ACTA
PROTOZOOLOGICA

Systematic Position and Phylogenetic Relationships of the Genera *Bursaridium, Paracondylostoma, Thylakidium, Bryometopus,* and *Bursaria* (Ciliophora: Colpodea)

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Summary. The morphology and infraciliature of *Paracondylostoma cavistoma oligostriatum* ssp. n. (differs from *P. cavistoma cavistoma* by non-overlapping morphometric characteristics), *P. setigerum chlorelligerum* ssp. n. (differs from *P. setigerum setigerum* by having symbiotic green algae), and *Bursaridium pseudobursaria* were studied in live and silver-impregnated specimens. *Paracondylostoma* and *Bursaridium* are sister groups due to a unique synapomorphy, namely, a circumoral ciliary ribbon produced by narrowly spaced somatic kinetids at the anterior end of the somatic kineties. *Bursaridium* differs from *Paracondylostoma* by the euplanktonic mode of life and the paroral membrane, the middle portion of which has very loosely spaced kinetids. Based on the morphological details discovered, a Hennigian phylogeny of the genera *Bursaridium, Paracondylostoma, Thylakidium, Bryometopus,* and *Bursaria* is proposed. These genera are linked by four synapomorphies, namely: (1) an apical oral opening secondarily lost in *Bryometopus*, which ventralized the oral apparatus; (2) a ventral vestibular cleft occupied by the ventralized oral structures in *Bryometopus*; (3) a conspicuous adoral zone of adoral organelles; and (4) a simple paroral membrane composed of a row of dikinetids secondarily amplified to a conspicuous field of short, dikinetidal kineties in *Bursaria*, which is thus derived.

Key words: Colpodea, Hennigian phylogeny, infraciliature, *Paracondylostoma cavistoma oligostriatum* ssp. n., *Paracondylostoma setigerum chlorelligerum* ssp. n.

INTRODUCTION

Colpodid ciliates have a fascinating morphological and ecological diversity, reviewed by Foissner (1993a). For instance, *Bursaria truncatella*, one of the largest (up to 1300 μm) ciliates known, is an omnivore living in astatic and permanent freshwater habitats, while *Nivaliella*

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plana, one of the smallest (10 - 25 μm) ciliates known, is a strict mycophage living exclusively in terrestrial biotopes. The phylogenetic relationships of the 60 genera and about 180 species presently assigned to the class (Foissner 1993a-c, 1994a, b, 1995) have been investigated with both classical morphological and modern molecular methods (Foissner 1993a, Lynn *et al.* 1998, Stechmann *et al.* 1998).

Lynn *et al.* (1998) used the small subunit rRNA gene sequences to test the Hennigian phylogeny of the colpodids suggested by Foissner (1993a), which makes three important predictions, namely: (1) that the kreyellid silverline

system separates bryometopids, such as *Bryometopus*, from all other colpodeans; (2) that the macro-micronuclear complex of cyrtolophosids, such as *Platyophrya*, is the next major synapomorphy; and (3) that the merotelokinetal stomatogenesis of colpodids *s. str.*, such as *Colpoda*, *Bresslaua*, and *Pseudoplatyophrya* is highly derived. The molecular tree topologies confirmed the two last mentioned synapomorphies, while the silverline system failed.

In the present paper, we analyze the morphology and evolution of a small group of colpodids having an apical vestibular opening with a more or less distinct ventral cleft. The investigation was stimulated by the rediscovery of *Paracondylostoma*, a rare genus, not found again since the original description by Foissner (1980).

MATERIALS, METHODS AND TERMINOLOGY

Paracondylostoma cavistoma oligostriatum was discovered in the bottom material of a dry rock-pool near Puerto Ayacucho, Venezuela. *Paracondylostoma setigerum chlorelligerum* was found in the mud of a moorland pond near Constance, Germany. For site details, see ecology and occurrence section in species descriptions. *Bursaridium pseudobursaria* occurred in the plankton of a small lake (Högelwörther See, N47°49'/E12°50') in southern Bavaria.

Specimens were studied *in vivo* using a high-power oil immersion objective and differential interference contrast. The ciliary pattern (infraciliature) and other cytological details were revealed by scanning electron microscopy and various silver impregnation techniques, preferably silver carbonate, all described in Foissner (1991); protargol does not work well with this group of ciliates.

Counts and measurements on silvered specimens were performed at a magnification of x 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 free-hand sketches and micrographs, 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 Foissner (1993a).

RESULTS

Paracondylostoma cavistoma oligostriatum ssp. n. (Figs. 1-17; Table 1)

Diagnosis: *in vivo* about 35 x 20 µm. 20 ciliary rows and 11 adoral organelles on average.

Type location: soil and sediment from rock-pools on a Laja near the farm of Mr. Eisenberg, vicinity of Puerto Ayacucho (W68°/N5°), Venezuela.

