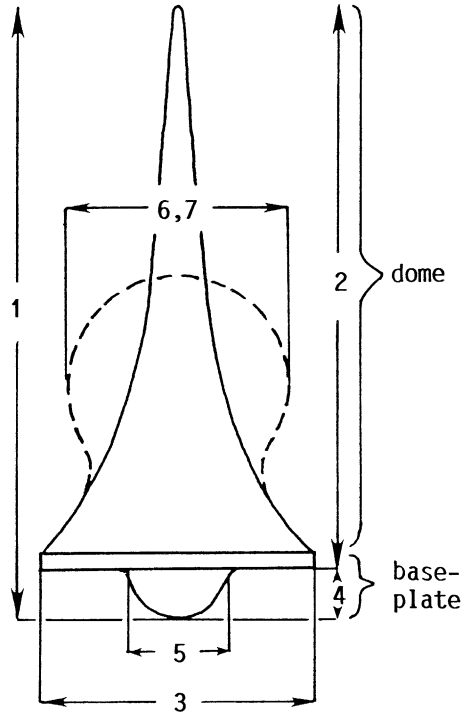


Fig. 1. Terminology and characteristics measured (numerals) in types V and VI lepidosomes of *S. pustulata* and *L. micelae* (see Table 1).

Results

Genus *Sleighophrys* nov. gen

Diagnosis: Trachelophyllidae Kent, 1881 with types I and V lepidosomes. Type I lepidosomes as diagnosed by Foissner et al. (2002). Type V lepidosomes upon a layer of type I lepidosomes, conspicuously hat-shaped, composed of a finely perforated, dish-shaped baseplate from which the coarsely and polygonally faceted, hemispherical dome emerges.

Type species: *S. pustulata* nov. spec.

Dedication: I dedicate this genus to Prof. Dr. Michael Sleigh (Southampton University), acknowledging his unforgettable protistological achievements and the excellent job he is doing as Managing Editor of the

European Journal of Protistology. The name is a composite of Sleigh and the Greek noun *ophrỳs* (eyebrow ~cilia ~ciliate) and has feminine gender.

Description of *Sleighophrys pustulata* nov. spec. (Figs. 2–43; Table 1)

Diagnosis: size about 180 × 23 μm in vivo, contractile; slenderly amphoriform. Two ellipsoidal, widely distant macronucleus nodules with a micronucleus each. Two types of oral bulge extrusomes: type 1 acicular, 12–16 μm long; type 2 rod-shaped, 2.5 μm long. On average 12 ciliary rows. Type I lepidosomes about 1.6 × 0.9 μm in SEM preparations, dome composed of an average of 16 polygons; type V lepidosomes about 7 × 7 μm in vivo (2.3 × 2.3 μm in SEM preparations), baseplate with distinct central convexity, distal dome surface thickened and finely faceted

Type locality: slightly saline surface mud and soil from temporary grassland puddles in the surroundings of the village of Chichiriviche, Maracay National Park, about 13 km inshore from the north coast of Venezuela, W67°13′N11°33′.

Type specimens: one holotype slide and two paratype slides with protargol-impregnated 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.

Etymology: *pustulata* refers to the pustular appearance of the species, especially in the scanning electron microscope.

Description: size of extended and/or slightly contracted specimens in vivo 160–230 × 15–40 μm (x̄ 185, M 180, SD 21.1, CV 11.4; x̄ 24.3, M 22.5, SD 8.0, CV 33.0; n 12), with a length:width ratio of 4.5–13.3:1 (x̄ 8.3, M 8.4, SD 2.6, CV 30.8; n 12); distinctly stouter in protargol preparations, likely due to some contraction and shrinkage: 152 × 28 μm, length:width ratio 5.7, that is, a change by 31% (Table 1)! Slenderly amphoriform to fusiform, middle third occasionally slightly narrowed, neck rounded and inconspicuously widened anteriorly gradually merging into broadened, fusiform trunk; up to 2:1 flattened dorsoventrally. Anterior end rather conspicuous due to the pin-shaped oral bulge, posterior narrowly rounded or tapered (Figs. 2, 9, 14, 15, 22, 25). Cells very flexible and contractile by up to 30%, fully contracted specimens bottle-shaped (Figs. 7, 8, 13); contracts and extends slowly, exact body shape and size thus difficult to determine. Nuclear apparatus in middle third of cell, that is, in trunk region (Figs. 2, 14, 23). Macronucleus nodules globular to ellipsoidal, on average broadly ellipsoidal, usually distinctly apart and never connected by a fine strand, stand out as bright blisters from granular cytoplasm. Usually, a globular to ellipsoidal micronucleus attached to each macronucleus nodule; rarely specimens occur without, with one, or with three micronuclei (Table 1). Contractile vacuole in posterior end, with single excretory pore in pole centre (Figs. 9 and 14). Cytopyge near contractile vacuole, faecal mass irregular and slimy (Fig. 7). Two types of extrusomes, not impregnating with the protargol method used, attached to oral bulge: type 1 conspicuous because acicular and 12–16 × 0.9–1.2 μm in size (x̄ 13.9, M 14, SD 1.1, CV 8.2; n 11); becomes club-shaped and up to 40 μm long when exploded (Figs. 2, 5, 6, 15, 26); type 2 extrusomes inconspicuous because only about 2.5 μm long and fine (Figs. 4 and 15). Cytoplasm colourless and usually turbid by globular and irregular lipid droplets 1–15 μm across, often a large defecation vacuole with food remnants above contractile vacuole. Mainly feeds on *Halteria grandinella*, but also on *Gonostomum affine* and the heterotrophic flagellate *Peranema* (Figs. 2, 3, 22, 23). Glides slowly on microscope slide and swims with rotation about main body axis.

Cortex thin and flexible, contains rows of pale granules < 0.5 μm across; covered by an up to 8 μm thick, mucilaginous layer of lepidosomes producing pustulate body margin in both in vivo and protargol preparations (Figs. 2, 3, 14, 17, 23, 29, 43) as well as in the scanning electron microscope (Fig. 25). Mucilaginous layer composed of two types of lepidosomes lying one upon the other. Individual lepidosomes elastic, that is, do not split when squashed by coverslip pressure (Figs. 28 and 29), become deformed even in fixed condition, viz., when contacting glue adhering cells to SEM stub; do not or only slowly dissolve when removed from cell (Figs. 29 and 30); impregnate more or less intensely with protargol (Fig. 43); specific structures anchoring lepidosomes to cell surface or lepidosome layer not recognizable.

Type I lepidosomes in two layers on body surface, except for oral bulge, tightly and irregularly spaced, usually difficult to recognize in both in vivo and SEM preparations because small, hyaline, and covered by type V lepidosomes; basic structure as described in Foissner et al. (2002); on average 1.6 × 0.9 μm in scanning preparations, dome slightly to hemispherically vaulted, composed of 16 large polygons on average (Figs. 3, 19, 26, 38, 41, 42; Table 1). Type V lepidosomes form single layer upon type I lepidosomes and detach easily, usually rare in distal third of neck, about 7 × 7 μm in vivo (2.3 × 2.3 μm in SEM preparations) and thus well recognizable in the light microscope; complex and beautiful, hat- to cupping glass-shaped when fully developed, baseplate margin thin performing undulating movements in strong water currents produced by beating cilia (Figs. 2, 3, 12, 14, 17, 20, 21, 23, 24, 28–30; Table 1). Baseplate circular to broadly elliptical, rarely fusiform, central third cup-like protruding; composed of minute, hexagonal meshes forming

honeycombed pattern; margin upright and usually more or less distinctly curved, composed of a single row of minute, rectangular meshes. Dome hemispherical and circular to slightly elliptical in transverse view, causes pustulate appearance of mucilage, distal surface thickened and perforated by minute, hexagonal openings gradually increasing to large, polygonal meshes proximally attached to baseplate margin (Figs. 20, 21, 24, 25, 27, 31–36, 39, 40; Table 1). Likely, type V lepidosomes develop from type I lepidosomes because many transition stages can be found, for instance, type I-like scales with some narrow central meshes and type V-like lepidosomes with a small, hill-shaped dome (Figs. 27, 37–40).

Cilia about 13 μm long in vivo, beat only in that portion which projects from mucilaginous layer, widely (about 6 μm) and unevenly spaced because ciliated kinetids irregularly alternate with slightly smaller, bare granules (Figs. 2 and 14; Table 1). Basal body-associated fibre system as described in *L. micelae* below. On average 12 meridional, equidistant ciliary rows about 5 μm apart from each other, three of them differentiated to inconspicuous dorsal brush anteriorly (Figs. 14, 16, 18; Table 1). Brush rows 1 and 2 dikinetidal and of similar length and structure, that is, anterior bristle of dikinetids slightly longer (2.5–3 μm) than posterior (2 μm); followed by some 1–1.5 μm long monokinetidal bristles, and then continue as ordinary somatic ciliary rows to posterior end of cell. Row 3 monokinetidal, extends to at least mid-body, main portion composed of about 5 μm long, rod-shaped bristles, at anterior end some 8 μm long and very narrowly spaced bristles recognizable also in SEM micrographs because slightly projecting from lepidosome layer (Fig. 26).

Oral bulge rather conspicuous because distinctly apart from body proper and refractive due to the extrusomes within; pin-shaped, about 4 × 1.5–2 μm in size, becomes conical under slight coverslip pressure and in preparations, usually not covered by lepidosomes, proximal half impregnates darker than distal (Figs. 2, 9, 13, 16, 22, 26; Table 1). Circumoral kinety composed of about 10 dikinetids having only the right basal body ciliated; gives rise to fine nematodesmata forming inconspicuous, slightly funnel-shaped oral basket (Figs. 16 and 17).

Occurrence and ecology: *S. pustulata* and *L. micelae* were discovered in a very rich sample that contained at least 80 ciliate species, several of which were undescribed. Whether they prefer limnetic or terrestrial environments is not known because of the specific habitat in which they were found. No other records of these species are known to me (see discussion); they did not even occur in a further sample from this area, where *Apofrontonia lametschwandtneri*, another flagship species was discovered (Foissner and Song 2002).

