

**Infraciliature and Systematic Position of the
Marine Interstitial Ciliates (Protozoa,
Ciliophora) *Lopezoterenia torpens* (Kahl, 1931)
Nov. Gen., Nov. Comb., *Discotricha papillifera*
Tuffrau, 1954, and *Paraspathidium fuscum*
(Kahl, 1928) Fjeld, 1955***

*Infraciliatura y Posición Sistemática de los Ciliados Marinos, Intersticiales
(Protozoa, Ciliophora) *Lopezoterenia torpens* (Kahl, 1931) Nov. Gen., Nov.
Comb., *Discotricha papillifera* Tuffrau, 1954 y *Paraspathidium fuscum*
(Kahl, 1928) Fjeld, 1955*

Wilhelm Foissner**

ABSTRACT

The morphology and infraciliature of *Lopezoterenia torpens* (Kahl, 1931) nov. gen., nov. comb. (basonym: *Trichopelma torpens* Kahl, 1931), *Discotricha papillifera* Tuffrau, 1954, and *Paraspathidium fuscum* (Kahl, 1928) Fjeld, 1955, some remarkable interstitial ciliates (Protozoa, Ciliophora) from the French Atlantic coast at Roscoff, were studied in live and protargol-impregnated specimens and with the scanning electron microscope. Most features of *T. torpens* are highly reminiscent of *D. papillifera*, namely the general ciliary pattern, the habitat, the cortical papillae containing fusiform trichocysts, the paroral membrane-like kinety at the upper right end of the oral field, the structure of the pharyngeal basket, and the lack of a postoral primordial field. Thus, *Trichopelma torpens* is assigned as a new genus, *Lopezoterenia* nov. gen., to the microthoracine family Discotrichidae. *Lopezoterenia* differs from *Discotricha* by the simple, holotrichous ciliature lacking compound, cirri-like cilia aggregates and details of the cortical ornamentation. A refined classification of the microthoracine nassulids is suggested. *Paraspathidium fuscum* has highly specialized cilia and kinetids in the anterior body portion, forming a dikinetidal circumoral kinety, a dikinetidal perioral ciliary corona, and a complex dorsal brush; furthermore, the perioral dikinetids bear nematodesmata, i.e. are oralized somatic kinetids, possibly because the cytopharyngeal basket is weakly developed. Most of these features are highly reminiscent of gymnostome haptorids, to which *Paraspathidium* is assigned as a new family, Paraspathidiidae nov. fam. (Acropisthiina (?) with apical, excavated oral opening surrounded by dikinetids forming conspicuous ciliary corona. Brosse and circumoral dikinetids bearing unique, highly specialized cilia).

Key words: *Discotricha papillifera*; infraciliature; *Lopezoterenia torpens* nov. gen., nov. comb.; microthoracids; *Paraspathidium fuscum*; gymnostomes.

* Dedicated to Professor Dr. Eucario López-Ochoterena on the occasion of his appointment as Honorary Member of the Sociedad Mexicana de Historia Natural.

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RESUMEN

La morfología e infraciliatura de *Lopezoterenia torpens* (Kahl, 1931) nov. gen., nov. comb. (basónimo: *Trichopelma torpens* Kahl, 1931), *Discotricha papillifera* Tuffrau, 1954 y *Paraspathidium fuscum* (Kahl, 1928) Fjeld, 1955, los ciliados (Protozoa, Ciliophora) intersticiales encontrados en Roscoff en la costa atlántica de Francia, fueron estudiados tanto en vivo, como impregnados con protargol y utilizando un microscopio electrónico de barrido. La mayor parte de los caracteres morfológicos de *L. torpens* son muy parecidos a los de *D. papillifera* y son: el patrón general de la infraciliatura, el hábitat, las papilas membranosas que contienen tricocistos fusiformes, la cinetia paroral en forma de membrana en el extremo superior derecho de la zona bucal, la estructura de la canasta faríngea y la falta de una zona primordial postoral. Por esta razón, *L. torpens* es asignado a la familia Discotrichidae perteneciente al suborden Microthoracina. *Lopezoterenia* difiere de *Discotricha* por la simple ciliatura holotrichida, la cual no posee compuestos de cilios agregados, parecidos a cirros y por algunos detalles referentes a la ornamentación cortical. Se sugiere una rectificación en la clasificación de los microthoracinos nassulidos. *Paraspathidium fuscum* tiene cilios y cinétidas altamente especializados en el antecuerpo formando una cinetia circumoral dicinétida, una corona ciliar perioral con dicinétidas y un cepillo dorsal complejo; además las periorales dicinétidas presentan nematodesmos, es decir que se trata de cinétidas somáticas oralizadas. Posiblemente esto se debe a que la canasta citofaríngea se encuentra poco desarrollada. Gran parte de estos caracteres son muy parecidos a los de los gymnostomátidos haptóridos, con quienes *Paraspathidium* es asignado a la nueva familia Paraspathidiidae nov. fam. (Acropisthiina (?)) la cual está constituida por un orificio oral apical en forma de caverna rodeada de dicinétidas formando una corona ciliar conspicua. El cepillo y las dicinétidas circumorales presentan unos cilios incomparables y altamente especializados).

Palabras clave: *Discotricha papillifera*; infraciliatura; *Lopezoterenia torpens* nov. gen., nov. comb.; microthoracidos; *Paraspathidium fuscum*; gymnostomátidos.

Introduction

It is not widely known that Kahl (1928, 1930, 1931, 1932, 1935) was the first who studied psammobiontic ciliates on a broader scale, possibly stimulated by the benchmark paper of Remane (1933). Kahl assigned most of the new species he found to common freshwater or marine genera, very likely because he often could not investigate them in detail due to their fragility and/or rareness. Later studies showed that most of Kahl's species were in fact representatives of new genera (Dragesco, 1960; Foissner, 1997; Noland, 1937; Song, 1990). The present paper provides a further example, viz. *Trichopelma torpens*, which Kahl (1931) properly placed in the Microthoracidae (syn.: Leptopharyngidae) but incorrectly assigned to *Trichopelma* (now *Leptopharynx* due to homonymy) because he did not recognize details of the somatic and oral ciliary pattern. Likewise, *Trachelocerca fusca* Kahl, 1928 was later recognized as representative of a new genus, *Paraspathidium* (Fjeld, 1955; Noland, 1937).

Both, *T. torpens* and *T. fusca* have rarely been studied with modern methods. Thus, their systematic position remained unclear (Corliss, 1979; Dragesco and Dragesco-Kernéis, 1986). The present investigations show that *T. torpens* represents a new genus within the microthoracine Discotrichidae, and that *Paraspathidium* should be assigned as a new family to the gymnostome haptorids.

Materials, Methods and Terminology

Lopezoterenia torpens, *Discotricha papillifera*, and *Paraspathidium fuscum* were found in September 1994 in the mesopsammon, i.e. in the upper 0-4 cm sand layer of the Atlantic coast at Roscoff, France (W4°, N48°50'). Samples were collected and treated as described by Fauré-Fremiet (1951). The upper 0-4 cm sand layer of shallow pools was taken with a shovel during the tide, put into a 1 litre jar, and allowed to settle for at least 24 hours. During this time many ciliates moved upwards and enriched in the upper 1 cm of sand. About 20 ml

sand and sea-water from this layer were collected with a large-bore (5 mm) pipette and mixed with about 5 ml of a 12% $MgCl_2$ solution to detach the ciliates. The mixture was then gently rotated in a petri dish so that the sand collected in the centre and the detached ciliates could be picked up with a pipette from the clear supernatant.

Cultures of *P. fuscum* were set up in petri dishes containing artificial sea-water and a few crushed wheat grains to support growth of indigenous bacteria and small ciliates which served as food organisms. *Paraspathidium fuscum* grew only slowly in such cultures and extincted after a few months.

Cells of *P. fuscum* were studied *in vivo* using a high-power oil immersion objective and differential interference contrast, and in the scanning electron microscope, as described in Foissner (1991). The infraciliature of *L. torpens*, *D. papillifera*, and *P. fuscum* was revealed by protargol impregnation [Foissner, 1991; protocol B (Wilbert's method)], using the fixative described by Foissner and Dragesco (1996): 5 ml glutaraldehyde (25%), 5 ml saturated, aqueous mercuric chloride, 3 ml aqueous osmium tetroxide (2%), and 1 ml glacial acetic acid are mixed just before use. This fixative preserves most mesopsammal ciliates very well, but does not prevent contraction in contractile species. Specimens were fixed for 10-15 min and washed three times in distilled water.

Counts and measurements on silvered specimens were performed at a magnification of X 1,000. *In vivo* measurements were conducted at magnifications of X 40-1,000. Although these provide only rough estimates, it is worth giving such data as specimens usually shrink in preparations and contract during fixation. Illustrations of live specimens were based on video records, those of impregnated cells were made with a camera lucida. All figures are oriented with the anterior end of the organism directed to the top of the page.

Terminology is according to Corliss (1979), Foissner (1985), and Foissner & Foissner (1988).

Results

Lopezoterenia nov. gen.

Diagnosis: Holotrichously ciliated Discotrichidae with distinct cortical furrows containing ciliary rows

composed of evenly spaced dikinetids. Cortex with conical interkinetal papillae.

Type species: *Trichopelma torpens* Kahl, 1931.

Etymology: Named in honour of Prof. Dr. López-Ochoterena, eminent Mexican protozoologist. Feminine gender according to article 30b of the ICZN.

Redescription of *Lopezoterenia torpens* (Kahl, 1931) nov. comb. (Figs. 1 - 11, Table 1)

Improved diagnosis: Size *in vivo* about 50 - 60 x 30 - 40 μm , up to 3:1 flattened laterally. Cortex with conical interkinetal papillae and conspicuous spines at margin of cell. 8 kineties on right side, 6 on left. 3 adoral membranelles, membranelle 1 smaller (comprising about 4 basal bodies) than membranelles 2 and 3 (each composed of three kineties with 3 basal bodies each) and far above cytopharyngeal opening near left anterior end of cell. Paroral membrane-like kinety above and left of cytopharyngeal opening, commences between adoral membranelles 1 and 2 and curves to upper margin of oral basket, composed of about 6 dikinetids and a monokinetidal tail comprising 2 - 3 basal bodies.

Specimens investigated and type material: The redescription is based on 6 well-impregnated specimens. No type material from *L. torpens* has been mentioned in the literature. Thus, I have deposited two neotype slides with specimens from Roscoff, prepared as described, in the Oberösterreichische Landesmuseum in Linz (1.1). Relevant specimens are marked by a black ink circle on the cover glass.