Type slides: two slides (1 holotype and 1 paratype) with protargol-impregnated specimens have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria, accession numbers: 1998/45, 46. The slides contain several specimens, with relevant cells marked by a black ink circle on the cover glass. *Paracondylostoma cavistoma oligostriatum* is difficult to impregnate with protargol and thus the type slides are of mediocre quality. Accordingly, we declare Figures 12-17 in the present paper as additional holotype material.

Etymology: composite of the Greek adjective *oligos* (few) and the Latin noun *striatus* (striae), meaning a *Paracondylostoma* with few ciliary rows.

Description: very fragile and thus difficult to observe *in vivo*, usually disintegrates when taken up with fine pipettes and/or observed under slight coverglass pressure. Size *in vivo* 25-40 x 18-25 µm, usually about 35 x 20 µm. Broadly ellipsoidal (1.5:1, Fig. 1), ellipsoidal (2:1, Fig. 3) or slightly conical (Fig. 2); anterior end slightly to distinctly broader than evenly rounded posterior, transverse truncate with dorsal side slightly longer than ventral, thus oblique when viewed laterally (Figs. 4, 10). Macronucleus usually in posterior body half, broadly ellipsoidal, contains many minute (about 0.3 µm) nucleoli. Two to three globular micronuclei (1.2 - 2µm, x̄ 1.7, n 13, protargol impregnation) attached to macronucleus, impregnate only faintly with protargol (Figs. 1, 8, 10, 15, 17). Contractile vacuole subterminal on ventral side. Cortex flexible and very fragile (see above), rather distinctly furrowed by ciliary rows, contains a stripe of minute (about 0.2 µm), colourless granules (mucocysts ?) between each two ciliary rows (Figs. 5, 6). Cytoplasm colourless, contains some bright fat globules and food vacuoles 4 - 8µm across with bacteria and granular material, very likely bacterial remnants. Swims rather fast by rotation about main body axis.

Somatic cilia about 8 µm long and rather evenly spaced, except for anterior end, where each row commences with three narrowly spaced cilia, forming rather distinct ribbon in live specimens. Ciliary rows distinctly separate from paroral membrane, equidistant and very slightly spiral, composed of dikinetids having only the posterior basal body ciliated (Figs. 1, 7-9, 12-17).