Sleighophrys pustulata and *L. micelae* occurred together with three other trachelophyllids, viz., *Bilamellophrya hawaiiensis*, *Spetazoon australiense*, and an *Enchelys vestita*-like ciliate. Unfortunately, these species were too rare to be checked with the scanning electron microscope, leaving considerable doubts about the identification. *Sleighophrys pustulata* and *L. micelae* were abundant in the non-flooded Petri dish culture six days after rewetting of the sample. Pure culture trials failed.

Both species prefer *H. grandinella* as a prey. This is surprising because they are slow mud inhabitants, while *H. grandinella* is mainly planktonic and can swim and jump very fast (Foissner et al. 1991).

Genus *Luporinophrys* nov. gen.

Diagnosis: Trachelophyllidae Kent, 1881 with types I, II, and VI lepidosomes. Types I and II lepidosomes as diagnosed by Foissner et al. (2002). Type VI lepidosomes scattered between type II lepidosomes, nail-shaped and higher than 5 μm in vivo; composed of a finely perforated, dish-shaped baseplate associated with a long, narrow cone consisting of fibrous stripes connected by polygonal meshes.

Type species: *L. micelae* nov. spec.

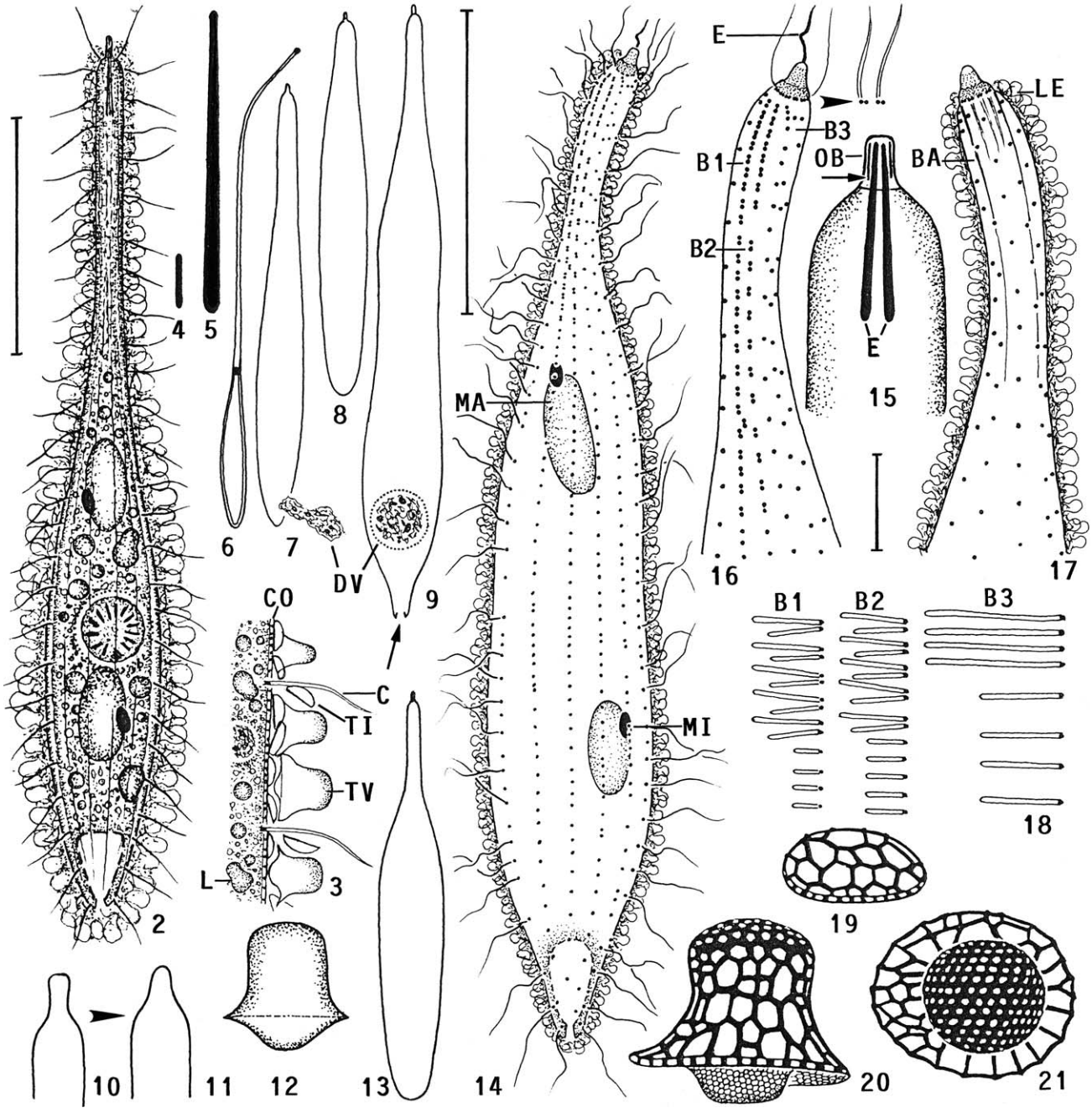
Dedication: I dedicate this genus to Prof. Dr. Pierangelo Luporini (Camerino University, Italy), acknowledging his excellent research on ciliates over many years and his efforts in organizing, together with his wife (see below), the Fourth European Congress of Protistology in August–September 2003. The name is a composite of *Luporini* and the Greek noun *ophrỳs* (eyebrow ~cilia ~ciliate) and has feminine gender.

Description of *Luporinophrys micelae* nov. spec. (Figs. 44–81; Table 1)

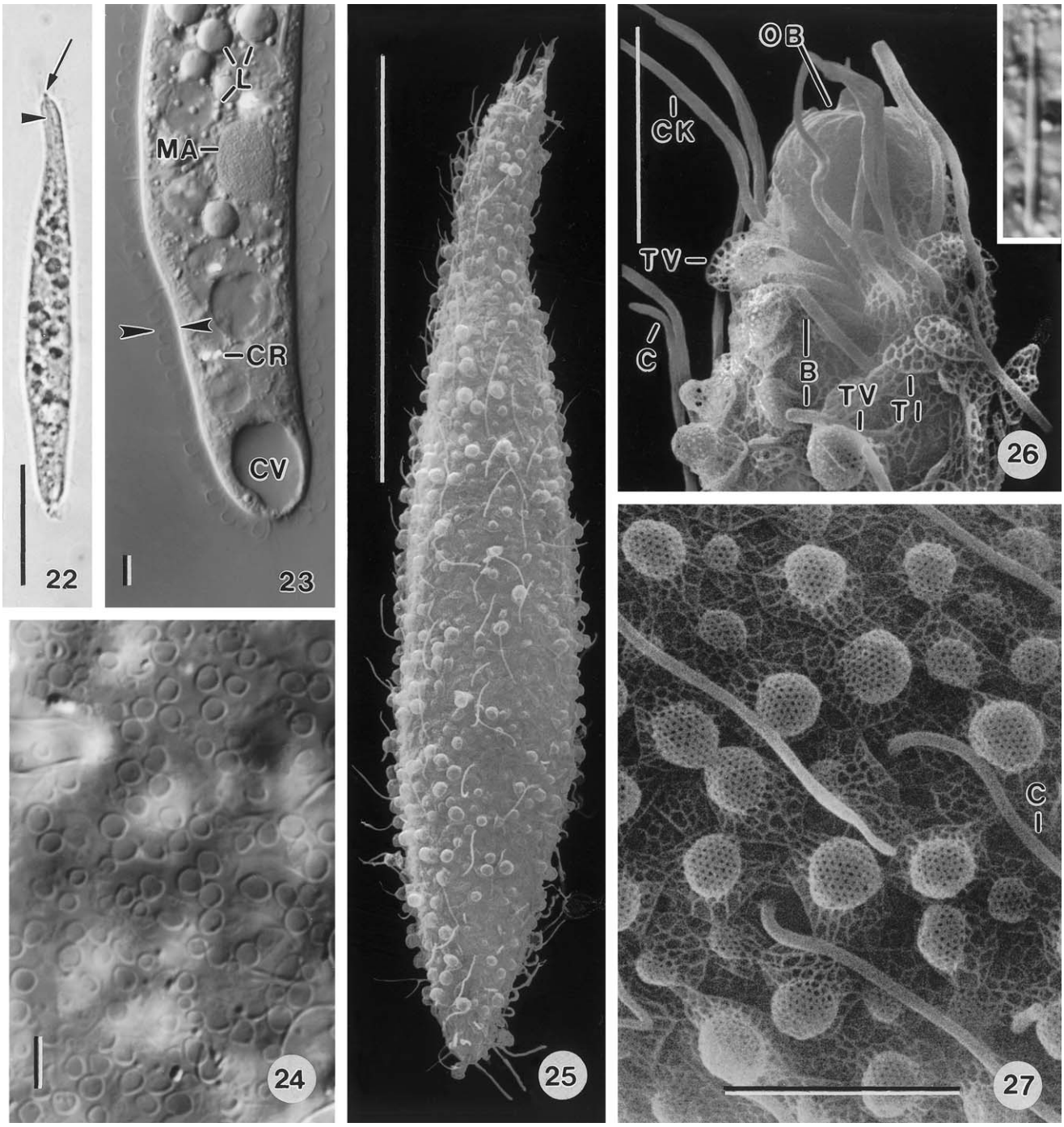
Diagnosis: size about 200 × 35 μm in vivo, contractile; slenderly amphoriform. Two ellipsoidal, widely distant macronucleus nodules with a micronucleus each. Two types of oral bulge extrusomes: type 1 acicular, about 23 × 0.6 μm in size; type 2 rod-shaped, 3 μm long. On average 21 ciliary rows. Type I lepidosomes on average 1.4 × 0.9 μm in SEM preparations, dome composed of an average of 10 polygons; type II lepidosomes on average 2.1 × 1.8 × 2 μm in SEM preparations (about 4 × 3 × 4 μm in vivo), drawing-pin shaped; type VI lepidosomes about 10 × 5 μm in vivo (4.7 × 2.1 μm in SEM preparations), baseplate with distinct central convexity.