Redescription: Morphometric data shown in Table 1 are repeated in this section only as needed for clarity. The redescription is based on protargol-impregnated specimens because I did not study live cells in detail.

Size of prepared specimens on average 50 x 30 μm . Cell outline roughly semicircular because of straight ventral and strongly convex dorsal side, both ends broadly rounded (Figs. 1, 6, 7, 8). Nuclear apparatus near body centre, usually weakly stained with protargol, macronucleus ellipsoidal (about 2:1),

micronucleus globular (Fig. 6). Pore of contractile vacuole, cytophyge, and extrusomes not stained with protargol, at least with the modification used. Cortex conspicuously ornamented by two kinds of processes, viz. up to 10 µm long spines forming two to three indistinct rows along body margin (Figs. 1, 3, 6, 11), and conical papillae arranged in two rows between two somatic kineties each; papillae 1 - 3 µm high, originate from deep, septate furrow extending between ciliary rows (Figs. 4, 7, 11). Food vacuoles contained filamentous cyanobacteria.

Holotrichously ciliated, except for centre of left side, where two kineties are partially reduced (Figs. 1, 2, 8, 10). Ciliary rows in deep, crenated furrows, larger anterior portion composed of ciliated dikinetids, smaller posterior portion made of ciliated monokinetids (Figs. 1, 2, 5, 8 - 10). Ventral ciliary rows (numbers 11 - 14) almost straight, commence close underneath adoral membranelle 3, i.e. left of pharyngeal opening; other kineties extend parallel to convex dorsal body margin, i.e. are increasingly curved and rather evenly spaced, except for kineties 5 and 6 near dorsal margin of left side, which are more narrowly spaced and commence preorally, forming indistinct suture with kineties 7 and 8 extending along dorsal margin of left side (Figs. 1, 2, 5, 7 - 10).

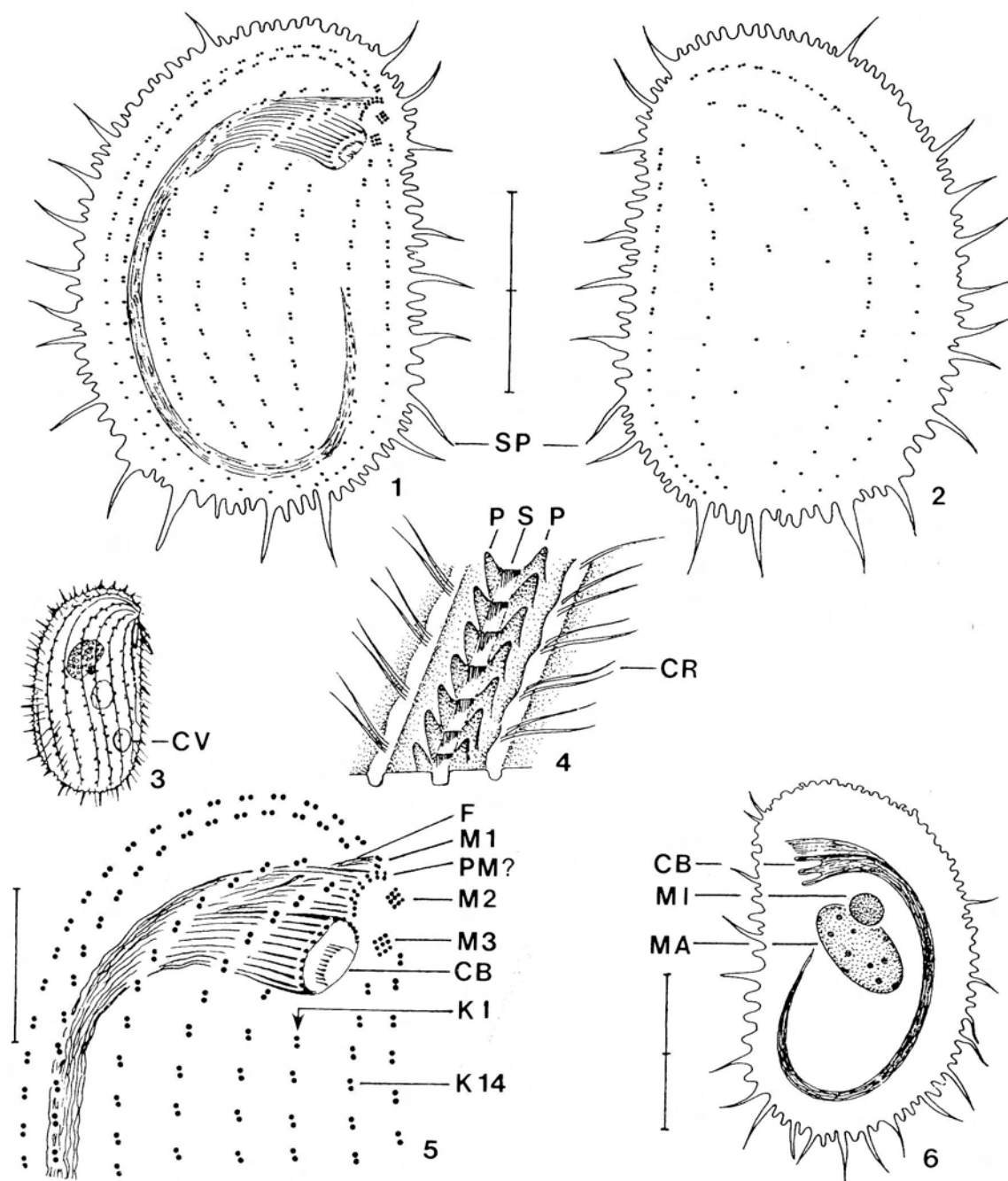
Oral opening near anterior left end of right side. Pharyngeal basket conspicuous because long and almost circular, commences subapically near left body margin and extends dorsally and posteriorly, where it curves ventrally and anteriorly to end near basket opening (Figs. 1, 6, 7, 9, 10); right half of basket composed of about 10 fine rods originating from minute granules [unciliated basal bodies (?) forming paroral membrane (?), as in *Pseudomicrothorax*; Peck (1974)], left half composed of very fine fibres, forming three to four digitate processes (rods ?) at pharyngeal opening; basket lumen with conical, finely striated structure (Figs. 5, 6, 9 - 11). Adoral membranelles left and above pharyngeal opening, minute (Figs. 1, 5, 9, 10): membranelle 1 near anterior end of somatic kineties 5 and 6, consists of only about four basal bodies; membranelles 2 and 3 square-shaped, each consisting of three kineties with three basal bodies each (Figs. 1, 5, 9, 10). Single, short, curved kinety (paroral membrane ?) above pharyngeal opening between and right of adoral membranelles 1 and 2, composed of about six dikinetids and a monokinetid tail comprising two or three basal bodies, associated with fine fibres merging into oral basket (Figs. 1, 5, 7, 9, 10).

Table 1. Morphometric data from *Lopezoterenia torpens*¹⁾

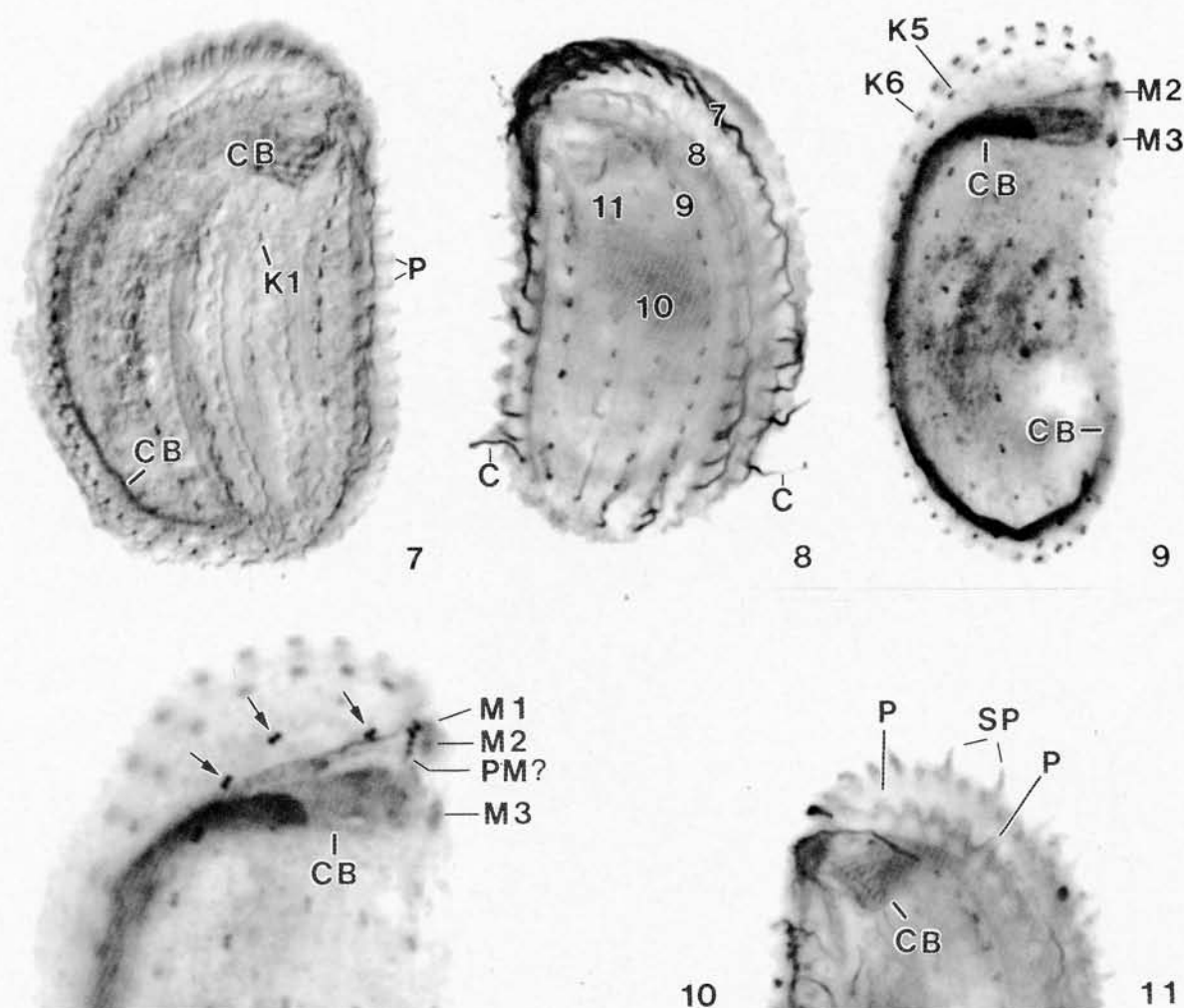
Character	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	49.0	50.0	2.4	0.9	5.0	45	51	7
Body, maximum width	29.9	29.0	3.2	1.2	10.8	27	36	7
Anterior end to proximal margin of adoral membranelle 3, distance	12.9	13.0	1.3	0.5	10.4	11	15	7
Cytopharyngeal basket, diameter ²⁾	7.0	7.0	0.8	0.3	11.7	6	8	7
Kineties on right side, number	8.0	8.0	0.0	0.0	0.0	8	8	6
Kineties on left side, number	6.0	6.0	0.0	0.0	0.0	6	6	6
Kinetids in kinety 1, number	10.5	10.5	2.3	1.0	22.3	8	14	6
Kinetids in kinety 5, number	26.3	26.5	5.2	2.1	19.8	21	34	6
Kinetids in kinety 14, number	12.7	12.0	2.6	1.1	20.3	10	17	6

1) Data based on protargol-impregnated and mounted specimens from field. 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 mean, $\bar{x}$ - arithmetic mean.