Oral (vestibular) opening on anterior end of cell, margin opaque and slightly indented in midline of ventral side by minute vestibular cleft. Vestibulum fragile, occupies circa 35% of body length, oblique conical, that is, straight ventrally and obliquely extending dorsally. Adoral zone of organelles (left polykinetid) on left wall of vestibulum, inconspicuous because short, narrow and oriented with the smaller side to the observer when the cell is viewed ventrally or dorsally (Figs. 1, 8, 13). Individual organelles
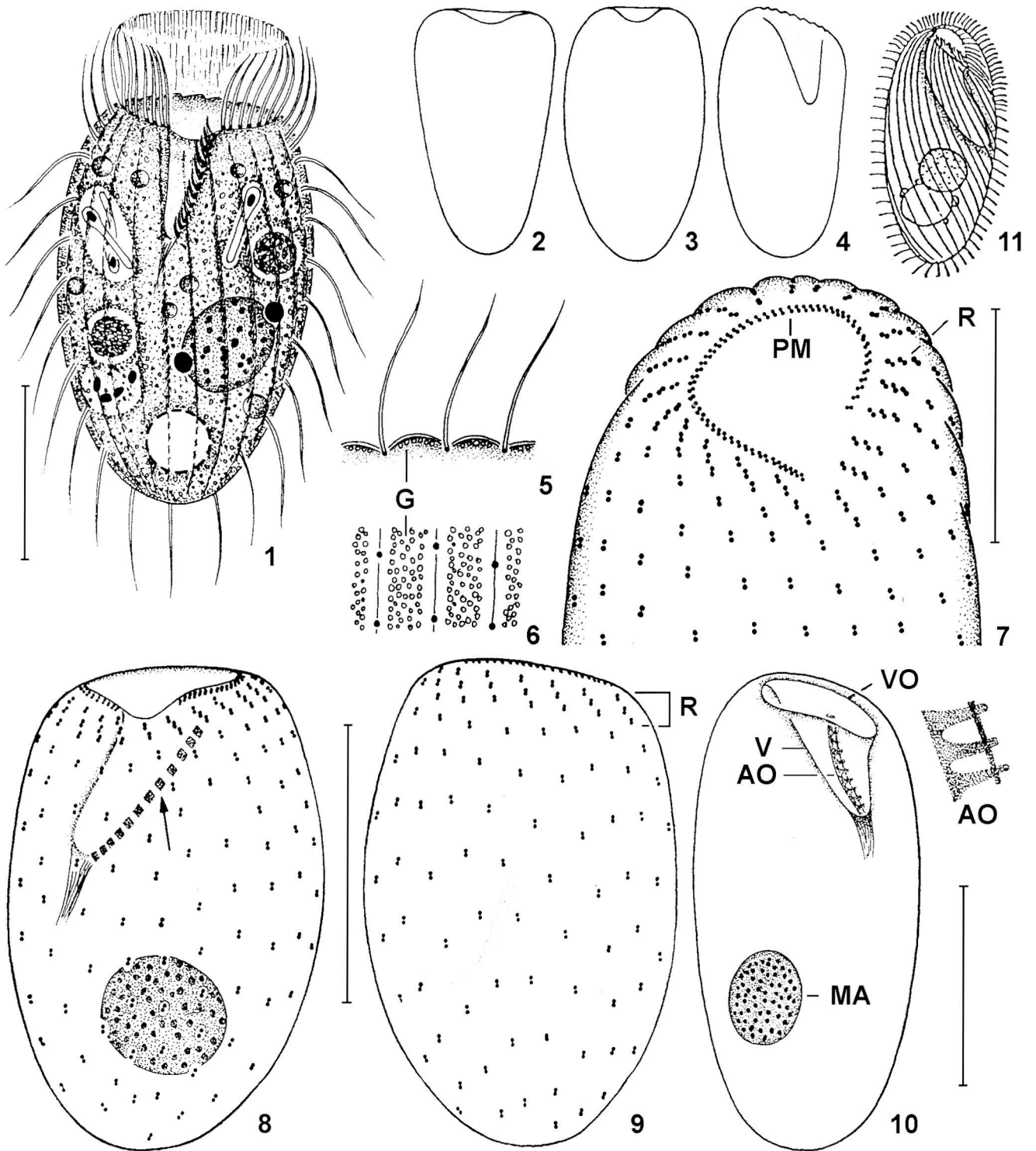
Figs. 1-11. *Paracondylostoma cavistoma oligostriatum* (1 - 10) and *P. cavistoma cavistoma* (11, from Gelei 1954) from life (1 - 6, 11) and after protargol impregnation (7 - 10). 1 - ventral view of a representative specimen containing sporulating bacteria; 2, 3 - funnel-shaped and obovate shape variants; 4 - ventrolateral view; 5, 6 - optical section and surface view of cortex, which contains stripes of minute granules; 7 - infraciliature of anterior ventral side; 8, 9 - infraciliature of ventral and dorsal side. Arrow marks zone of adoral organelles; 10 - lateral view showing location of main cell organelles, 11 - *P. cavistoma cavistoma*. Ventro-lateral view of a mercuric chlorid fixed specimen, length 