Type locality: slightly saline surface mud and soil from temporary grassland puddles in the surroundings of the village of Chichiriviche, Maracay National Park, about 13 km inshore from the north coast of Venezuela, W67°13′N11°33′.

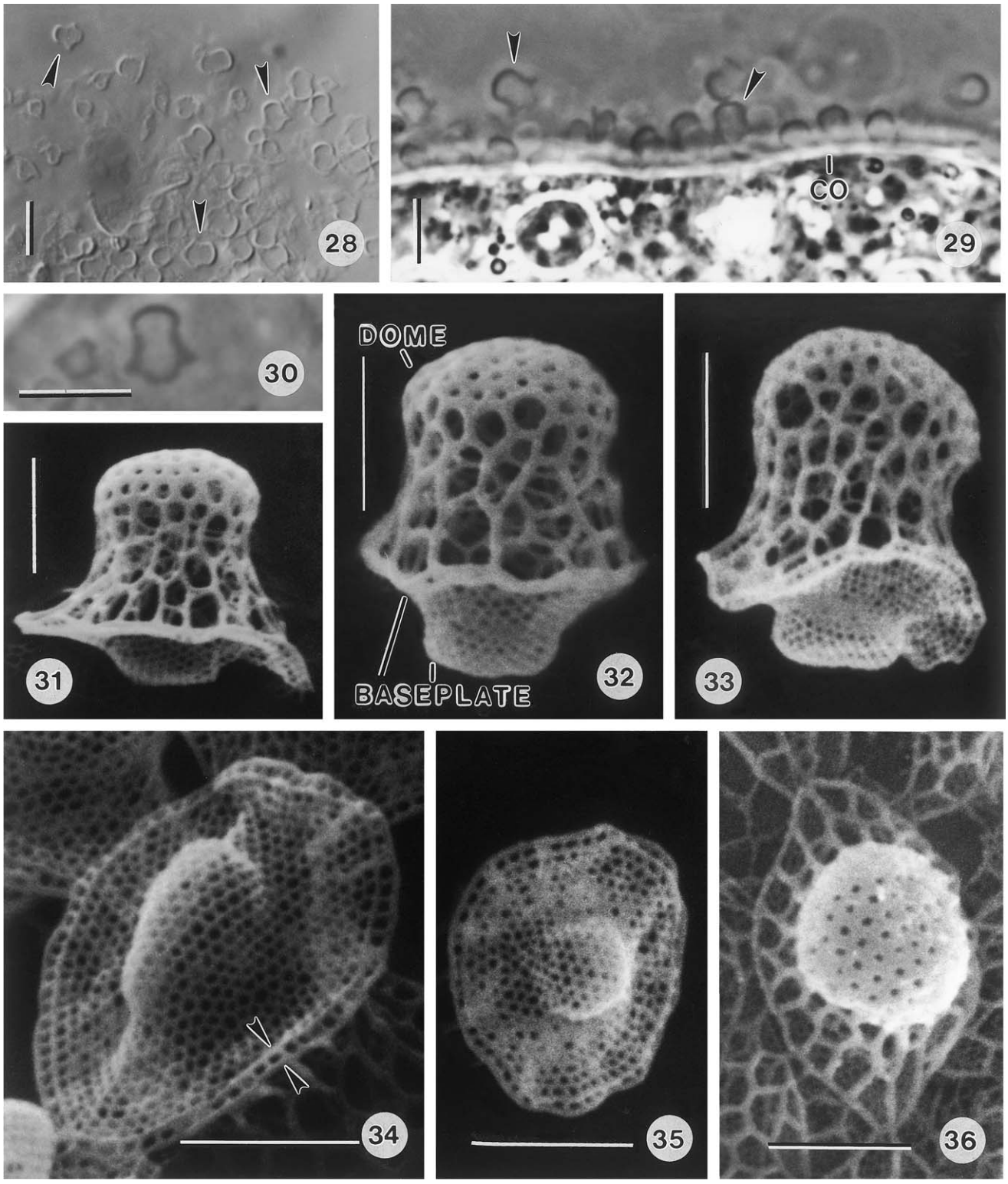
Type specimens: one holotype slide and three paratype slides with protargol-impregnated specimens have been



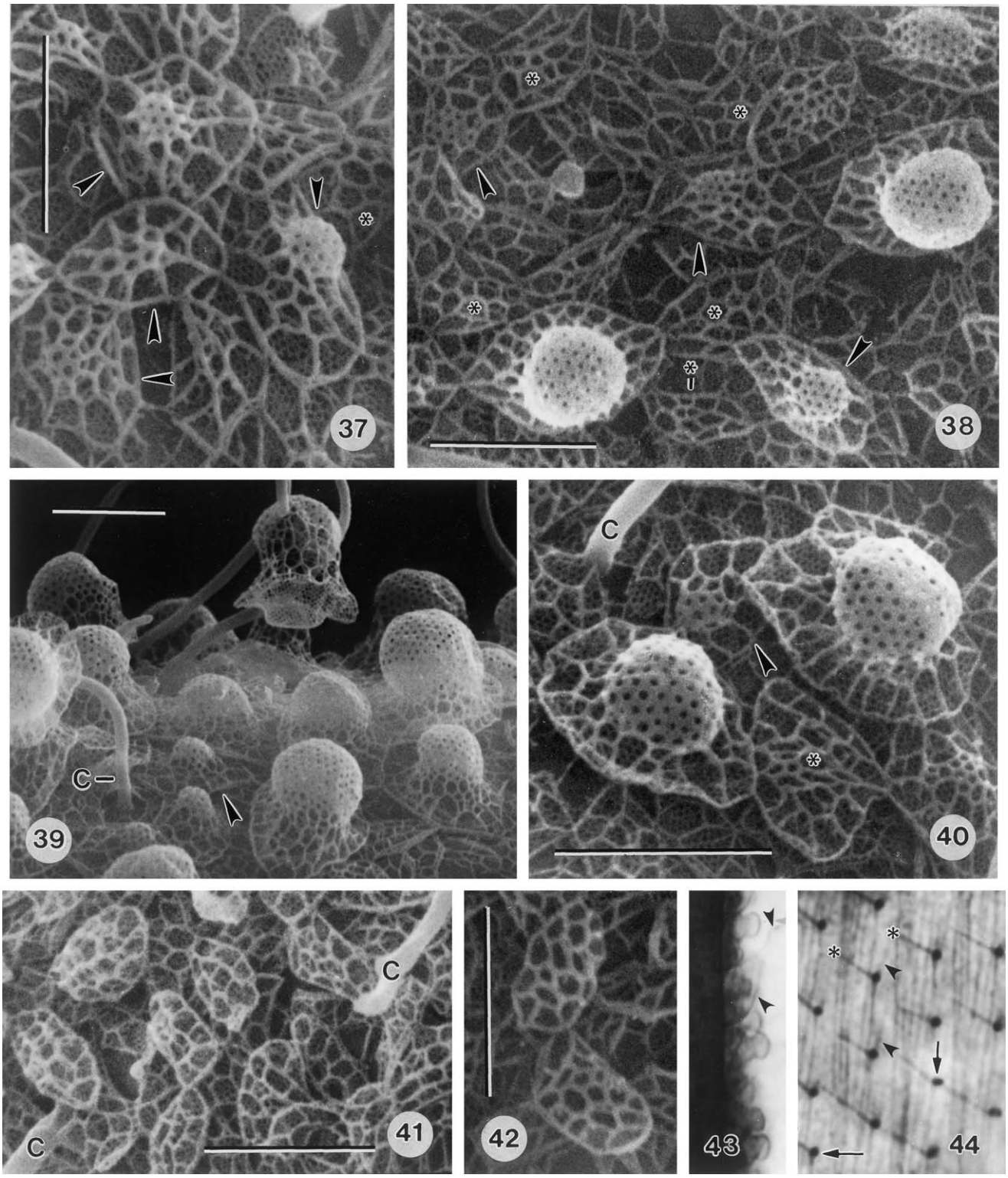
Figs. 2–21. *Sleighophrys pustulata* from life (2–13, 15, 18), after protargol impregnation (14, 16, 17), and in the SEM (19–21). **2**: Ventral view of a representative specimen, length 185 μm. A just ingested *H. grandinella* is shown in mid-body. **3**: Optical section of cortex. **4**: Type 2 oral bulge extrusome, length 2.5 μm. **5, 6**: Resting (15 μm) and exploded (40 μm) type 1 oral bulge extrusome. **7**: A defecating specimen. **8, 13**: Slightly and strongly contracted specimens. **9**: Outline of a frequent shape variant. Arrow marks excretory pore. **10, 11**: The pin-shaped oral bulge becomes conical in slightly disturbed specimens. **12**: Type V lepidosomes are 7 μm high and thus well recognizable in the light microscope. **14, 16, 17**: Dorsal (14, 16) and ventral (17) view of ciliary pattern and nuclear apparatus of holotype specimen, length 170 μm. **15**: Anterior body portion. The fine, short type 2 extrusomes (arrow) are difficult to recognize. **18**: Posterior region of dorsal brush; slightly schematized. Bristles up to 8 μm long and drawn to scale. **19**: Oblique surface view of a type I lepidosome, length 1.6 μm in the SEM. **20, 21**: Side and surface view of the hat-shaped type V lepidosomes, height 2.3 μm in the SEM. B1-3—dorsal brush rows, BA—oral basket, C—somatic cilium, CO—cortex, DV—defecation vacuole, E—extrusomes, L—lipid droplet, LE—lepidosome layer, MA—macronucleus nodule, MI—micronucleus, OB—oral bulge, TI, TV—types I and V lepidosomes. Scale bars 50 μm (2, 14) and 10 μm (16, 17).