2) Including rods originating from paroral kinety-like ciliary row.



Figs. 1 - 6. *Lopezoterenia torpens* from life (3) and after protargol impregnation (1, 2, 4 - 6). 1, 2. Infraciliature of right and left side. 3. Right lateral view, length 60 μm (from Kahl, 1931). 4. Cortical ornamentation. 5. Anterior body portion at higher magnification showing details of somatic and oral infraciliature. 6. Left lateral view showing nuclear apparatus and left side of pharyngeal basket. CB - cytopharyngeal basket, CR - ciliary row, CV - contractile vacuole, F - fibres originating from adoral membranelle 1, K1, 14 - somatic kineties 1 and 14, MA - macronucleus, MI - micronucleus, M1, M2, M3 - adoral membranelles, P - cortical papillae, PM? - paroral membrane, S - septate furrow, SP - cortical spines. Scale bar division 10 μm .



Figs. 7 - 11. *Lopezoterenia torpens*, somatic and oral infraciliature after protargol impregnation. 7, 8. General right and left lateral views. Note highly ornamented cortex. Numbers denote kineties. 9. Ventrolateral view showing long, curved oral basket (CB). 10, 11. Right and left anterior end showing details of oral apparatus and cortical ornamentation. Arrows mark somatic dikinetids. C - cilia, CB - cytopharyngeal basket, K1 - 10 - somatic kineties, M1, M2, M3 - adoral membranelles, P - cortical papillae, PM? - paroral membrane, SP - cortical spines.

Occurrence and ecology: *Lopezoterenia torpens* is a very rare species, having been recorded only five times. Kahl (1931) discovered few specimens in the sandy mud of the Alster, a brackish tributary to the River Elbe near Hamburg (Germany). Later, Lackey and Lackey (1963, 1970) reported it from sand and mud flats near Plymouth (England) and from Logy Bay, Newfoundland. Burkovsky (1970) found sparse numbers rather frequently in the fine sand (0.25 - 0.5 mm) of the Kandalaksha Gulf, White Sea. My population occurred in the sandy mud of the Atlantic coast at Roscoff (France).

Discotricha papillifera Tuffrau, 1954 (Figs. 12 - 26, Table 2)

This species has been well described by Tuffrau (1954), Dragesco (1965), and Wicklow and Borror (1977), using live observation, silver nitrate impregnation, and transmission electron microscopy (Figs. 12, 16). However, protargol impregnation (voucher slides deposited in the Oberösterreichische Landesmuseum in Linz) revealed several new details, which are summarized

in the following paragraphs (terminology after Wicklow and Borror, 1977):

1. *Discotricha papillifera* invariably has nine kineties on the right side (Figs. 17, 19, 22, Tab. 2). On the left side, the ciliation is very sparse and most of the kinetids are unciliated, except those of the conspicuous frontal row (Figs. 18, 26).

2. The dikinetids in kinty 2 are more irregularly arranged than depicted by Wicklow and Borror (1977) and those at the ends of kineties 3 - 6 (Figs. 15 - 17, 19, 21).

3. The cytopharyngeal basket is circular and, like that of *Lopezoterenia torpens*, asymmetrical, i.e. its right half is formed by about eight fine rods while the left half consists of very fine fibres forming three to four digitate processes (rods?) at the pharyngeal opening (Figs. 17, 18, 19, 22, 23, 26).

4. Adoral membranelle 1 is smaller than the membranelles 2 and 3, which invariably consist of three kineties, each comprising three basal bodies (Figs. 15, 17, 22, 23).

5. There is a special field of fine, rod-shaped extrusomes (?) at the left margin of the central portion of somatic kinty 2 (Figs. 15, 20, 21).

6. The extrusomes, located in conspicuous papillae, are nail-shaped, i.e. have a distinct head, at least after protargol impregnation (Figs. 13, 15, 21, 22, 24, 25).

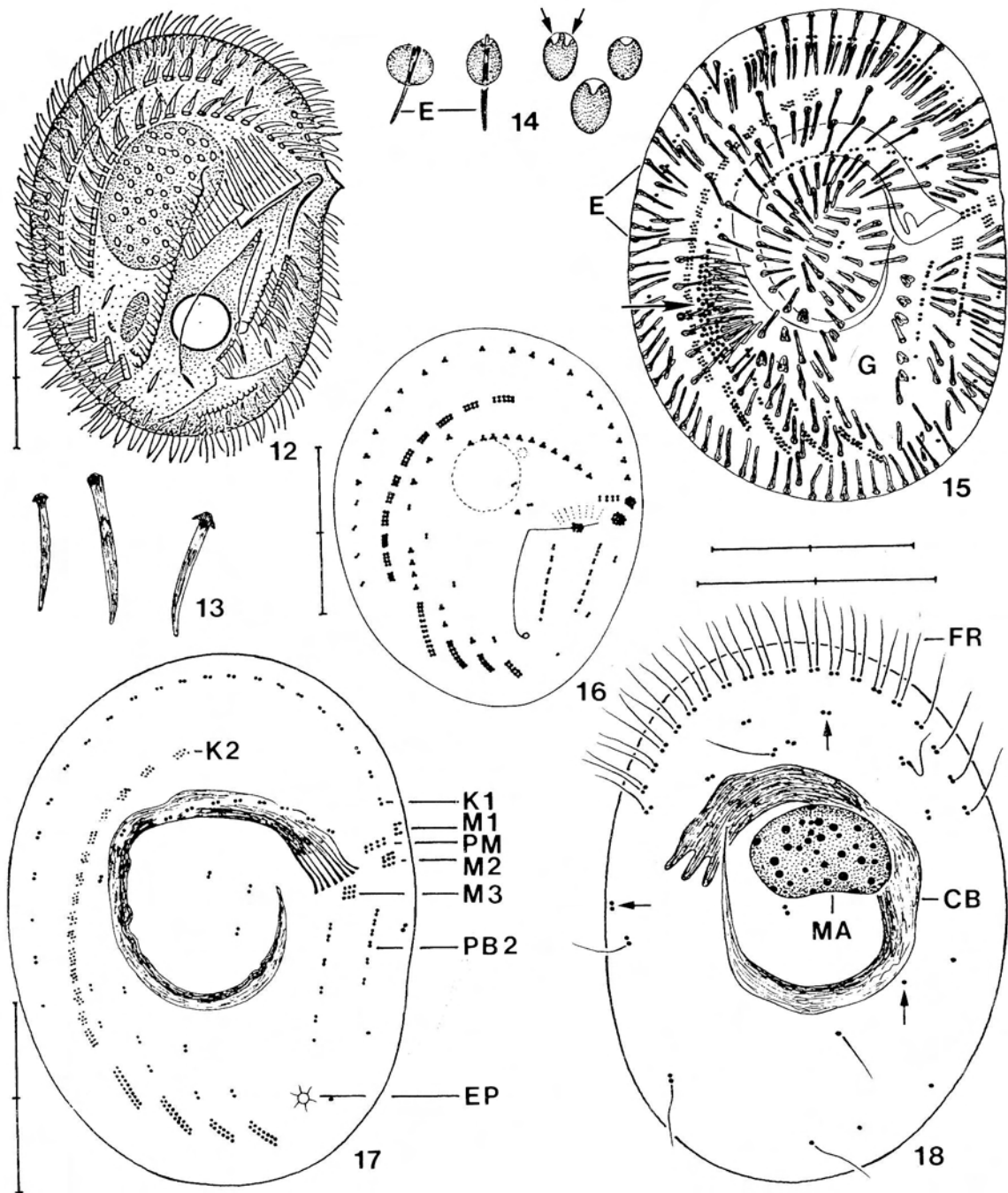
Occurrence and ecology: Although sometimes numerous, *D. papillifera* is very likely a rare species, like *Lopezoterenia torpens*, because it has been discovered rather recently and, since then, has been recorded only six times. Tuffrau (1954) discovered great numbers of *D. papillifera* in marine sand at Pointe de Raguénès near Concarneau, France. Likewise, Dragesco (1965) found great numbers in marine sand at Port-Etienne, Mauritania (Africa). Fenchel (1968) observed a few specimens in the Øresund, Denmark. Wicklow and Borror (1977) and Borror (1980) found *D. papillifera* near mean tidal level at Foss beach (New Hampshire) in the top 3 cm of sand (mean grain size 0.36 mm) in an area of high interstitial water content with a salinity of 30 ‰. Small *et al.* (1985) isolated *D. papillifera* from fine coastal marine sands of Tom's Cove, Assateague Island, Virginia (USA), and Sudzuki (1979) reported a *Discotricha* (?) sp. from Japan. I found sparse numbers in coastal marine sands at Roscoff (France), where it occurred together with *L. torpens* and many karyorelictids.