60 μm. AO - adoral organelles, MA - macronucleus, PM - paroral membrane, R - ribbon of three narrowly spaced dikinetids, V - vestibulum, VO - vestibular opening. Scale bars - 15 μm (Figs. 1, 8-10) and 10 μm (Fig. 7)
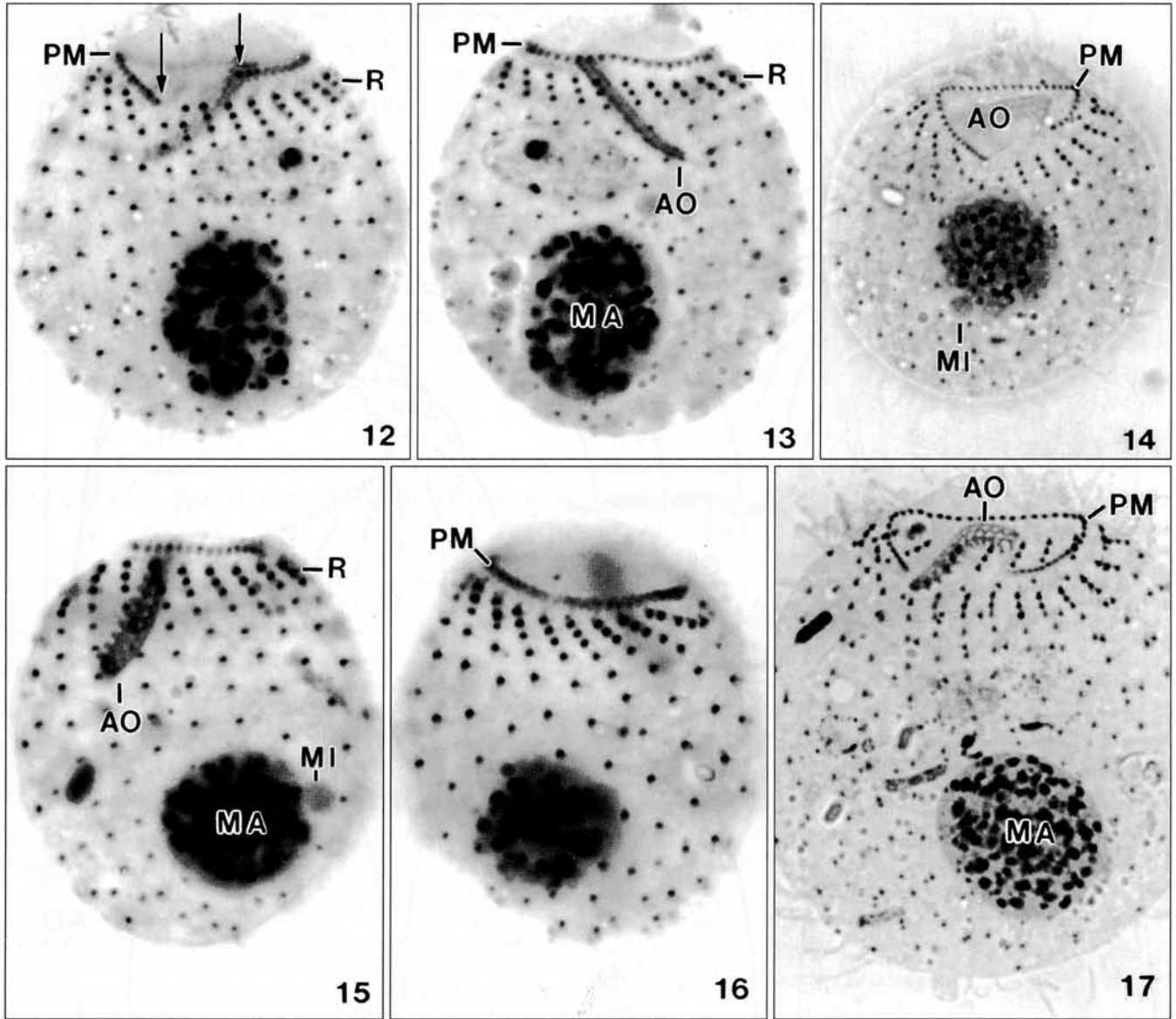
Figs. 12-17. *Paracondylostoma cavistoma oligostriatum*, oral and somatic infraciliature and nuclear apparatus after silver carbonate impregnation. To reveal details, specimens were strongly flattened by the cover glass. 12, 13 - ventral and dorsal view of same specimen, where the adoral zone of organelles is directed toward the observer with the smaller side and thus appears as narrow band (cp. Fig. 15, 17). Arrows mark ends of paroral membrane. Note the distinct ciliary ribbon formed by three narrowly spaced dikinetids each at the anterior end of the somatic kineties; 14, 17 - oblique ventral anterior polar views. Twelve adoral organelles, which form a reticulate structure, are recognizable in Fig. 17; 15, 16 - dorsolateral view of same specimen, where the adoral zone of organelles is directed toward the observer with the wider side and thus appears as broad band. AO - adoral zone of organelles, MA - macronucleus, MI - micronucleus, PM - paroral membrane, R - ribbon of three narrowly spaced dikinetids