Figs. 22–27. *Sleighophrys pustulata* from life (22–24, inset in 26) and in the SEM (25–27). **22**: A freely motile, slightly contracted specimen with many food inclusions. The arrow denotes the pin-shaped oral bulge containing the anterior end of the extrusome bundle (arrowhead). **23**: Posterior body portion with lepidosome layer marked by arrowheads. **24, 27**: Surface views showing the cell covered with type V lepidosomes, the domes of which appear as ring-shaped structures in optical section. **25**: Overview showing the pustulate appearance of *S. pustulata* due to the type V lepidosomes. The specimen is rather distinctly contracted and strongly shrunken due to the preparation procedures. **26**: Dorsal view of anterior body end at high magnification. The inset shows a 15 μm long, acicular type 1 extrusome. B—dorsal brush bristles, C—ordinary somatic cilia, CK—cilia of circumoral kinety, CR—crystals, CV—contractile vacuole, L—lipid droplets, MA—macronucleus nodule, OB—oral bulge, TI, TV—types I and V lepidosomes. Scale bars 50 μm (22, 25), 10 μm (23, 24), 5 μm (26, 27).



Figs. 28–36. *Sleighophrys pustulata*, type V lepidosomes from life (28–30) and in the scanning electron microscope (31–36). **28–30**: The lepidosomes have a height of about 7 μm. Thus, their hat-like shape (arrowheads) can be easily recognized in the interference (28, 30) and phase contrast (29) microscope. **31–33**: Side views. **34, 35**: Baseplate views. The baseplate is hexagonally faceted, convex in the centre, and the upright margin consists of slightly larger, rectangular meshes (arrowheads). Accordingly, the ''plate'' is a ''dish''. **36**: Dome view of a lepidosome with fusiform baseplate. CO—cortex. Scale bars 10 μm (28–30) and 1 μm (31–36). Note that the lepidosomes are shrunken by about 50% in the SEM preparations.



Figs. 37–44. *Sleighophrys pustulata*, lepidosomes in the SEM (37–42) and after protargol impregnation (43). **37–40**: Incompletely (arrowheads) and fully developed type V lepidosomes. Asterisks mark type I lepidosomes, which are often difficult to distinguish from incompletely developed type V lepidosomes (arrowheads). **41, 42**: Type I lepidosomes cover the cell in two layers. **43**: Optical section showing impregnated type V lepidosomes. Arrowheads mark cilia. **44**: Cortical fibre system of *L. micelae*. Arrows mark basal bodies. Arrowheads denote an anteriorly extending fibre. Asterisks mark interkinetal fibres. C—somatic cilia. Scale bars 2 μm.

Table 1. Morphometric data on *Sleighophrys pustulata* (upper line) and *Luporinophrys micelae* (lower line)

Characteristics[a]	x̄	M	SD	SE	CV	Min	Max	*n*
Body, length	152.3	150.0	24.3	5.3	15.9	120.0	207.0	21
	160.2	158.0	24.3	5.6	15.2	125.0	215.0	19
Body, width (without lepidosome layer)	27.8	28.0	4.3	1.0	15.6	20.0	35.0	21
	35.9	35.0	8.3	1.9	23.2	21.0	56.0	19
Body length:width, ratio	5.7	5.6	1.4	0.3	24.7	3.4	8.6	21
	4.7	4.4	1.2	0.3	26.2	3.2	6.9	19
Oral bulge, height (distal end to circumoral kinety)	3.8	4.0	0.7	0.2	17.7	2.5	5.0	21
	4.4	4.5	0.5	0.1	10.2	4.0	5.0	19
Oral bulge, width at circumoral kinety	4.4	4.5	0.4	0.1	9.2	4.0	5.0	21
	6.7	7.0	1.3	0.3	19.3	5.0	9.0	19
Anterior body end to first macronucleus nodule, distance	48.4	50.0	11.0	2.4	22.7	25.0	65.0	21
	63.3	61.0	12.4	2.9	19.6	44.0	85.0	19
Circumoral kinety to last dikinetid of brush row 1, distance	34.0	32.0	5.4	1.2	16.0	25.0	47.0	21
	35.4	35.0	5.9	1.3	16.6	27.0	45.0	19
Brush row 1, number of dikinetids	20.5	20.0	3.3	0.7	15.9	15.0	25.0	21
	17.1	17.0	3.1	0.7	18.3	13.0	23.0	19
Circumoral kinety to last dikinetid of brush row 2, distance	33.4	34.0	4.6	1.0	13.7	28.0	45.0	21
	49.5	49.0	5.8	1.3	11.7	40.0	63.0	19
Brush row 2, number of dikinetids	17.8	18.0	1.5	0.3	8.4	15.0	21.0	21
	23.1	23.0	4.1	0.9	17.5	14.0	32.0	19
Anterior macronucleus nodule, length	14.5	15.0	2.7	0.6	18.5	10.0	22.0	21
	16.8	16.0	3.6	0.8	21.2	12.0	26.0	19
Anterior macronucleus nodule, width	9.2	9.0	1.4	0.3	14.9	6.0	11.0	21
	10.7	10.0	2.5	0.6	23.4	6.0	18.0	19
Macronucleus nodules, distance in between	32.5	34.0	9.0	2.0	27.7	17.0	50.0	21
	23.1	22.0	13.3	3.0	57.6	0.0	65.0	19
Macronucleus nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
Anterior micronucleus, length	4.5	4.0	0.9	0.2	19.9	3.0	6.0	21
	6.2	6.0	1.4	0.3	23.1	4.0	9.0	19
Anterior micronucleus, width	3.5	3.5	0.4	0.1	12.9	3.0	4.0	21
	3.3	3.0	0.7	0.2	20.0	2.0	4.0	19
Micronuclei, number	1.9	2.0	0.5	0.1	28.3	0.0	3.0	21
	2.2	2.0	0.8	0.2	37.0	1.0	4.0	19
Somatic ciliary rows, number	11.6	12.0	0.6	0.1	5.1	11.0	13.0	21
	20.8	21.0	1.4	0.3	6.8	18.0	24.0	19
Kinetids in a ventral kinety, total number	35.1	33.0	7.2	1.6	20.4	26.0	54.0	21
	31.3	29.0	7.7	1.8	24.6	22.0	53.0	19
Ciliated kinetids in a ventral kinety, number	26.7	25.0	4.2	0.9	15.8	21.0	35.0	21
	27.5	26.0	6.4	1.5	23.4	17.0	41.0	19
Dikinetidal brush rows, number[b]	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Type I lepidosomes, length[c]	1.6	1.6	0.2	0.1	15.7	1.1	2.2	30
	1.4	1.4	0.3	0.1	20.2	0.7	2.0	19
Type I lepidosomes, width	0.9	0.9	0.2	0.1	22.0	0.6	1.5	30
	0.9	0.9	0.4	0.1	40.3	0.4	1.8	19
Type I lepidosomes, number of dome polygons	16.3	16.5	4.6	0.8	28.4	7.0	25.0	30
	9.9	9.0	2.2	0.5	22.1	6.0	15.0	19
Types V and VI lepidosomes, character 1[c]	2.3	2.2	0.5	0.1	21.3	1.6	3.4	19
	4.7	4.7	0.7	0.2	14.0	3.6	5.8	19
Types V and VI lepidosomes, character 2	1.8	1.7	0.5	0.1	25.4	1.2	2.8	19
	4.0	4.0	0.7	0.2	16.2	2.9	5.1	19
Types V and VI lepidosomes, character 3	2.3	2.2	0.5	0.1	21.7	1.6	3.4	19
	2.1	2.1	0.2	0.1	11.1	1.5	2.6	19
Types V and VI lepidosomes, character 4	0.4	0.4	0.2	0.1	39.6	0.2	0.7	19
	0.7	0.7	0.1	0.1	16.6	0.5	0.8	19
Types V and VI lepidosomes, character 5	1.0	1.0	0.2	0.1	23.8	0.6	1.3	19
	1.1	1.2	0.2	0.1	18.7	0.6	1.4	19

Table 1. (*continued*)

Characteristics[a]	x̄	M	SD	SE	CV	Min	Max	*n*
Types V and VI lepidosomes, character 6 (dome, long axis)	1.5	1.4	0.4	0.1	23.1	1.1	2.4	19
	—	—	—	—	—	—	—	—
Types V and VI lepidosomes, character 7 (dome, short axis)	1.4	1.2	0.3	0.1	23.8	1.0	2.3	19
	—	—	—	—	—	—	—	—
Type V lepidosomes, baseplate view, long axis	2.4	2.4	0.4	0.1	15.2	1.6	3.2	19
	—	—	—	—	—	—	—	—
Type V lepidosomes, baseplate view, short axis	1.8	1.8	0.3	0.1	18.3	1.0	2.4	19
	—	—	—	—	—	—	—	—
Types II and VI lepidosomes, ratio of baseplate and baseplate convexity	2.1	2.1	0.4	0.1	17.2	1.7	2.8	11
	1.8	1.8	0.2	0.1	9.2	1.5	2.0	18
Type II lepidosomes, long axis	—	—	—	—	—	—	—	—
	2.1	1.9	0.4	0.1	20.5	1.3	3.0	19
Type II lepidosomes, short axis	—	—	—	—	—	—	—	—
	1.8	1.7	0.5	0.1	25.5	1.2	3.0	19
Type II lepidosomes, height	—	—	—	—	—	—	—	—
	2.0	1.8	0.6	0.1	29.0	1.0	3.2	19

[a]Data based, if not mentioned otherwise, on mounted, protargol-impregnated, and selected specimens (cells inflated by large food inclusions or with different nuclear pattern, likely exconjugants, were excluded; see text) from a non-flooded Petri dish culture. Measurements in µm. CV — coefficient of variation in %, M — median, Max — maximum, Min — minimum, — number of specimens investigated, SD — standard deviation, SE — standard error of arithmetic mean, x̄ — arithmetic mean.

[b]Row 3 is monokinetidal (see descriptions).

[c]All lepidosome measurements are from SEM micrographs of at least four specimens. The characteristics measured in types V and VI lepidosomes are shown in Fig. 1.

deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Dedication: I dedicate this species to Prof. Cristina Miceli (Camerino University, Italy), an excellent ciliate researcher, for her successful efforts in organizing the Fourth European Congress of Protistology in August–September 2003.

Description: the silver slides contain many small exconjugates with deviating nuclear pattern. These and specimens with large food inclusions were excluded from the morphometric analysis.