Table 2. Morphometric data from *Discotricha papillifera*¹⁾

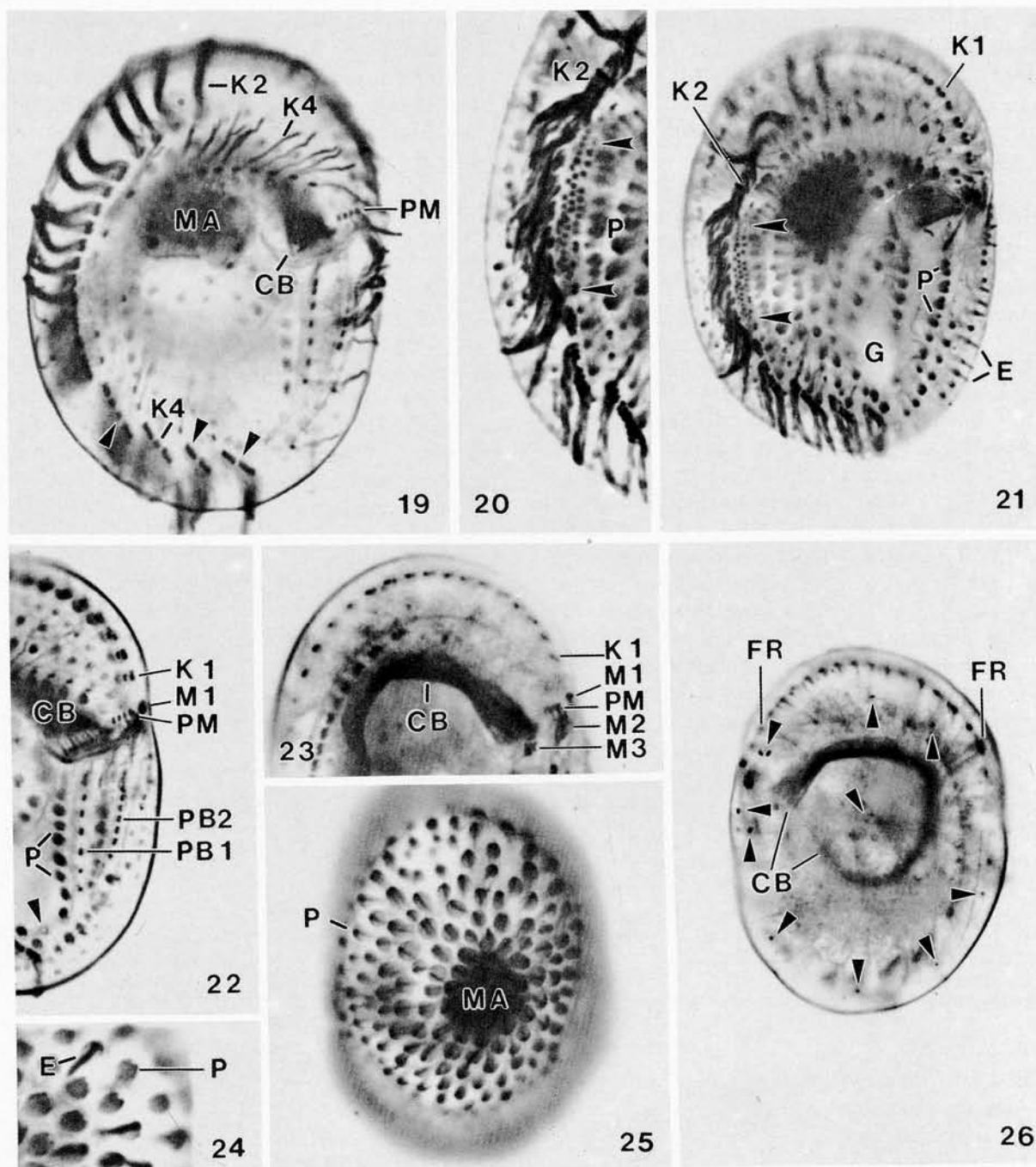
Character	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	47.8	48.0	5.1	1.4	10.6	41	56	13
Body, maximum width	35.8	35.0	4.9	1.4	13.7	29	45	13
Anterior end to proximal margin of adoral membranelle 3, distance	22.4	22.0	3.5	1.0	15.6	17	29	13
Anterior end to pore of contractile vacuole, distance	40.3	40.0	4.5	1.3	11.3	31	46	13
Macronucleus, length	11.4	11.0	2.0	0.7	17.5	9	15	8
Macronucleus, width	8.2	8.5	1.3	0.5	15.6	6	10	8
Cytopharyngeal opening, diameter	5.9	5.0	1.3	0.4	22.4	5	9	13
Kineties on right side, number	9.0	9.0	0.0	0.0	0.0	9	9	13
Kinetids in kinty 1, number ²⁾	23.5	22.0	4.8	1.3	20.3	16	35	13
Kinetid groups in kinty 2, number	14.2	15.0	2.5	0.7	17.5	11	19	13
Kinetids in post-buccal kinty 2, number	7.2	6.0	1.8	0.5	24.6	6	12	13
Kinetids in paroral membrane, number	4.0	4.0	0.0	0.0	0.0	4	4	13

1) Data based on protargol-impregnated and mounted specimens from field. 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 mean, $\bar{x}$ - arithmetic mean.

2) Terminology and kinty numbering according to Wicklow and Borror (1977).



Figs. 12 - 18. *Discotricha papillifera* from life (12) and after protargol (13 - 15, 17, 18) and silver nitrate (16) impregnation. 12. Right lateral view of African population (from Dragesco, 1965). 13. Extrusomes (cp. Fig. 15). 14. Extrusomes within cortical papillae and empty papillae. Usually, each papilla contains a single extrusome, rarely two (arrows). 15. Extrusome and ciliary pattern. Arrow marks special extrusome field (cp. Figs. 20, 21). 16. Infraciliature of right side of New Hampshire population (from Wicklow and Borror, 1977). 17, 18. Infraciliature of right and left side of Roscoff population. Arrows mark unciliated kinetids. CB - cytopharyngeal basket, E - extrusomes, EP - pore of contractile vacuole, FR - frontal ciliary row, G - groove (cp. Fig. 12), K1, 2 - somatic kineties, MA - macronucleus, M1, M2, M3 - adoral membranelles, PB2 - post-buccal kinety 2, PM - paroral membrane. Scale bar division 10 μ m.



Figs. 19 - 26. *Discotricha papillifera*, somatic and oral infraciliature after protargol impregnation. 19. General right side view. Arrowheads mark cirri-like cilia aggregates at posterior end of somatic kineties 3 - 6. Note also distinct "cirri" in kinety 2. 20, 21. Right side views showing general organization and details from a field of special extrusomes (arrowheads) left of kinety 2. 22, 23. Right side views showing details of somatic and oral infraciliature. Arrowhead marks pore of contractile vacuole. 24. Full (i.e. containing an extrusome) and empty cortical papillae. 25. Left side view showing cortical papillae each containing an extrusome. 26. The left side is sparsely ciliated (arrowheads), except at the anterior margin, where a conspicuous frontal ciliary row extends. Note circular pharyngeal basket. CB - cytopharyngeal basket, E - extrusomes, FR - frontal ciliary row, G - groove (cp. Fig. 12), K1, 2, 4 - somatic kineties, MA - macronucleus, M1, M2, M3 - adoral membranelles, P - cortical papillae, PB1, 2 - post-buccal kineties, PM - paroral membrane.

No detailed ecological data are available for *D. papillifera*. I can confirm the observations of Tuffrau (1954), Dragesco (1965), and Fenchel (1968) that it feeds on diatoms. The records from Eurasia and Africa indicate that it is cosmopolitan.

Redescription of *Paraspathidium fuscum* (Kahl, 1928) Fjeld, 1955 (Figs. 27 - 64, Table 3)

Identification: This species has been investigated by several authors (Agamaliyev, 1968, 1983; Biernacka, 1963; Czapik and Jordan, 1976; Dragesco, 1960, 1963; Dragesco and Dragesco-Kernéis, 1986; Fjeld, 1955; Hartwig, 1973a, 1980; Kahl, 1930; Noland, 1937; Petzold, 1956). However, most redescriptions added little, if any, to Kahl's rather detailed original description, and none recognized the features important for a reliable classification, as also emphasized by Dragesco and Dragesco-Kernéis (1986). Thus, I provide a complete redescription with copious figure documentation, which should be helpful to future revisers of the genus in deciding about synonymy of *P. fuscum* Kahl, 1928, *P. trichostomum* Noland, 1937, and *P. obliquum* Dragesco, 1963. For the present, I agree with Fjeld (1955) that at least *P. trichostomum* should be considered as a junior synonym of *P. fuscum*.

Type material: No type material from *P. fuscum* has been mentioned in the literature. Thus, I have deposited four neotype slides with protargol-impregnated cells in the Oberösterreichische Landesmuseum in Linz (LI). Relevant specimens are marked by a black ink circle on the cover glass.

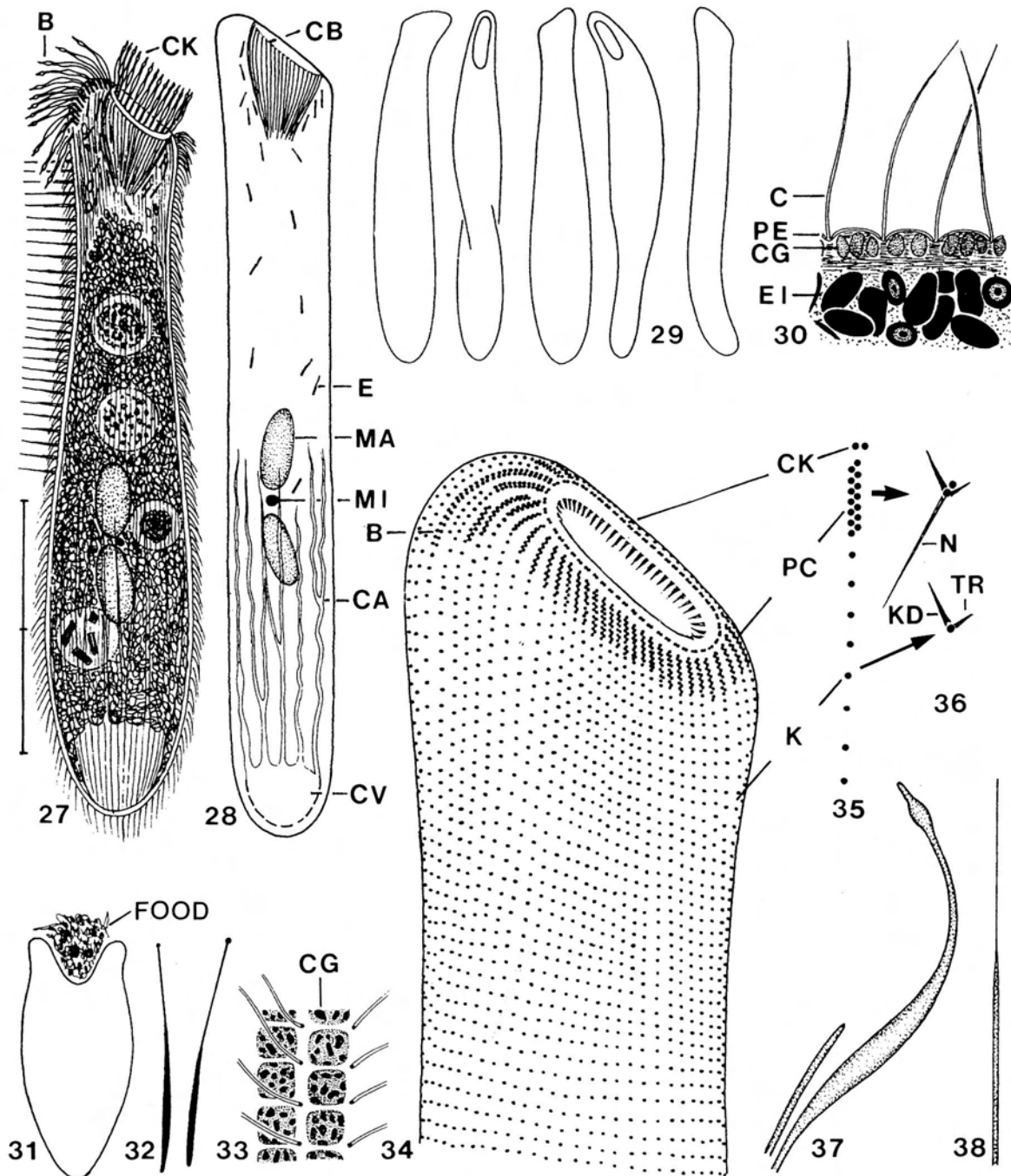
Redescription: Morphometric data shown in Table 3 are repeated in this section only as needed for clarity. The redescription is based on cultured specimens studied in live and with the scanning electron microscope as well as on protargol and silver carbonate-impregnated cells. However, *P. fuscum* is very difficult to stain. Thus, Figures 34-36 are composites from several specimens and the neotype slides mentioned above are only mediocre in quality. The best results were obtained from heavily squashed, unmounted specimens (Figs. 49, 50, 54, 56, 59).