slightly cuneate, touch each other proximally, connected by fine line distally, forming reticulate pattern (Figs. 10, 15, 17). Paroral membrane encircles anterior body end, except for ventral cleft, where about 10 dikinetids are lacking; consists of dikinetids, whose cilia form, together with the ciliary ribbon produced by the narrowly spaced

cilia at the anterior end of the somatic kineties, a conspicuous corona (Figs. 1, 7, 12 - 17).

Ecology and occurrence: as yet found only at type location, that is, a large granitic rock (Laja) with many dry pools containing up to 5 cm thick layers of greybrown, sandy soil and sediment with many roots from plants of

Table 1. Morphometric data from *Paracondylostoma cavistoma oligostriatum* (PC) and *P. setigerum chlorelligerum* (PS)

Character[*]	Species	Method[**]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	PC	P	29.0	28	4.2	1.2	14.5	20	36	13
	PS	V	74.2	73	6.2	1.4	8.4	65	88	21
Body, maximum width	PC	P	17.5	17	1.3	0.4	7.2	16	20	13
	PS	V	31.8	30	3.6	0.8	11.3	28	43	21
Anterior end to proximal end of	PC	P	10.0	10	1.9	0.5	18.7	6	13	13
adoral zone, distance	PS	V	35.8	36	3.8	0.8	10.6	28	42	21
Anterior end to macronucleus,	PC	P	16.2	16	3.1	0.9	19.1	10	22	13
distance	PS	V	39.5	40	6.5	1.4	16.5	25	50	21
Anterior end to contractile										
vacuole, distance	PS	V	51.6	52	7.7	1.7	14.9	35	73	21
Macronucleus, length	PC	P	7.5	8	1.5	0.4	19.3	5	10	13
	PS	V	13.3	13	1.1	0.2	8.3	11	15	21
Macronucleus, width	PC	P	6.5	6	1.1	0.3	16.2	5	8	13
	PS	V	11.2	10	1.8	0.4	16.1	9	15	21
Normal somatic cilia, length	PS	V	5.1	5	-	-	-	5	6	21
Tactile cilia, length	PS	V	19.9	20	2.7	0.6	13.6	15	25	20
Symbiotic algae, length	PS	V	5.1	5	-	-	-	5	6	21
Symbiotic algae, width	PS	V	4.1	4	-	-	-	4	5	21
Symbiotic algae, number	PS	V	31.3	29	12.6	2.7	40.3	18	64	21
Macronuclei, number	PC	P	1.0	1	0.0	0.0	0.0	1	1	13
	PS	V	1.0	1	0.0	0.0	0.0	1	1	21
Micronuclei, number	PS	V	2.3	3	-	-	-	1	3	21
Somatic kineties, number	PC	P	19.5	20	0.8	0.2	4.0	18	21	13
	PS	SC	46.7	47	1.7	0.6	3.6	45	49	7
Dikinetids in a somatic	PC	P	12.8	12	1.5	0.4	11.6	11	17	13
kinety, number	PS	SC	34.7	35	2.6	1.0	7.9	33	38	7
Adoral organelles, number	PC	P	11.5	11	0.9	0.3	7.9	10	13	13