Size of extended or slightly contracted specimens 150–250 × 25–55 µm in vivo, usually about 200 × 35 µm, as calculated from some in vivo measurements and the morphometric data (Table 1). Length:width ratio near 5:1 in both in vivo and protargol preparations. Slenderly amphoriform to roughly fusiform, neck roundish to transversely truncate and slightly widened anteriorly gradually merging into broadened, fusiform trunk; both body ends narrowly rounded; up to 3:1 flattened dorsoventrally (Figs. 45, 48, 49, 58, 64, 69, 70). Cells very flexible and contractile by up to 40%, fully contracted specimens fusiform to claviform, about 120 × 60 µm (Figs. 49–51); contracts and extends slowly, exact body shape and size thus difficult to determine. Nuclear apparatus on average in middle and anterior portion of rear third, that is, in trunk region (Figs. 45, 58, 64, 65; Table 1). Macronucleus nodules globular to ellipsoidal, on average broadly ellipsoidal, less than 10 µm apart in two out of 19 specimens analysed; never connected by a fine strand, stand out as bright blisters from granular cytoplasm. Micronuclei globular to elongate ellipsoidal, sometimes flattened 2:1, in vivo rather conspicuous because about 7 × 3.5 µm in size; usually one micronucleus attached to each macronucleus nodule, but half of specimens have one, three or four micronuclei. Contractile vacuole in posterior end, with single, tubular excretory pore in pole centre (Figs. 45 and 58). Two types of fine extrusomes, both usually not impregnated with the protargol method used, attached to oral bulge: type 1 conspicuous because forming a refractive bundle in oral area and 22–24 × 0.6 µm in size, acicular and slightly curved, numerous also in cytoplasm, where certain developmental stages impregnate faintly (Figs. 45, 46, 48, 62, 65, 68); type 2 extrusomes rod-shaped, inconspicuous because only 3 µm long and fine (Figs. 47 and 48). Cytoplasm colourless and usually rather hyaline, contains lipid droplets 0.5–3 µm across and food vacuoles with rather loose content. Mainly feeds on the heterotrophic flagellate *Peranema* and the ciliate *H. grandinella*, but larger ciliates, likely hypotrichs, are also attacked and digested in up to 40 µm-sized vacuoles. Glides slowly on microscope slides and between soil particles.

Cortex thin and flexible, contains rows of pale granules about 0.5 × 0.25 µm in size; covered by an up

to 12 µm thick, mucilaginous layer of lepidosomes producing spinose body margin in both in vivo and protargol preparations (Figs. 45, 54, 64–67) as well as in the SEM (Fig. 69). Mucilaginous layer composed of three types of lepidosomes forming a 3–5 µm thick, tangled mass from which the thin, up to 8 µm long cones of the type VI lepidosomes protrude (Figs. 45, 54, 64–66); individual lepidosomes elastic, that is, do not split when squashed by coverslip pressure (Fig. 65), become deformed even in fixed condition, viz., when contacting glue adhering cells to SEM stub (Fig. 79); do not or only slowly dissolve when removed from cell; impregnate faintly with protargol (Fig. 67); specific structures anchoring lepidosomes to cell surface or lepidosome layer not recognizable.

Type I lepidosomes in two layers on body surface, except for oral bulge, tightly and irregularly spaced, usually difficult to recognize in both in vivo and SEM preparations because small, hyaline, and covered by types II and VI lepidosomes; basic structure as described in Foissner et al. (2002), frequently somewhat distorted, that is, stretched and/or wrinkled due to the preparation procedures; on average 1.4×0.9 µm in scanning preparations, dome slightly to hemispherically vaulted and composed of 10 large polygons on average (Figs. 54, 55, 71–73; Table 1). Type II lepidosomes in single layer upon type I lepidosomes, about 4×4 µm in vivo ($2.1 \times 1.8 \times 2$ µm in SEM preparations) and thus well recognizable in the light microscope; basic structure as described in Foissner et al. (2002), that is, drawing-pin shaped with baseplate convexity occupying 49% of total diameter on average; dome often slightly curved and usually narrow, that is, rises rather abruptly from baseplate occupying less than one third of its diameter, composed of about 20 longitudinal fibres forming circa eight stripes consisting of two to five fibres each (Figs. 54, 56, 65, 66, 70–73, 76, 81; Table 1).

Type VI lepidosomes beautiful and conspicuous because complex and $7–12 \times 4–6$ µm in size, occupy space between domes of type II lepidosomes, less numerous than type I and II lepidosomes, usually lacking in oral region and partially lost during preparation procedures; conical portion delicate, swinging forwards and backwards in water currents produced by cell gliding and beating cilia; on average 4.7 µm high and 2.1 µm wide in scanning preparations. Baseplate circular to broadly elliptical, central 58% cup-like protruding and thus considerably larger than in type II lepidosomes (49%); composed of minute, hexagonal meshes forming honeycombed pattern; margin upright and more or less sigmoidal, composed of a single row of minute, rectangular meshes. Dome narrowly conical (~2:1), causes the spinose appearance of the mucilage, composed of many more or less bundled, longitudinal fibres connected by small and large polygons in proximal half (Figs. 45, 54, 57, 61, 64–66, 69–71, 74, 76–80; Table 1). Possibly, type VI lepidosomes develop from type II lepidosomes because intermediates occur (Fig. 75); nonetheless, the two are distinct as shown by Figs. 71 and 76.

Cilia about 12 µm long in vivo, beat only in distal half projecting from lepidosome mass, widely (circa 7 µm) and unevenly spaced because ciliated kinetids irregularly alternate with slightly smaller, bare granules (Figs. 45, 58, 63; Table 1). Ciliated basal bodies associated with three types of fibres, as in most other trachelophyllids (Foissner et al. 2002): (i) a long, probably postciliary microtubule ribbon extending slightly obliquely posteriorly, forming a distinct stripe between adjacent ciliary rows together with the ribbons of 5–10 neighbouring kinetids; (ii) a short, faintly impregnated (transverse?) fibre extending slightly obliquely anteriorly for one to two kinetids; and (iii) a short, strongly impregnated (kinetodesmal ?) fibre, present also in bare basal bodies, crossing the interkinetal space at almost right angles (Figs. 44 and 63). On average 21 meridional, equidistant ciliary rows about 4 µm apart from each other, three of them differentiated to rather complex dorsal brush anteriorly (Figs. 52, 58, 61, 70; Table 1). Brush row 1 distinctly shorter than row 2, dikinetidal with about 2.5 µm long, slightly curved, motionless bristles covered by the lepidosome layer. Brush row 2 similar to row 1, but longer and anterior bristle of dikinetids shortenend by approximately 40%. Brush row 3 monokinetidal, composed of a very short anterior portion and a long "tail" extending to near body end, bristles up to 8 µm long and thus projecting from lepidosome layer (Fig. 70): anterior portion slightly convex and composed of 5–10 very narrowly spaced, about 8 µm long, distinctly beating cilia; posterior portion composed of comparatively widely spaced, about 6 µm long, acicular, stiff bristles beating slowly forwards and backwards.

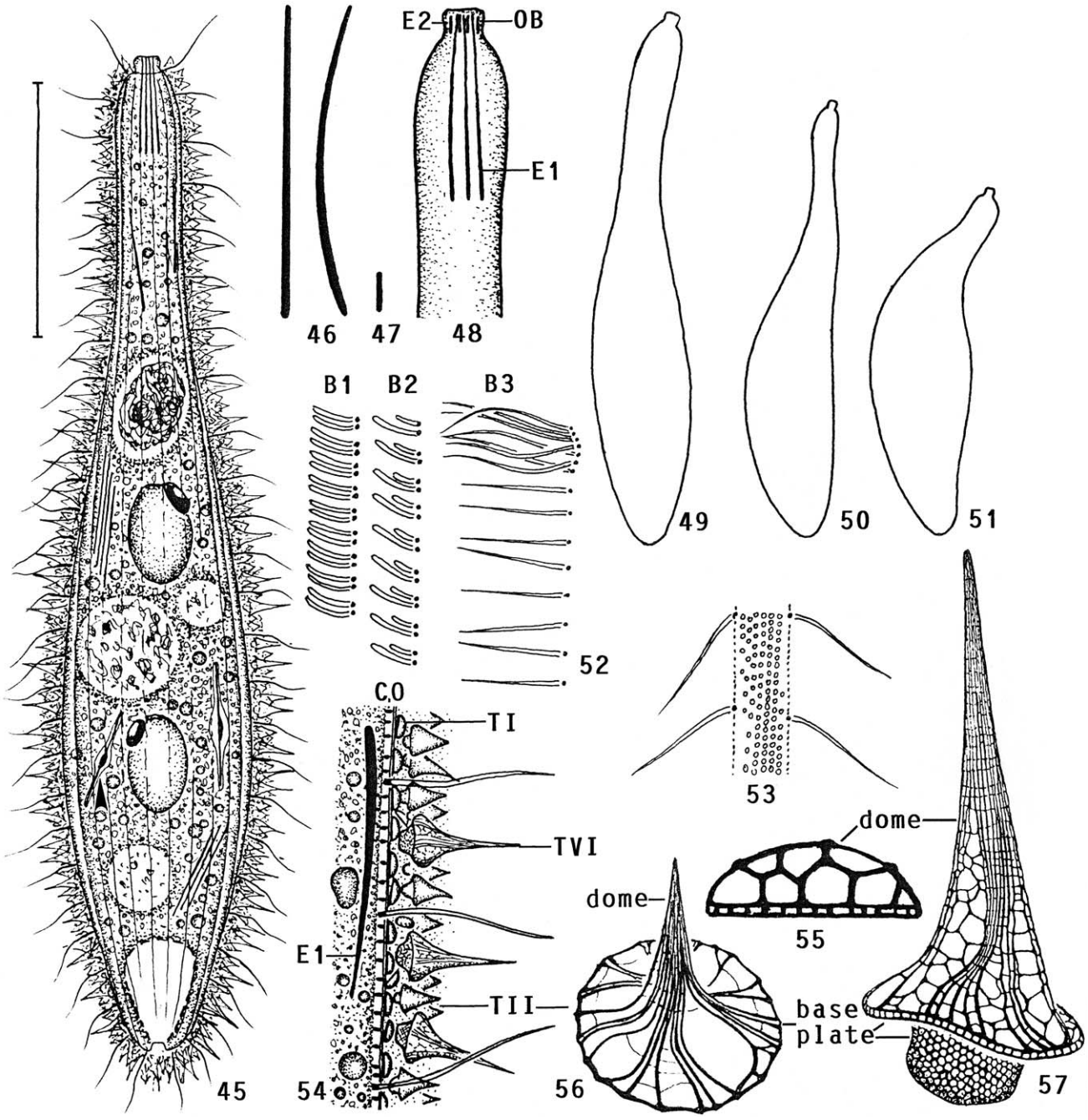
Oral bulge about 5×5 µm in vivo, inconspicuous because gradually merging into neck; usually not covered by lepidosomes; contains the short extrusomes, which occasionally impregnate with the protargol method used, and the top of the long extrusomes (Figs. 45, 48, 58, 61, 62, 64, 70; Table 1). Circumoral kinety composed of approximately 12 dikinetids having only the right basal body ciliated, gives rise to rather conspicuous nematodesmata forming cylindroidal oral basket (Figs. 60–62). Nematodesmata bifurcated, forming distinct bundles as shown in Figs. 59 and 62.