Size, length:width ratio, and shape highly variable, as also indicated by literature data (200-500 μm , 8-13:1; Agamaliyev, 1968, 1983; Dragesco, 1960; Fjeld, 1955; Kahl, 1928; Noland, 1937). Cultured Roscoff specimens *in vivo* about 220-350 x 40-60 μm , length:width ratio 4:1-9:1, on average 6.5:1 ($n = 11$; Figs. 27-29); contract slightly during fixation, prepared specimens thus stouter than live cells (length:width ratio 3.5-6:1, on average 5:1, Tab. 3; Figs. 39-41, 51). *In vivo* very flexible and about 30% contractile, especially in anterior half, as also observed by Kahl (1928) and Biernacka (1963);

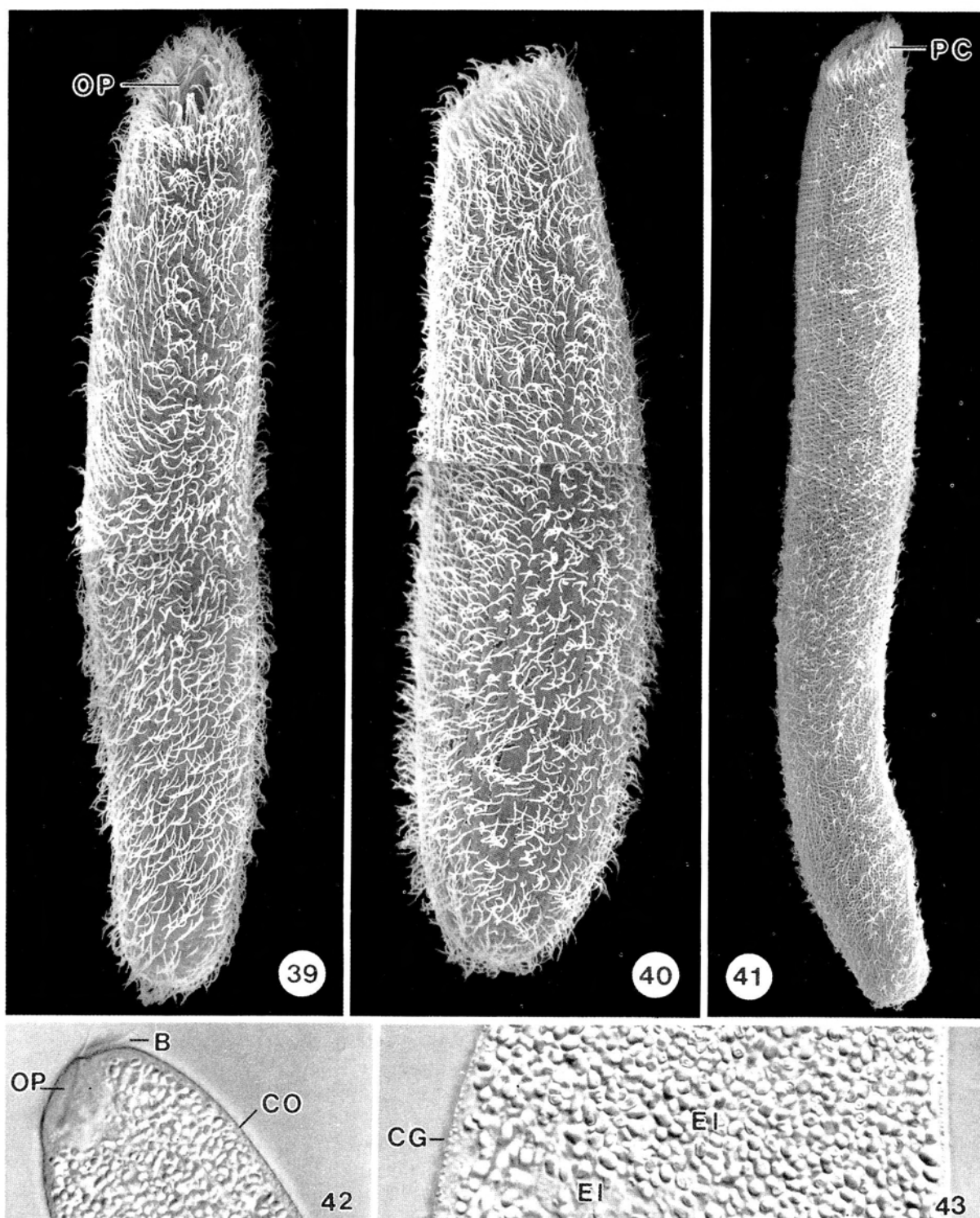
Table 3. Morphometric data from *Paraspathidium fuscum*¹⁾

Character	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	282.8	290.0	34.2	6.4	12.1	220	335	29
Body, maximum width	59.7	60.0	5.2	1.0	8.6	50	70	29
Anterior end to nuclear apparatus, distance	155.1	160.0	30.4	5.6	19.6	75	225	29
Macronuclear nodule, length	25.9	25.0	4.2	0.8	16.4	19	35	29
Macronuclear nodule, width	11.1	11.0	0.9	0.2	8.1	9	13	29
Micronucleus, length	4.2	4.0	0.5	0.1	11.1	4	6	29
Micronucleus, width	3.2	3.0	0.4	0.1	13.3	3	5	29
Somatic kineties, number	55.2	55.0	2.6	0.5	4.7	50	60	29
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2	2	29
Micronuclei, number	1.0	1.0	0.0	0.0	0.0	1	1	29

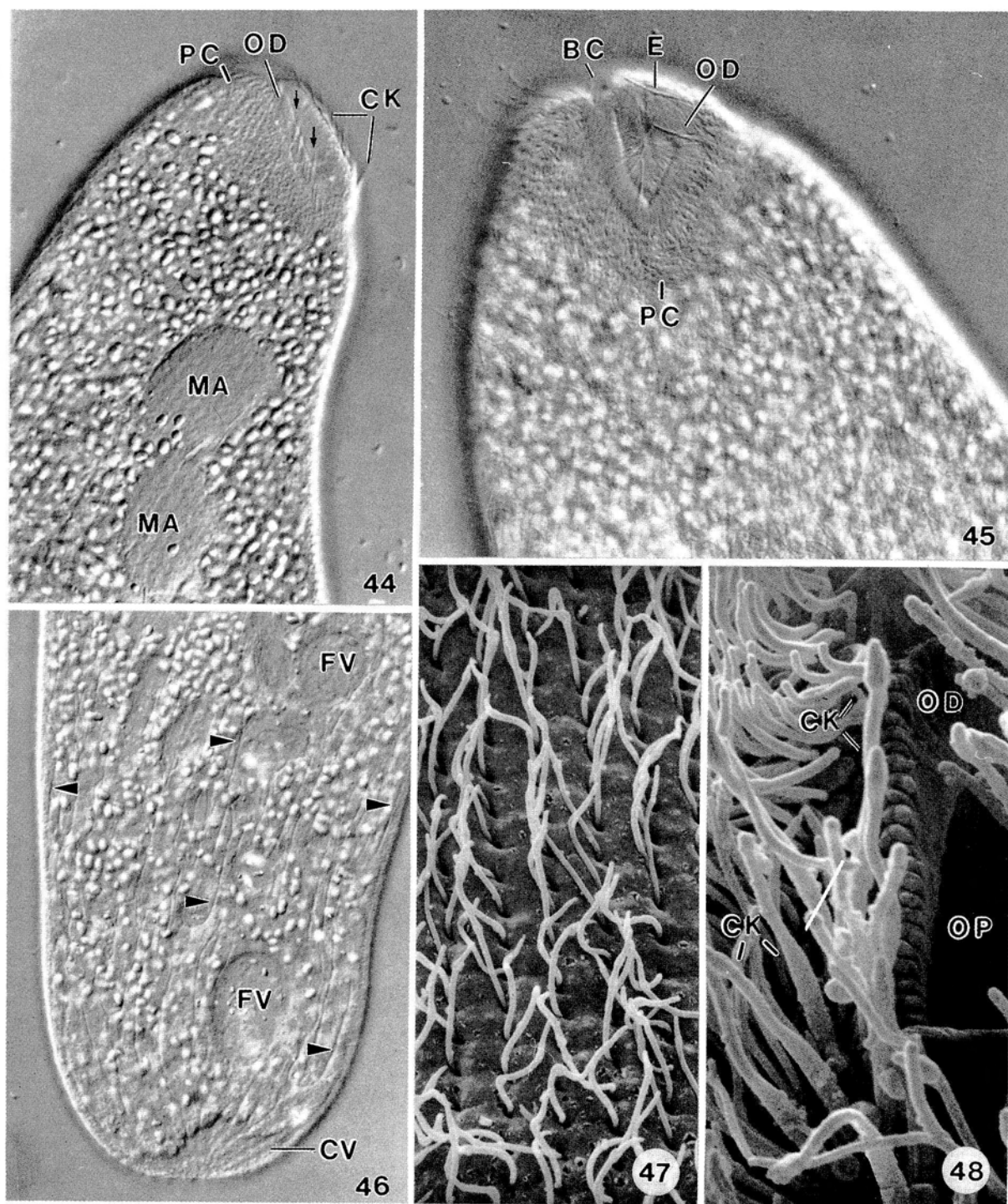
1) Data based on protargol-impregnated and mounted, cultured specimens. Measurements in μm . CV - coefficient of variation in %, M - median, Max - maximum, Min - minimum, n - number of individuals investigated, SD - standard deviation, SE - standard error of mean, $\bar{x}$ - arithmetic mean.