[*] 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
[**] P - protargol impregnation (Foissner's protocol), mounted specimens; SC - silver carbonate impregnation; V - *in vivo*

the endemic Velloziaceae family. The rock-pools were dry and the bottom partially covered by minute mosses when the sample was taken. In the Petri dish, most specimens of *P. cavistoma oligostriatum* were found in a mossy patch, indicating that it prefers this habitat.

Comparison with related species: *Paracondylostoma cavistoma oligostriatum* is very likely closely related to *Cyrtolophosis cavistoma*, discovered by Gelei (1954) in a temporary pool in Hungary (Fig. 11). Gelei (1954) mentioned that he did not study the species, especially its oral structures, in detail. Our investigations confirm Foissner (1993a), who transferred Gelei's species to *Paracondylostoma*.

Gelei's species (Fig. 11) and the Venezuelan population (Figs. 1, 8, 9) differ mainly in some morphometric characteristics: size about 60x30 µm vs. about 35x20 µm, 30-34 distinctly spiral ciliary rows vs. 18-21 almost straight rows. Thus, we separate the Venezuelan population only at subspecies level. A more distinct character

would be the dwelling tube *P. cavistoma cavistoma* inhabits. However, we cannot exclude that *P. cavistoma oligostriatum* also produces a dwelling tube, although we did not find any, because it was rare and fragile and thus could not be studied in great detail.
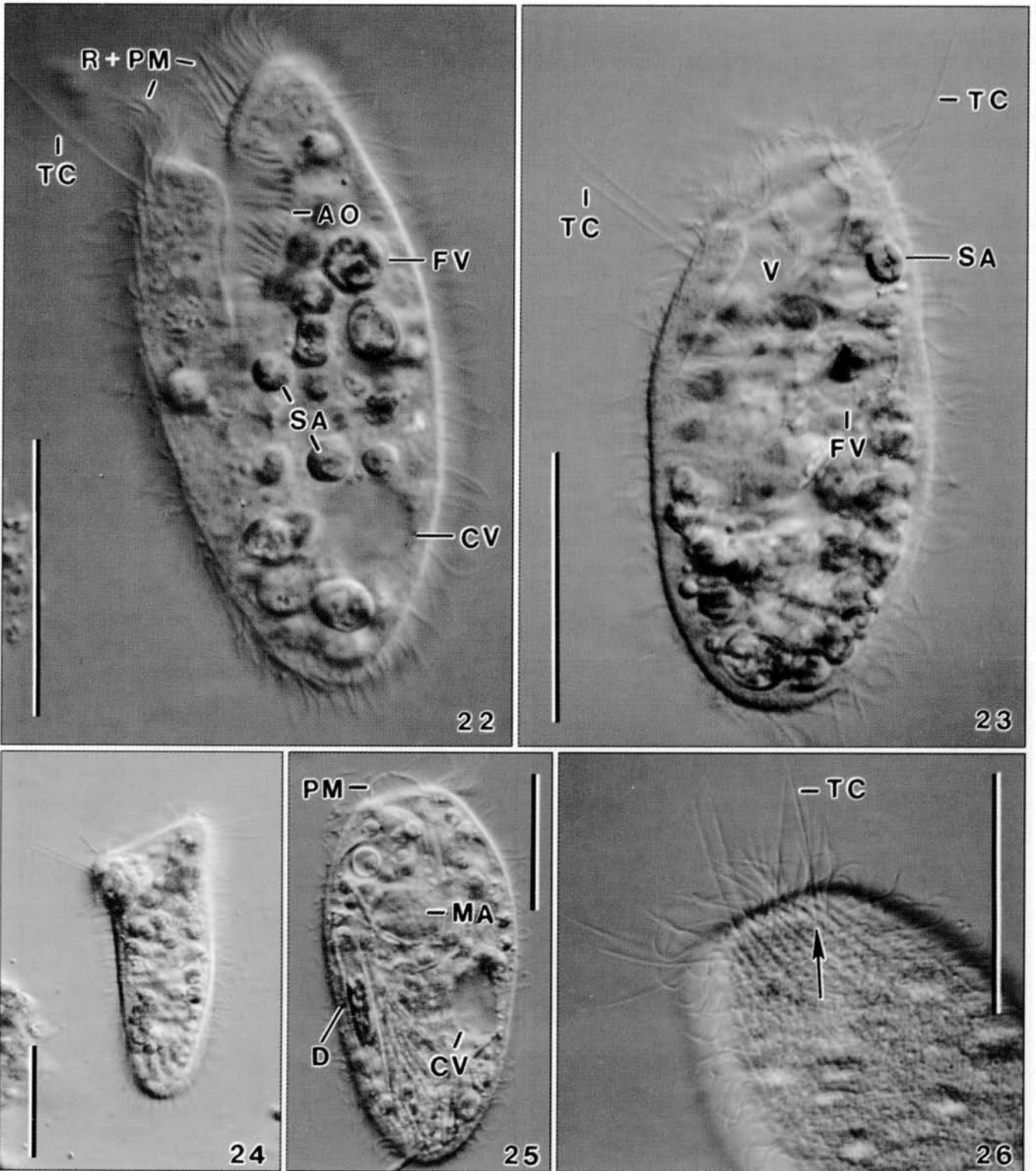
Paracondylostoma setigerum setigerum and *P. setigerum chlorelligerum* have a length of 65-90 µm, 45-50 ciliary rows, and 30-40 adoral organelles, whereas *P. cavistoma oligostriatum* is 25-40 µm long and has 18-21 ciliary rows and 10-13 adoral organelles. These differences are large enough to classify both types as distinct species.