Occurrence and ecology: see *S. pustulata*.

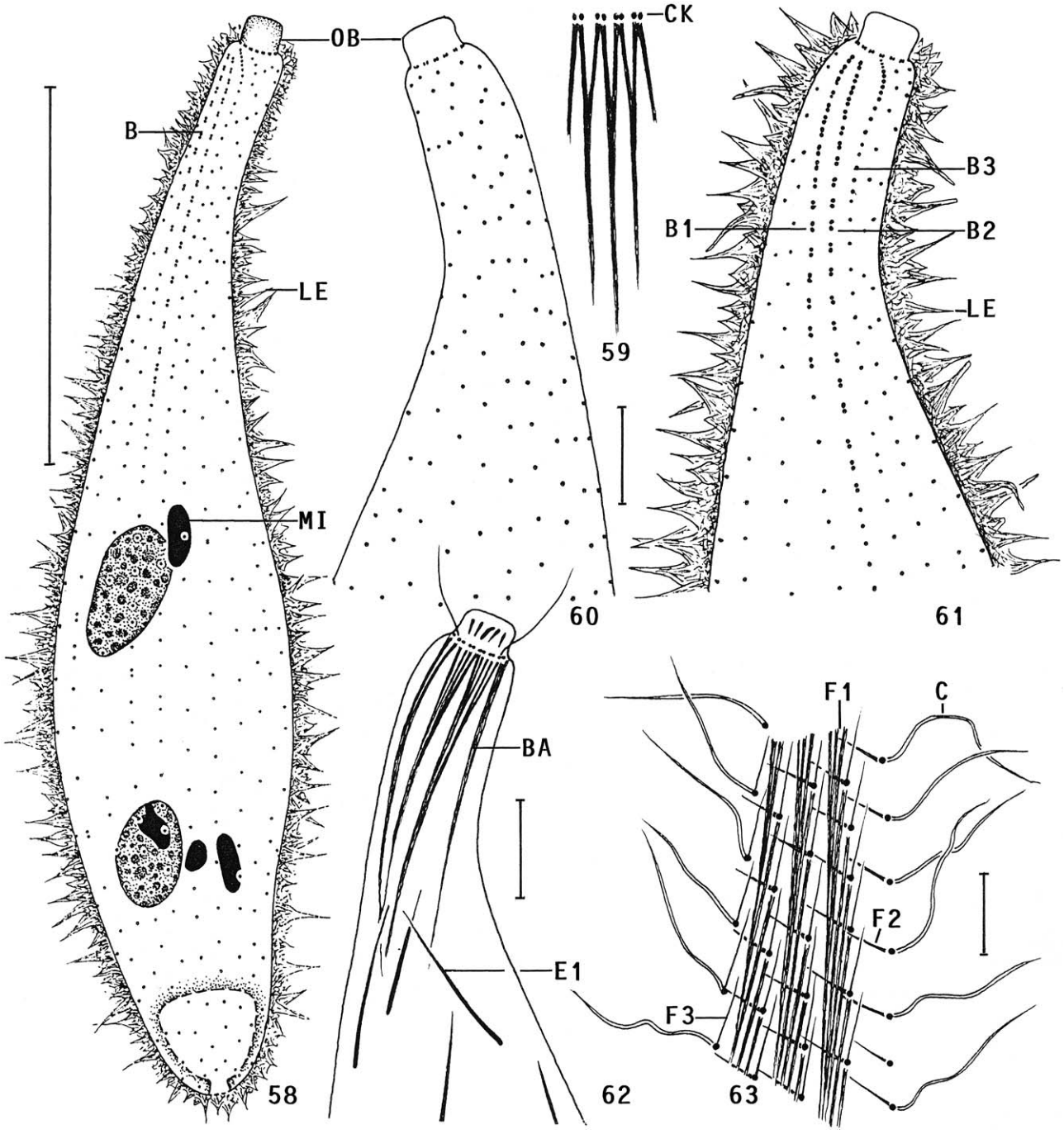
Discussion

Classification of the Trachelophyllina Grain, 1994

Foissner et al. (2002) diagnosed a new suborder, Trachelophyllina, as "Spathidiida with epicortical scales". However, Grain (1994) established the same



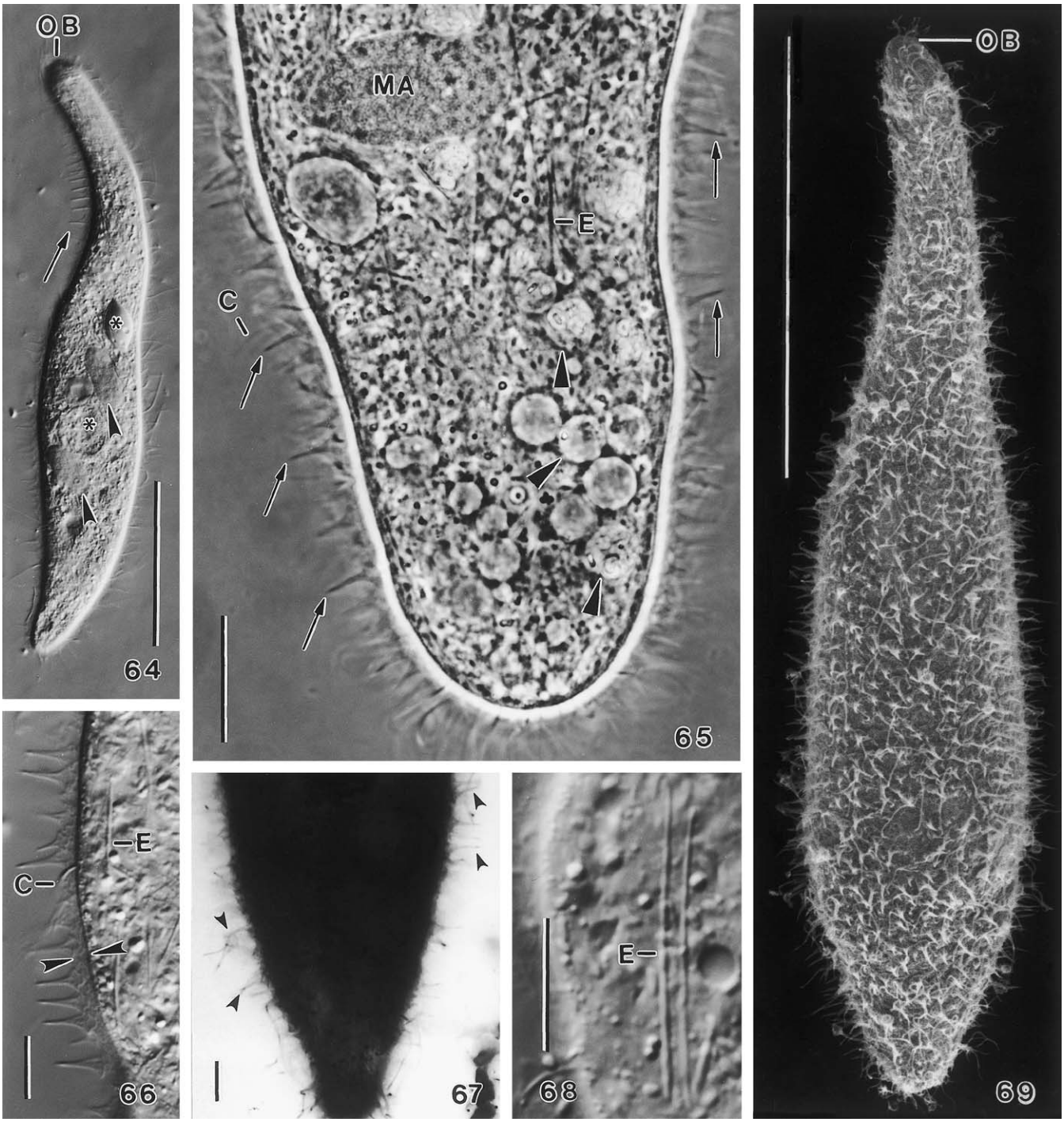
Figs. 45–57. *Luporinophrys micelae* from life (45–54) and in the SEM (55–57). **45**: Ventral view of a representative specimen, length 200 μm. The up to 12 μm long type VI lepidosomes make the species spinose. The arrowhead marks a developing extrusome. **46**: Type 1 oral bulge extrusomes, length about 23 μm. **47**: Type 2 oral bulge extrusome, length about 3 μm. **48**: Anterior body region showing the shape of the oral bulge and the location of the types 1 and 2 extrusomes. **49–51**: A contracting specimen (redrawn from micrographs). **52**: Anterior portion of dorsal brush, bristles drawn to scale and up to 8 μm long in vivo. Note brush row 3, which has an anterior condensation of flexible, about 8 μm long bristles, followed by inflexible, acicular, 6 μm long bristles which can move only forwards and backwards. **53**: Surface view showing cortical granulation. **54**: Optical section showing the conspicuous epicortical mucilage composed of three types of lepidosomes (drawn to scale, type VI about 10 μm long in vivo). **55, 57**: Side view of a type I and a type VI lepidosome, height only about 0.4 μm and 4.7 μm in the SEM due to strong shrinkage by about 50%. **56**: Oblique surface view of a type II lepidosome, height about 2 μm in the SEM. B1-3—dorsal brush rows, CO—cortex, E1, 2—extrusome types, OB—oral bulge, TI, II, VI—lepidosome types. Scale bar 50 μm.