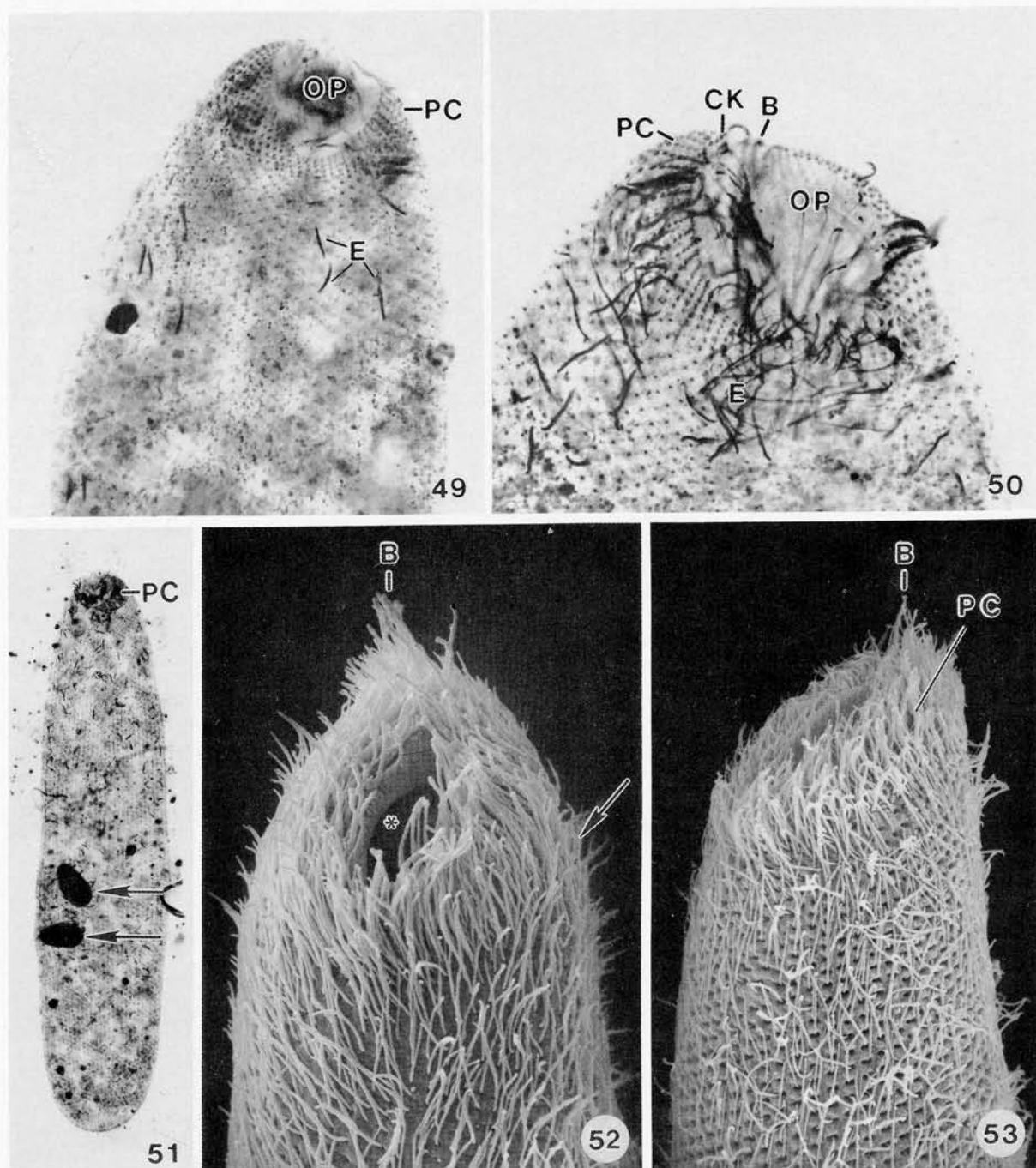
Figs. 27 - 38. *Paraspithidium fuscum* from life (27 - 34, 37, 38) and after protargol (34, 35) and silver carbonate (36) impregnation. 27, 28. Right lateral views of typical specimens. Scale bar division 45 μ m. 29. Shape variants in lateral and ventral views (redrawn from video records). 30, 33. Transverse section and surface view of cortex. 31. Shape of feeding cell. 32. Extrusomes, length 10 μ m. 34. Infraciliature of right anterior end (composite from several stains and specimens). 35, 36. Details of kinetid structure. 37, 38. Brush cilia, length up to 25 μ m (cp. Fig. 27). B - dorsal brush, C - cilium, CA - canals of contractile vacuole, CB - cytopharyngeal basket, CG - cortical granules, CK - circumoral kinety, CV - contractile vacuole, E - extrusomes, EI - highly refractile cytoplasmic inclusions, K - somatic kineties, KD - kinetodesmal fibre, MA - macronucleus, MI - micronucleus, N - nematodesma, PC - perioral ciliary corona, PE - pellicle, TR - transverse microtubule ribbon.



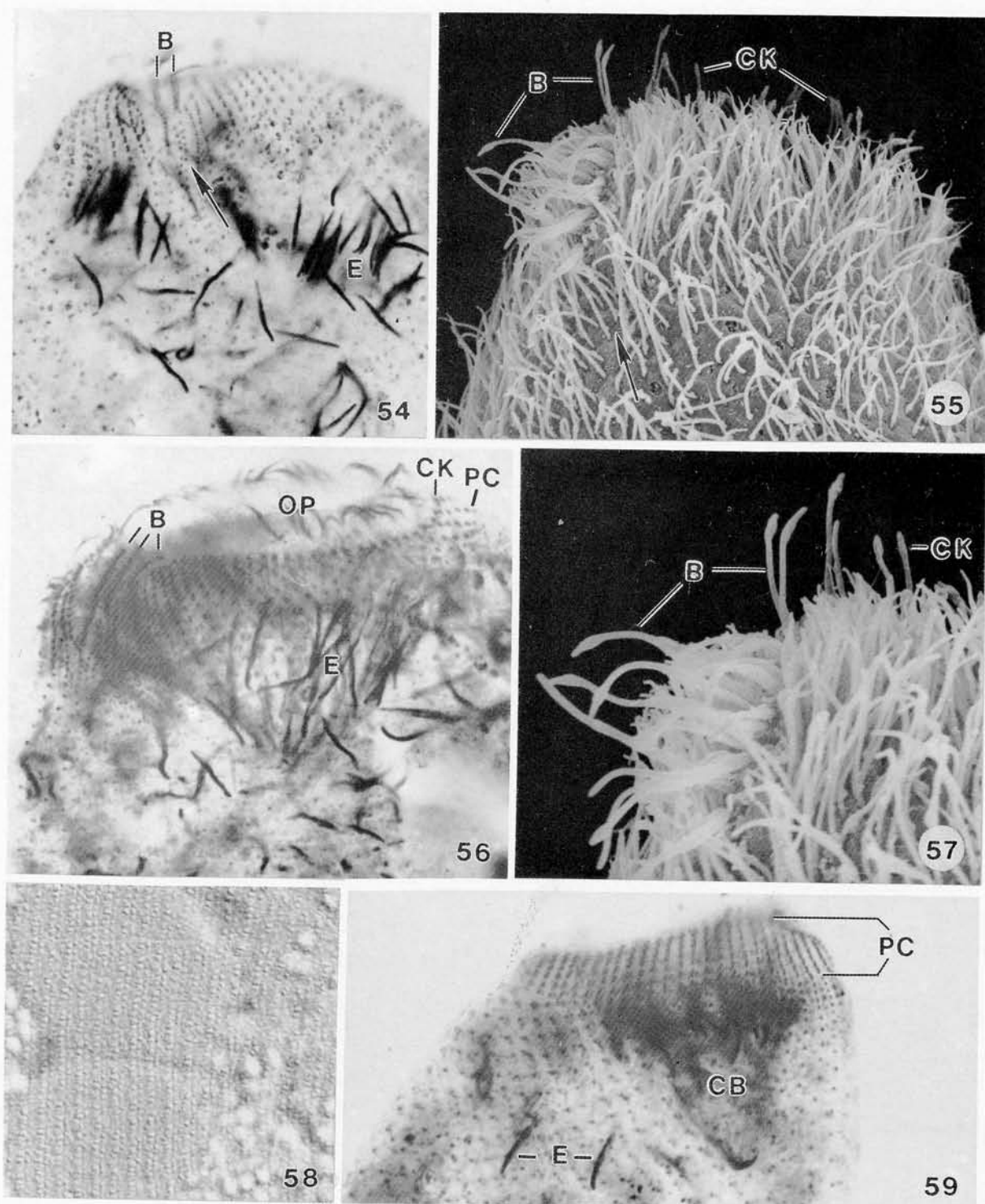
Figs. 39 - 43. *Paraspithidium fuscum* in the scanning electron microscope (39 - 41) and from life (42, 43). 39. Ventral view of typical specimen. 40, 41. Left lateral views of a broad and a slender specimen. 42. Anterior body end. 43. Cytoplasmic inclusions in mid-body. B - dorsal brush, CG - cortical granules, CO - gelatinous cortex, EI - highly refractile cytoplasmic inclusions, OP - oral opening, PC - perioral ciliary corona.