Paracondylostoma setigerum chlorelligerum ssp. n. (Figs. 18-30; Table 1)

Diagnosis: as *P. setigerum setigerum* Foissner, 1980, but with symbiotic green algae.
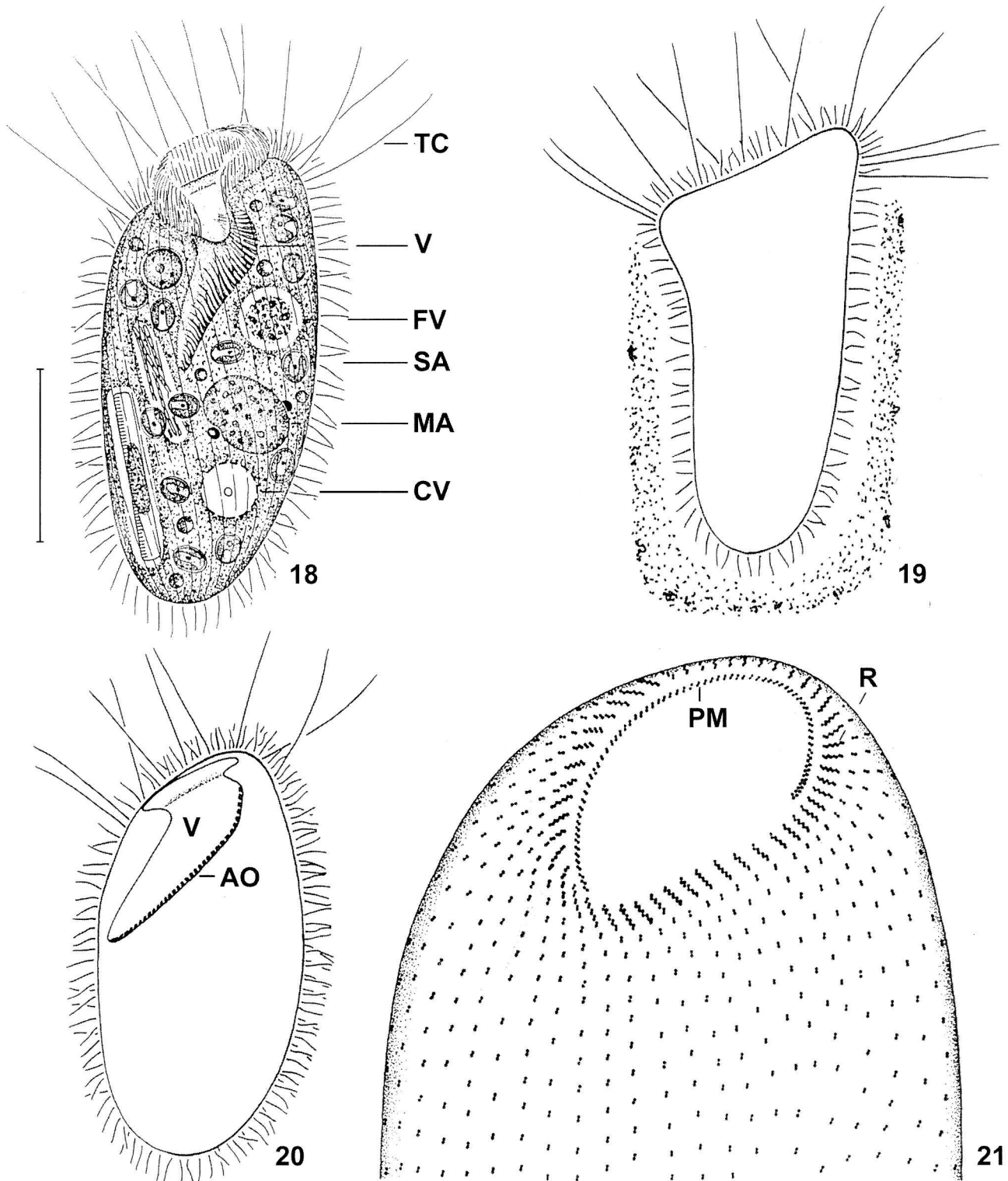
Figs. 18 - 21. *Paracondylostoma setigerum chlorelligerum* from life (18 - 20) and after silver carbonate impregnation (21). 18, 20 - ventral and lateral view of representative specimens with slightly contracted vestibular opening; 19 - specimen with fully extended anterior portion and very hyaline dwelling tube (cp. Fig. 24); 21 - infraciliature of ventral anterior portion (redrawn from squashed specimen). AO - adoral zone of organelles, CV - contractile vacuole, FV - food vacuole, MA - macronucleus, PM - paroral membrane, R - ribbon of narrowly spaced dikinetids, SA - symbiotic algae; TC - tactile cilia, V - vestibulum. Scale bar - 30 μm