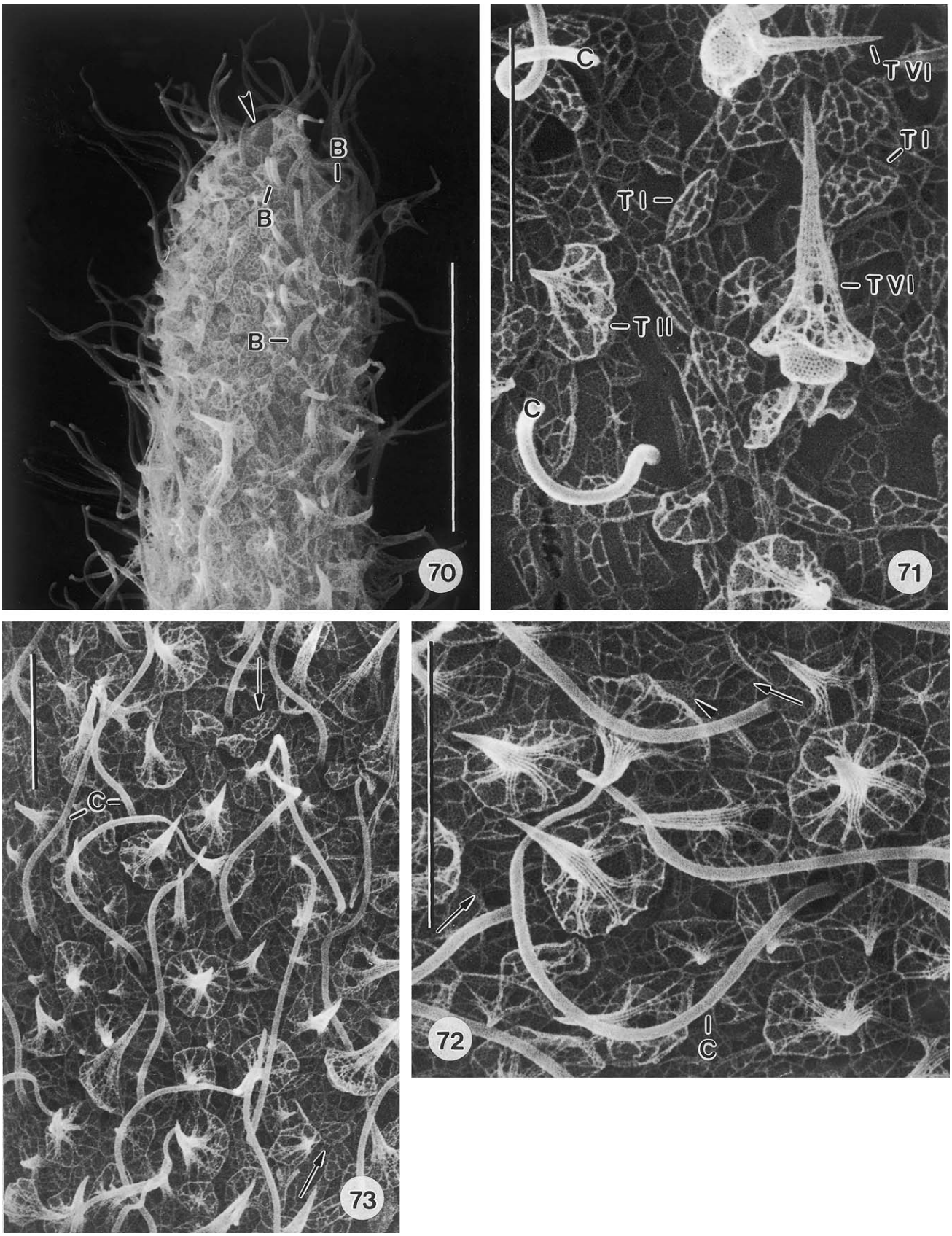
Figs. 58–63. *Luporinophrys micelae*, oral and somatic infraciliature after protargol impregnation. **58**: Dorsal overview of holotype specimen, length 145 µm. The lepidosome layer impregnates faintly, and the long type VI lepidosomes are well recognizable. **59, 62**: The oral basket is composed of bifurcated nematodesmata originating from the circumoral kinety. **60, 61**: Ventral and dorsal ciliary pattern in anterior body region of a paratype specimen. Dorsal brush row 1 is distinctly shorter than row 2, and both are composed of dikinetids. Brush row 3, in contrast, is monokinetidal, but has a convex, densely ciliated anterior end (further details, see Fig. 52). **63**: The cortical fibre system consists of three distinct components. BA—oral basket, B(1-3)—dorsal brush (rows), C—ordinary somatic cilium, CK—circumoral kinety, E1—type 1 extrusome, F1-3—fibre systems, LE—lepidosome layer, MI—micronucleus, OB—oral bulge. Scale bars 50 µm (58) and 10 µm (60–63).

suborder earlier, albeit with a different and rather vague diagnosis not including the lepidosomes which are, in my opinion, the main diagnostic feature. Nonetheless, Grain (1994) has nomenclatural priority.

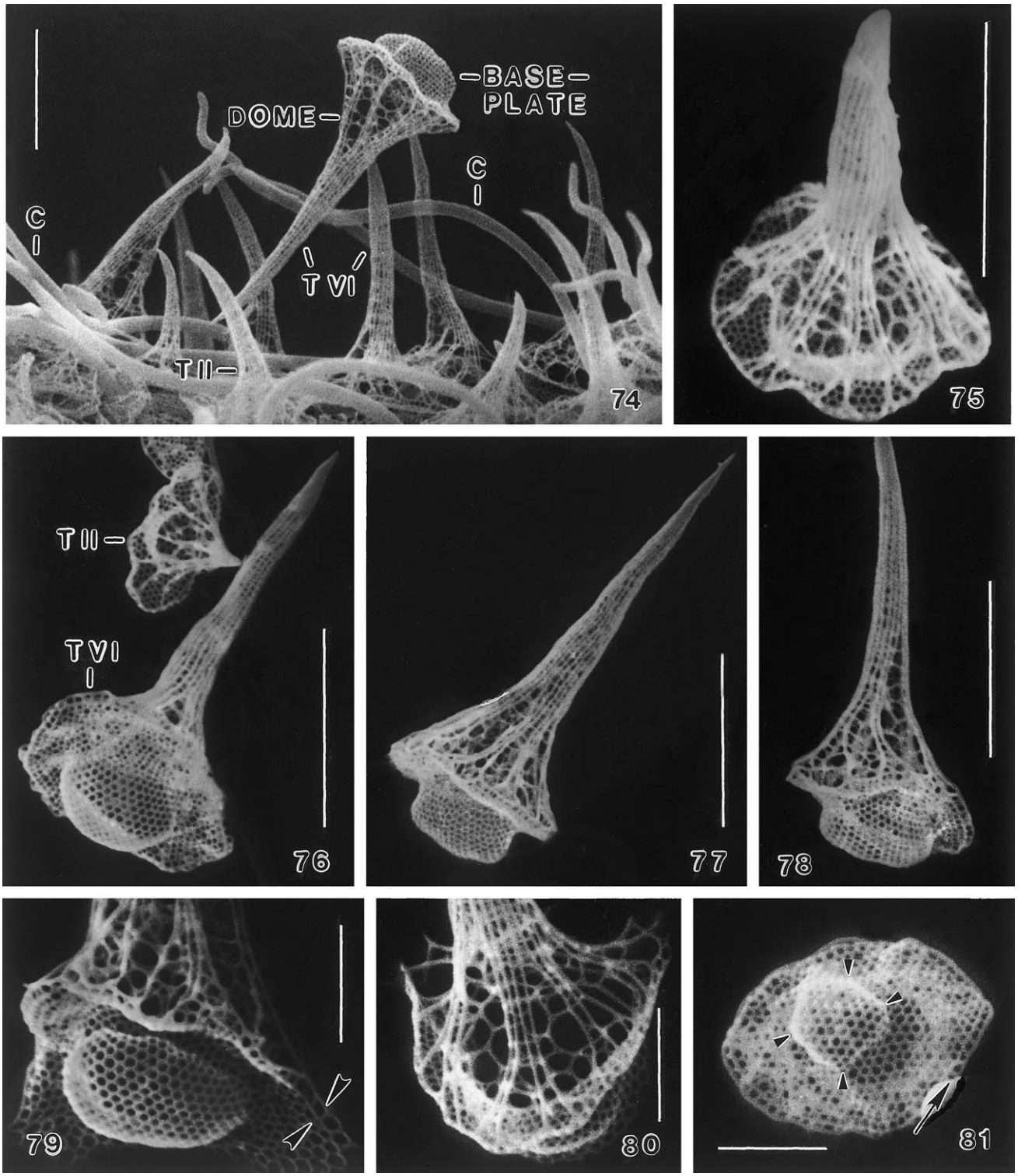
Grain (1994) and Foissner et al. (2002) classify the trachelophyllids into the haptorids, and Foissner et al. (2002) relate them to the Spathidiina because of distinct similarities in the oral and somatic infraciliature.