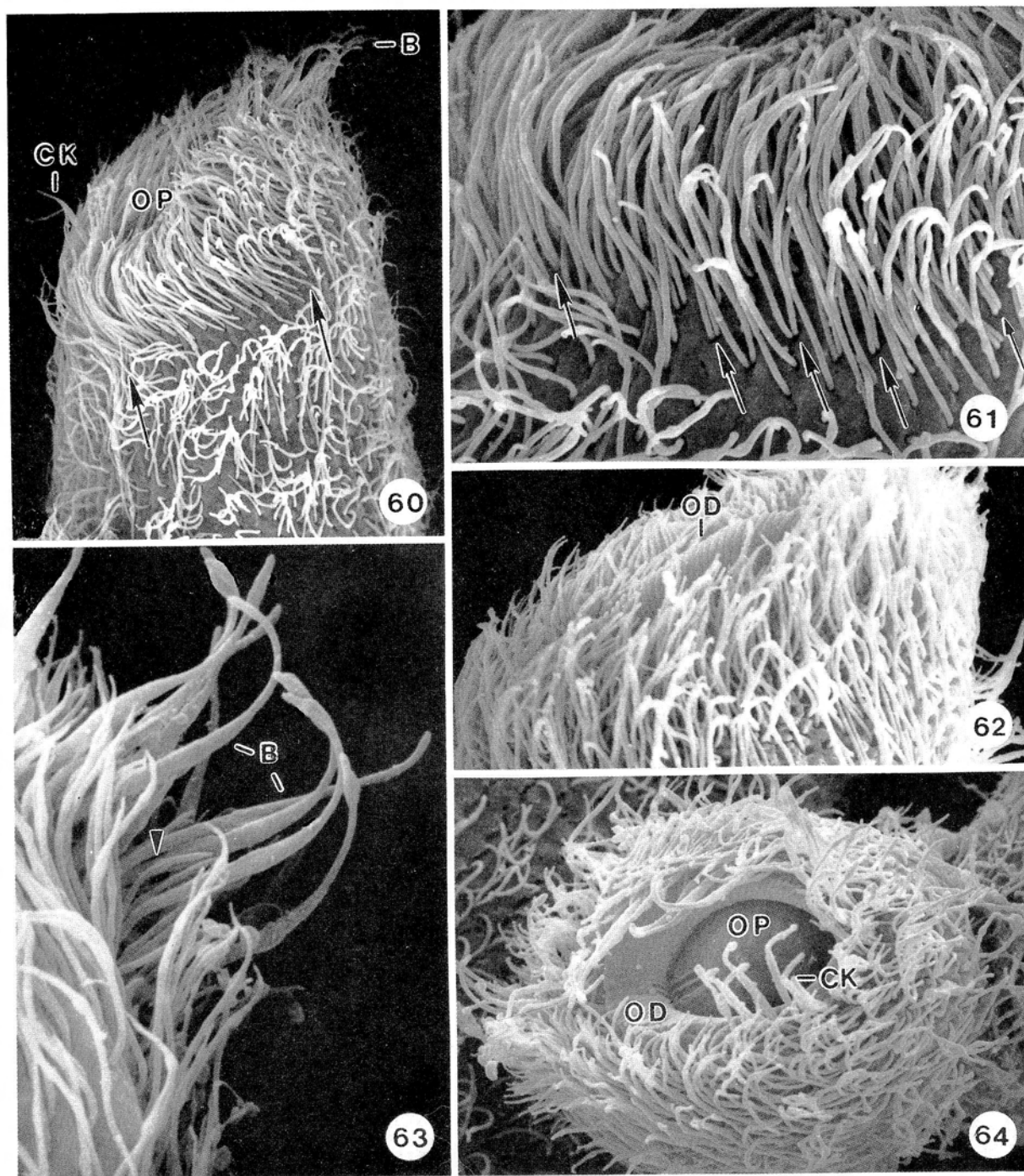
Figs. 44 - 48. *Paraspithidium fuscum* from life (44 - 46) and in the scanning electron microscope (47, 48). 44, 45, 48. Right lateral and ventral views of anterior body portion showing details of oral apparatus. Arrows mark inflated cilia of circumoral kinety. 46. Posterior body portion showing long, fine canals (arrowheads) originating from contractile vacuole and extending to mid-body. 47. Surface view in mid-body. The somatic ciliature consists of single cilia (monokinetids), which originate from deep, cortical pits. BC - brush cleft, CK - circumoral kinety with inflated cilia, CV - contractile vacuole, E - extrusome, FV - food vacuoles, MA - macronuclear nodules, OD - oral dome, OP - oral opening, PC - perioral ciliary corona.



Figs. 49 - 53. *Paraspithidium fuscum*, oral and somatic infraciliature after protargol impregnation (49 - 51) and in the scanning electron microscope (52, 53). 49, 50. Ventral views of anterior body portion. 51. General view showing macronuclear beads (arrows) in typical sub-equatorial location. 52, 53. Ventral and left lateral view of anterior body portion. Asterisk marks excavated oral opening. Arrow denotes transition zone of somatic dikinetids, producing conspicuous perioral ciliary corona, and somatic monokinetids. The cilia are very regularly arranged and originate from deep pits producing cross-hatched, symmetrical pattern (Fig. 53). B - dorsal brush, CK - circumoral kinety, E - extrusomes, OP - oral opening, PC - perioral ciliary corona composed of oralized somatic dikinetids.



Figs. 54 - 59. *Paraspithidium fuscum* from life (58), after protargol impregnation (54, 56, 59), and in the scanning electron microscope (55, 57). 54 - 57. Dorsal views showing details of brush and circumoral kinety. Arrows mark two shortened, monokinetidal kineties underneath left brush row. 58. Surface view showing cortical bolsters containing irregular granules (cp. Figs. 30, 33). 59. Infraciliature of left anterior body portion. B - dorsal brush, CB - cytopharyngeal basket, CK - circumoral kinety, E - extrusomes, OP - oral opening, PC - perioral ciliature.



Figs. 60 - 64. *Paraspithidium fuscum*, details of oral apparatus and dorsal brush in the scanning electron microscope. 60, 61. The oral opening (cp. Fig. 64) is surrounded by a corona of ciliated dakinets (arrows). 62, 64. The excavated oral opening is surrounded by an unciliated dome at the base of which the circumoral kinety extends. 63. The cilia of the dorsal brush are distinctly elongated (20 μ m) and have, like those of the circumoral kinety (cp. Figs. 48, 57, 60, 64), a very peculiar shape. The arrowhead marks a short, distally inflated cilium in front of a long dorsal brush cilium. B - dorsal brush, CK - circumoral kinety, OD - oral dome, OP - oral opening.

however, later Kahl (1930) stated that *P. fuscum* can contract up to 2/3 of its length. This is not unlikely because feeding specimens strongly contract becoming urceolate (Fig. 31). Shape likewise fairly variable, usually, however, cylindrical or slightly bursiform and highly reminiscent of slender spathidiids (cp. Kahl, 1930); anterior mouth-bearing portion more or less distinctly widened and obliquely truncate, posterior end narrowly rounded, laterally slightly flattened (Figs. 27 - 29, 39 - 41). Nuclear apparatus on average slightly underneath mid-body, invariably consisting of two ellipsoidal (about 2:1) macronuclear nodules with a single micronucleus in between (Figs. 27, 28, 44, 51; Tab. 3). Contractile vacuole in posterior end, associated with many fine and anastomosing collecting canals extending to at least mid-body (Figs. 27, 28, 46); very likely, these canals were interpreted as satellite vacuoles by Dragesco (1960, 1963). Extrusomes in vivo about 10 x 0.5 µm, concentrated around pharyngeal basket and scattered throughout cytoplasm, consist of fusiform posterior half, which stains with protargol, and filiform anterior portion having minute globule on top (Figs. 28, 32, 45, 49, 50, 54, 56). This particular shape of the extrusomes, highly reminiscent of exploded toxicysts, was seen in 10 specimens and thus very likely represents the resting state. Cortex about 2 µm thick, stands out as bright fringe from darkly granulated cytoplasm (Figs. 27, 42, 43), distinctly punctate by deep ciliary pits (Figs. 41, 53), very flexible and gelatinous, contains innumerable tiny granules in small bolsters between ciliary rows (Figs. 30, 33, 43, 58); cortical granules irregularly shaped, 0.1 - 2 µm across, stain blue with methyl green-pyronin but are not extruded when dye is added. Cells, respectively, cytoplasm conspicuously dark at X 100 due to countless, highly refractive inclusions; mouth region, macronuclear nodules, contractile vacuole, and food vacuoles stand out as bright blisters; inclusions colourless, ellipsoidal to roughly globular, some possibly hollowed, 3 - 6 x 2 - 4 µm in size (Figs. 27, 30, 43). Slowly gliding on bottom of culture dishes or swimming by rotation about main body axis, usually, however burrowing in and under mats of sulphur bacteria ingesting small ciliates (mainly *Euplotes*), which break in pieces when touching mouth opening (Fig. 31).

Somatic cilia 8-10 µm long, very regularly arranged in bipolar and transverse rows, originate from deep cortical pits producing curious, cross-hatched

cortical pattern (Figs. 34, 41, 47, 53, 59), as already noted by Kahl (1928) and Noland (1937). Cilia single (monokinetids), except at anterior end of kineties, where 5-10 narrowly spaced, ciliated dikinetids occur producing conspicuous perioral ciliary corona (Figs. 34, 35, 41, 44, 47, 49, 52, 53, 59, 60, 61). Anterior dikinetids associated not only with the usual set of fibres (short, anteriorly directed kinetodesmata and very short transverse microtubule ribbon), but also with long nematodesma supporting cytopharyngeal basket (Fig. 36; oralized somatic kinetids, see Foissner and Foissner, 1988). Dorsal brush highly complex, difficult to study because short and in deep cleft at dorsal anterior end of cell, consists of two or three rows of transversely oriented dikinetids bearing up to 25 µm long, curiously vase-shaped cilia (Figs. 27, 34, 37, 42, 45, 50, 52, 54 - 57, 63); left row with monokinetidal tail extending above mid-body and bearing 15 - 20 µm long cilia having filiform process (Figs. 27, 38). Long, vase-shaped brush cilia accompanied by about 5 µm long, rod-shaped cilia (Figs. 37, 63).

Oral apparatus in widened anterior end of cell. Oral opening apical, elliptical, excavated (i.e. not closed), surrounded by inconspicuous oral dome (Figs. 28, 39, 42, 44, 45, 48, 49 - 53, 62, 64). Circumoral kinety at base of oral dome, made of dikinetids having, like dorsal brush, about 15 µm long, vase-shaped cilia (Figs. 27, 34, 35, 44, 48, 50, 55 - 57, 60, 64). Inner wall of oral dome striated by fine fibres forming inconspicuous, campanulate cytopharyngeal basket (Figs. 27, 28, 34, 48, 62).

Occurrence and ecology: There are about 50 records of *P. fuscum* in the literature, including Mexico (Aladro-Lubel *et al.*, 1990) and South America (Kattar, 1970), indicating that it has a world-wide distribution (for reviews, see Agamaliyev, 1983; Detcheva, 1992; Dragesco and Dragesco-Kernéis, 1986; Hartwig, 1973a, 1974, 1980; Hartwig and Parker, 1977). Some details on the ecology of *P. fuscum* have been reported, mainly by Fenchel (1969) and Hartwig (1973b). Fenchel (1969) found a low tolerance to H₂S (< 0.1 g/l) and up to 30 ind./cm² in the Helsingør Beach (Denmark). Hartwig (1973b), working at Sylt (Germany), observed that *P. fuscum* preferred the lentic zones and migrated from the 0-5 cm top sediment layer to the 5-10 cm layer during the cold season. 10-100 ind./100 ml sediment were common throughout the year, with peaks of up to 1500 cells in September. Petzold

(1956) observed *P. fuscum* in brackish water (5.4‰) at Hiddensee, a small island at the north coast of Germany. This agrees with data from Biernacka (1963), who observed *T. fuscum* at 7‰ and 9.5–14°C at the Polish coast. Thus, *T. fuscum* is a euryhaline halobiont.

Paraspathidium fuscum feeds on algal debris, euglenoid flagellates, and ciliates (Kahl, 1928, 1930; present data). More detailed observations were performed by Fenchel (1968). According to this author, *P. fuscum* is a histophage which is quickly attracted to small metazoans torn to pieces with needles. The vacuole contents of 33 individuals from Nivå Bay, the Helsingør Beach, and Askø Harbor were investigated. In most cases they contained material of animal origin, in one case a bristle of the oligochaete *Paranais littoralis*. Often the vacuoles also contained material of vegetable origin, mostly dinoflagellates, rarely diatoms, and in some cases the vacuoles contained remains of ciliates.

Discussion

Systematic position of *Lopezoterenia torpens* and comparison with related genera

Lopezoterenia torpens has three minute adoral membranelles and a conspicuous pharyngeal basket composed of fine rods (Figs. 1, 5, 6, 9). Thus, it belongs to the Nassophorea Small and Lynn, 1981. Within this assemblage, *L. torpens* is most closely related to the microthoracids, as already mentioned by Kahl (1931), because it is small and strongly flattened laterally, has a richly ornamented cortex (Figs. 4, 7, 11), somatic monokinetids and dikinetids (Figs. 1, 2), three minute adoral membranelles (Figs. 5, 9, 10), and a strongly curved pharyngeal basket (Figs. 1, 6, 9). Three families have been recognized within the Microthoracina (Foissner, 1985): Microthoracidae (with reduced somatic ciliature and three preoral kineties; extrusomes with anchor-like processes), Pseudomicrothoracidae (holotrichously ciliated; ciliary rows in deep furrows and abutting preorally; without preoral kineties; extrusomes with anchor-like processes), Discotrichidae (with reduced somatic ciliature; cilia partially fused to cirri-like organelles; without preoral kineties; extrusomes fusiform, i.e. without anchor-like processes). *Lopezoterenia* lacks preoral kineties and compound

ciliary organelles (Figs. 1, 2), indicating that it could belong to the Pseudomicrothoracidae. However, most other characters are highly reminiscent of *Discotricha papillifera*, as redescribed by Wicklow and Borror (1977) and in the present paper (Figs. 12–26), namely the simple, fusiform trichocysts (Kahl, 1931; Wicklow and Borror, 1977; but see present data, Figs. 13, 15, 24), the paroral membrane-like kinety at the upper right end of the oral field (Figs. 5, 10), the cortical papillae (Figs. 4, 7, 11), the structure of the pharyngeal basket (Figs. 5, 6, 17, 18), and the lack of a postoral primordial field typically found in *Pseudomicrothorax* (Peck, 1974). Thus, *L. torpens* is very likely more closely related to *D. papillifera* than to *Pseudomicrothorax* spp., especially because of the highly characteristic (paroral?) kinety at the upper right end of the oral area (Figs. 5, 10, 17, 19) and the specific structure of the pharyngeal basket (Figs. 5, 6, 17, 18). Furthermore, both *Lopezoterenia* and *Discotricha* inhabit marine sands, whereas *Pseudomicrothorax* spp. have as yet been recorded only from freshwater and terrestrial habitats (Corliss, 1958; Foissner *et al.*, 1994).

Both, the Pseudomicrothoracidae and Discotrichidae are monotypic (Deroux, 1994; Foissner, 1985), i.e. contain only a single genus each, viz. *Pseudomicrothorax* Mermod, 1914 and *Discotricha* Tuffrau, 1954. *Lopezoterenia* differs from both very distinctly, i.e. is a solid new genus: from *Discotricha* mainly by the simple, holotrichous ciliature lacking compound, cirri-like aggregates (cp. Figs. 1, 2, 17, 18) and by details of the cortical pattern [cp. Fig. 4 and Tuffrau (1954) and Wicklow and Borror (1977)]; from *Pseudomicrothorax* by the paroral membrane-like kinety at the upper right end of the oral field (Figs. 5, 10), the simple extrusomes (Kahl, 1931), details of the cortical pattern [cp. Fig. 4 and Peck *et al.* (1991)], and by the pharyngeal basket, which is homomorphic [made of many identical rods; Hausmann and Peck (1978)] in *Pseudomicrothorax* and heteromorphic (right half made of many fine rods, left of few thick processes; Figs. 5, 6) in *Lopezoterenia*.

Classification of the Microthoracina

A refined classification of the microthoracids is possible (Table 4), using the present and literature data (Augustin *et al.*, 1987; Foissner, 1985). Except for *Hemicyclium*, at least one representative of each

genus has been investigated with modern methods. Thus, the group is well-known. The genus *Trochiliopsis* Penard, 1922 has been resurrected by Augustin *et al.* (1987) and Foissner *et al.* (1988). It is closely related to *Stammeridium*. See Corliss (1979) and Foissner (1985) for diagnoses of taxa, synonymy, and nomenclature. Only the Discotrichidae need to be redefined to include *Lopezoterenia*: Microthoracina with strongly ornamented cortex and paroral membrane-like kinety at upper right end of oral area. Ciliary rows in conspicuous furrows forming more or less distinct preoral suture. Cytopharyngeal basket almost circular and heteromorphic, i.e. right half made of many fine rods, left of very fine fibres forming few digitate processes at pharyngeal opening. Extrusomes without anchor-like processes.

Corliss (1979) and Deroux (1994) suggested a slightly different classification, uniting *Leptopharynx* and *Pseudomicrothorax* in the family Leptopharyngidae. This is certainly an artificial grouping not taking account the differences in the preoral ciliature and extrusomes.

Table 4. Classification of microthoracids¹⁾

Suborder Microthoracina Jankowski, 1967
Family Microthoracidae Wrześniowski, 1870 ²⁾
Genera <i>Drepanomonas</i> Fresenius, 1858
<i>Hemicyclium</i> Eberhard, 1862
<i>Leptopharynx</i> Mermod, 1914
<i>Microthorax</i> Engelmann, 1862
<i>Trochiliopsis</i> Penard, 1922
<i>Stammeridium</i> Wenzel, 1969
Family Pseudomicrothoracidae Jankowski, 1967
Genus <i>Pseudomicrothorax</i> Mermod, 1914
Family Discotrichidae Foissner, 1985 ³⁾
Genera <i>Discotricha</i> Tuffrau, 1954
<i>Lopezoterenia</i> nov. gen. (this paper)

1) Based on Foissner (1985). Key literature (mainly containing descriptions and/or redescrptions of type species): Augustin *et al.* (1987), Corliss (1958), Deroux (1994), Foissner (1985), Foissner *et al.* (1988, 1994), Leitner and Foissner (1997), Njine (1979), Peck (1974), Prella (1968), Tuffrau (1954), Wenzel (1953), Wicklow and Borror (1977).

2) First mentioned, but not discussed, in Wrześniowski (1866).

3) First mentioned (name only), but not diagnosed, by Jankowski (1975). Recently erected as a new family by Deroux (1994), without reference to Jankowski (1975) and Foissner (1985). However, Foissner (1985) was the first who provided an appropriate diagnosis and should thus probably credited with this family.

Systematic position of *Paraspathidium* and characterization of the family Paraspathidiidae nov. fam.

Paraspathidium has a complex dorsal brush (Figs. 27, 34, 54 - 57) and oralized somatic kinetids (Figs. 35, 36). Both features are typically found in gymnostome haptorids (Foissner, 1984, 1987, 1996; Foissner and Foissner, 1988). Further, minor characters supporting this assignment are the short transverse microtubule ribbons (Fig. 36; cp. Williams *et al.*, 1981), the toxicysts (Figs. 32, 45, 50), the small but numerous cortical granules (Figs. 30, 33, 43, 58), and the great overall similarity with spathidiid gymnostomes (Figs. 27, 28, 41, 44). Thus, *Paraspathidium* very likely belongs to the gymnostome haptorids, as first suggested by Noland (1937). A relationship with trachelocercids, as proposed by Kahl (1928, 1930), can be definitely excluded because trachelocercids have a glabrous stripe bordered by a highly specific bristle kinety (Foissner and Dragesco, 1996).

There are, however, some features which are reminiscent of the prostomatids, especially the complex contractile vacuole and the dikinetidal perioral ciliary corona (Figs. 28, 34; cp. Hiller 1993a, b). However, a highly evolved contractile vacuole apparatus is found also in various gymnostomes, e.g. *Loxophyllum* (Foissner *et al.*, 1995), and dikinetids at the anterior end of the somatic kineties occur, e.g. in *Lacrymaria* (Foissner *et al.*, 1995).

Within the gymnostomes, *Paraspathidium* matches the Acropisthiina as characterized by Foissner and Foissner (1988): "Cytostome apical, round or oval; nematodesmal bundles originate from typical haptorid oral dikinetids and from ciliated oralized somatic monokinetids. Dorsal brush consists of two or three kineties". However, the general appearance of *Paraspathidium* is more similar to the Spathidiida than the Acropisthiina. Possibly, the specific character combination of the Acropisthiina evolved in several evolutionary lines of the gymnostomes. Thus, a definite intraclass assignment of *Paraspathidium* requires ontogenetic and transmission electron microscopic studies.

Certainly, *Paraspathidium* has a unique combination of characters, warranting separation at familial level. I characterize the Paraspathidiidae nov. fam. as follows: Acropisthiina (?) with excavated oral opening and dikinetidal perioral

ciliature. Brush two or three-rowed, consists of highly specialized, vase-shaped cilia. Jankowski mentioned a family Paraspastidiidae already in 1975. However, he provided the name only, i.e. did not characterize it. Thus, it is a nomen nudum.

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