Figs. 64–69. *Luporinophrys micelae* from life (64–66, 68), after protargol impregnation (67), and in the SEM (69). **64, 69**: Overviews of representative specimens, showing the spiny appearance at even low magnification. Arrow denotes a region where the type VI lepidosomes look like stiff cilia. Arrowheads mark the two macronucleus nodules. Asterisks denote food inclusions. Note the comparatively broad oral bulge (OB). **65**: Phase contrast micrograph of posterior region of a specimen strongly flattened by coverslip pressure. The cell surface is conspicuously spinose due to the up to 12 μm high type VI lepidosomes (arrows). The cytoplasm contains many vacuoles with more or less distinct food remnants (arrowheads). **66, 67**: Optical sections showing the up to 12 μm high, spiny type VI lepidosomes, which are conspicuous both in vivo and after protargol impregnation. Opposed arrowheads mark mucilaginous layer composed of types I and II lepidosomes. **68**: Type 1 extrusomes are acicular and 22–24 μm long. C—somatic cilia, E—extrusomes, MA—macronucleus nodule, OB—oral bulge. Scale bars 10 μm (66–68), 20 μm (65), 50 μm (64, 69).



Figs. 70–73. *Luporinophrys micelae* in the SEM. **70**: Dorsal view showing brush (B) and oral bulge (arrowhead). **71**: The three lepidosome types. **72, 73**: A region covered mainly by type II lepidosomes, which cover type I lepidosomes (arrows). Arrowhead marks baseplate of a type II lepidosome. B—dorsal brush, C—cilia, TI, II, VI—lepidosome types. Scale bars 5 μm (71–73) and 10 μm (70).



Figs. 74–81. *Luporinophrys micelae*, types II and VI lepidosomes in the SEM. Structures are shrunken by about 50% due to the preparation procedures! **74**: Cell margin with a detached type VI lepidosome. **75**: A stout type VI or a large type II lepidosome. **76**: Oblique view of a type II and type VI lepidosome. **77, 78**: Type VI lepidosomes. **79**: Oblique posterior polar view showing the baseplate margin (arrowheads) of a type VI lepidosome. **80**: Dome base of a type VI lepidosome. **81**: Posterior polar view of a type II lepidosome, showing the baseplate margin (arrow) and the central convexity (arrowheads). C—cilia, T II, VI—lepidosome types. Scale bars 1 μm (79–81) and 2 μm (74–78).

However, the present data indicate a relationship with the Lacrymariina Lipscomb and Riordan, 1990 because bifurcated nematodesmata are clearly recognizable in *L. micelae* (Fig. 59). Unfortunately, bifurcated nematodesmata occur in various haptorid families, including acropisthinids with oralized somatic monokinetids (Foissner 1996; Grain 1994; Lipscomb and Riordan 1990). Thus, they probably evolved convergently in various haptorids and cannot be used for higher phylogenetic analyses. As concerns the trachelophyllids, the bifurcated nematodesmata were probably overlooked or misinterpreted in our previous investigations (Foissner 1994; Foissner et al. 2002).

Familiar and generic classification of trachelophyllids

The Trachelophyllidae Kent now consists of six genera with 12 well-investigated and some poorly known nominal species (Table 2). Several other haptorids with lepidosomes, but different general organization probably constitute a further distinct family (Foissner et al. 2002). The six trachelophyllid genera appear confamiliar, if traditional features and the infraciliature are considered, and no correlations are recognizable between the various features, for instance, number of ciliary rows and brush pattern (Table 2). However, two groups can be distinguished with the lepidosomes, viz., an assemblage having only one type (*Trachelophyllum*, *Epitholiolus*, *Spetazoon*) and another having two or three types (*Bilamellophrya*, *Sleighophrys*, *Luporinophrys*). In my opinion, each lepidosome type represents a distinct genus (Fig. 82; Table 2), while further investigations are required for the estimation of the systematic significance of having one or more types of lepidosomes.

Sleighophrys pustulata and *Luporinophrys micelae* as new species

The two species have a distinct mucilaginous layer easily recognizable also with an ordinary bright field

Table 2. Comparison of main taxonomic features in 12 well-investigated trachelophyllids

Species[a]	Average size (μm)	Nucleus pattern[b]	Extrusome size and shape	Ciliary rows, number	Brush row 2 distinctly longer than 1	Oral bulge shape	Lepidosome types[c]
Bilamellophrya australiensis	200 × 30	Ordinary	Rod-shaped, >10 μm	24	Yes	Anvil-shaped	I, II
Bilamellophrya etoschensis	140 × 15	Ordinary	Rod-shaped, <10 μm	11	No	Conical	I, II
Bilamellophrya hawaiiensis	150 × 25	Ordinary	Acicular, >10 μm	13	No	Cylindroidal	I, II
Epitholiolus chilensis	95 × 10	Different	Acicular, ≙ 10 μm	9	Yes	Cylindroidal	III
Luporinophrys micelae	190 × 30	Ordinary	Acicular, >10 μm	21	Yes	Cylindroidal	I, II, VI
Sleighophrys pustulata	180 × 23	Ordinary	Acicular, >10 μm	12	No	Pin-shaped	I, V
Spetafoon australiense	250 × 55	Ordinary	Acicular, >10 μm	31	No	Conical	IV
Trachelophyllum africanum	200 × 25	Ordinary	Narrowly lanceolate, <10 μm	13	Yes	Cylindroidal	I
Trachelophyllum apiculatum	150 × 25	Ordinary	Rod-shaped, >10 μm	13	No	Cylindroidal	I
Trachelophyllum costaricanum	180 × 15	Ordinary	Obclavate, >10 μm	9	Yes	Cylindroidal	I
Trachelophyllum lineare	280 × 60	Ordinary	?	30	?	?	I
Trachelophyllum pannonicum	200 × 20	Ordinary	Acicular, ≙10 μm	11	Yes	Cylindroidal	I

[a]Most data are from Foissner et al. (2002) and the present investigation; those on *S. australiense* are from Foissner (1994), and those on *T. lineare* (junior synonym: *L. fornicis*; see Foissner 1994 and Foissner et al. 2002) are from Nicholls and Lynn (1984).

[b]Ordinary: two widely separate macronucleus nodules with a micronucleus each. Different: two narrowly spaced macronucleus nodules with a single micronucleus in between.

[c]See Fig. 82.

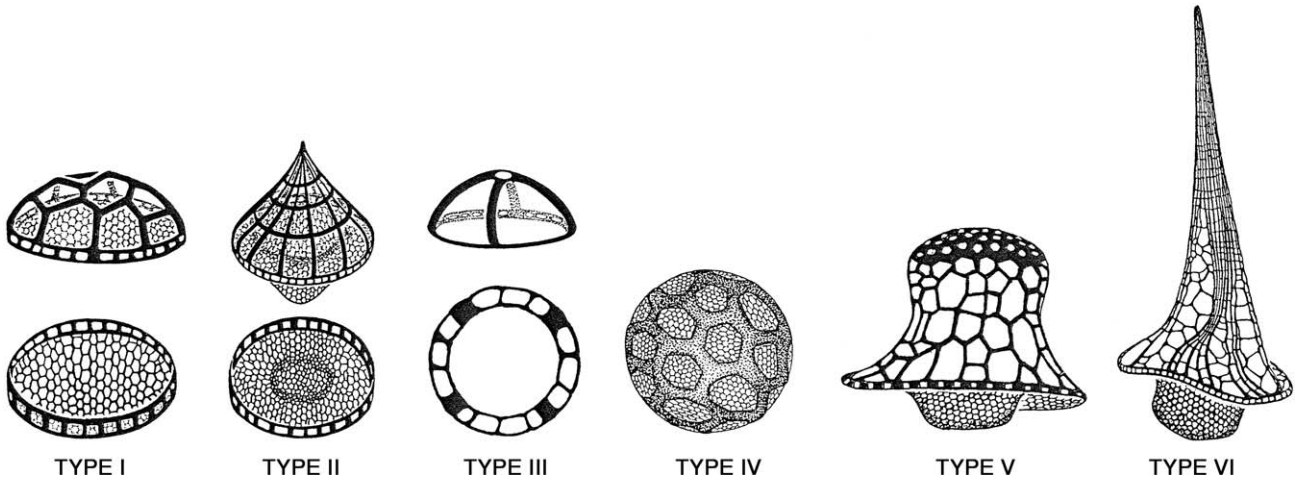


Fig. 82. Lepidosome types in trachelophyllid ciliates (from Foissner et al. 2002, supplemented). Type I: side view and baseplate of *Trachelophyllum* spp. Type II: side view and baseplate of *Bilamellophrya* spp Type III: side view and baseplate of *Epitholiolus chilensis*. Type IV: *Spetazoon australiense*. Type V: side view of *Sleighophrys pustulata*. Type VI: side view of *Luporinophrys micelae*.

microscope. Indeed, mucilaginous layers have been described already by Stokes (1884), Kahl (1930), Lepsi (1960), and Foissner (1983) in *Trachelophyllum vestitum*, *T. sigmoides*, and *T. lineare*. The individual lepidosomes of *T. vestitum* are too small to be clearly seen with the light microscope (Foissner 1983), while the lepidosomes of *T. sigmoides* are mushroom-shaped and about 3.5 µm in size (Foissner, unpubl. observ.). *Trachelophyllum lineare* is the senior synonym of *Lepidotrachelophyllum fornicis* and has only type I lepidosomes (Foissner 1994; Foissner et al. 2002; Nicholls and Lynn 1984). Thus, none of these species can be identical with *S. pustulata* or *L. micelae*. Likewise, I could not find any other similar species in the literature. Thus, *S. pustulata* and *L. micelae* are new species well defined by their large, conspicuous lepidosomes.

Sleighophrys pustulata and *Luporinophrys micelae* as biogeographic flagships

There is now an exciting discussion whether or not microscopic organisms have biogeographies (for reviews, see Foissner 2004; Papke and Ward 2004). *Sleighophrys pustulata* and *L. micelae* have the potential to cast some light on this matter because they are "flagships" in a biogeographical context, that is, have highly complex lepidosomes and are large enough (~200 µm) to be recognized easily. I did not find them in over 2000 limnetic samples from Austria and Germany and in about 1000 soil samples collected globally (Foissner 1998). Further, they were not found by any other ciliate taxonomist because they are new species (see above). Thus, I believe that *S. pustulata* and *L. micelae* are either extremely rare (but they were numerous in the raw culture), or, more likely, have a restricted geographic distribution.

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