Figs. 22 - 26. *Paracondylostoma setigerum chlorelligerum*, electronic flash micrographs of live specimens. 22, 23 - ventral and lateral view of specimens with slightly contracted anterior end; 24 - fully extended specimen within very hyaline, mucous dwelling tube; 25 - specimen packed with food items and distinct paroral membrane (kindly supplied by P. Mayer, Germany); 26 - dorsal anterior end showing tactile cilia (arrow) originating at the posterior border of the ciliary ribbon surrounding the oral opening. AO - adoral zone of organelles, CV - contractile vacuole, D - diatom, FV - food vacuoles, MA - macronucleus, R + PM - cilia of somatic ribbon and paroral membrane, SA - symbiotic algae, TC - tactile cilia, V - vestibulum. Scale bars - 30 μm
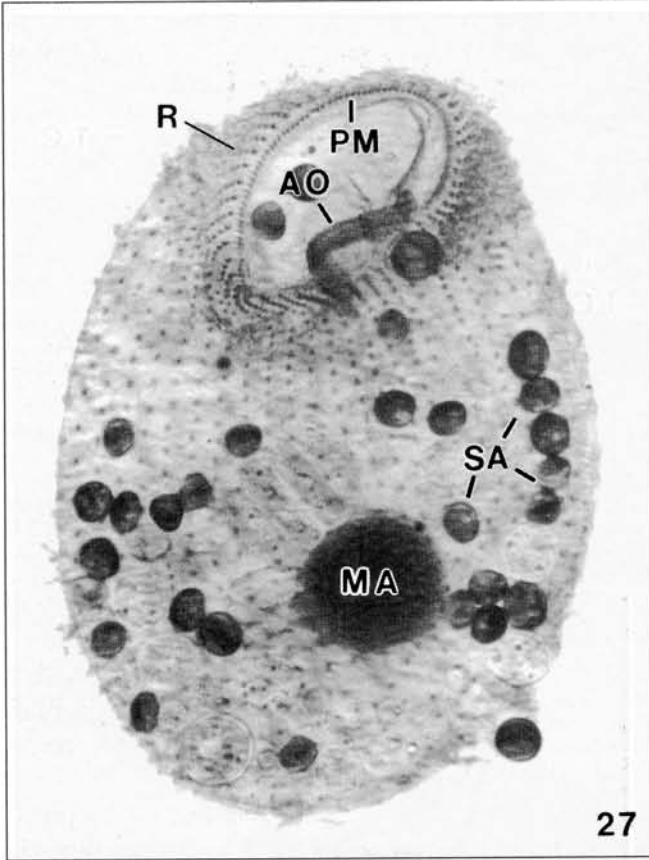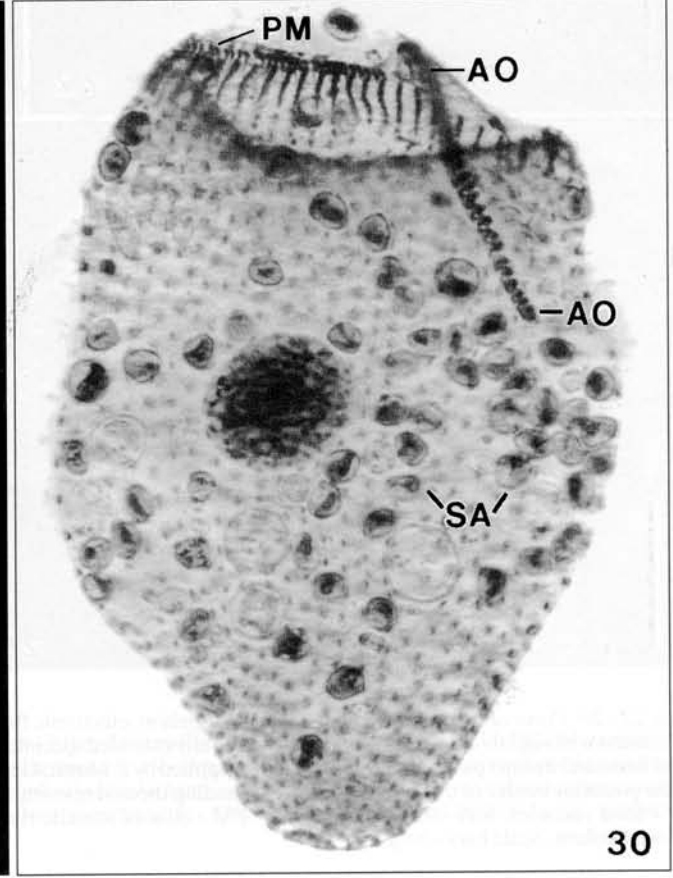
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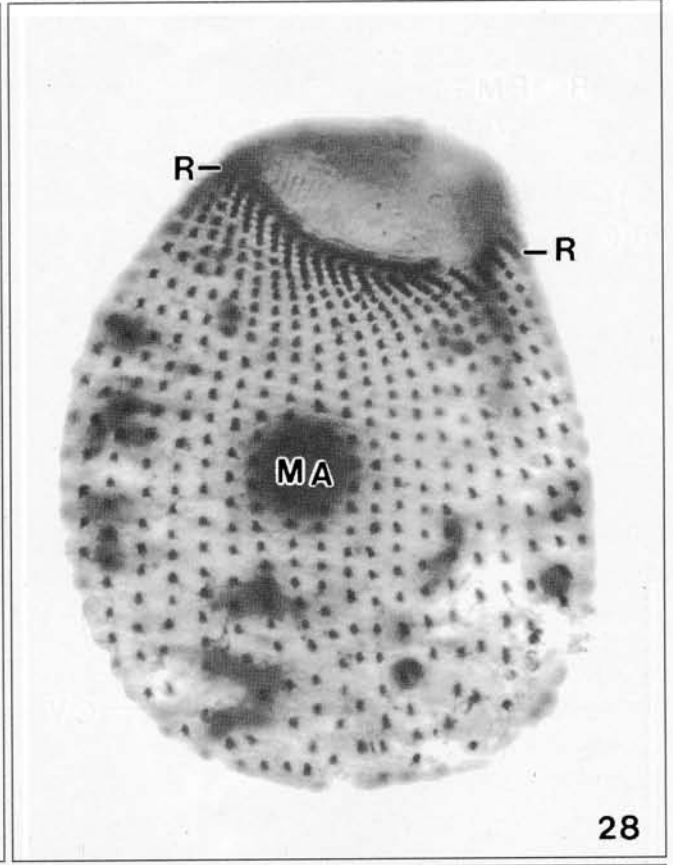
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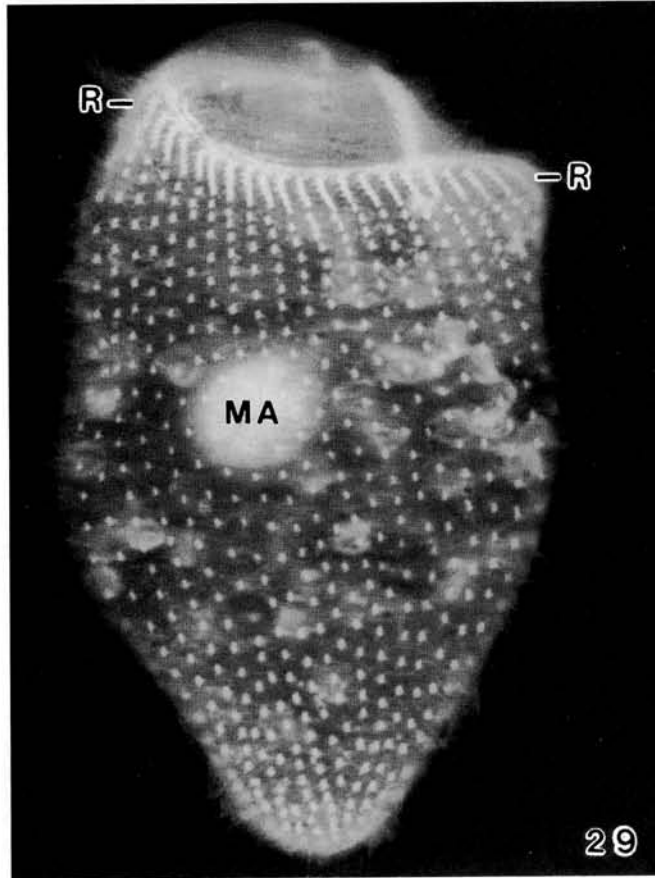
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Type location: pond mud near Hegne, a suburb of Constance, Germany (E9°10'/ N47°40').

Type slides: no permanent slides were made. Thus, the figures in this paper must serve as type material.

Etymology: *chlorelligerum* (bearing chlorellae) refers to the main subspecies character, that is, the symbiotic green algae.

Description: size *in vivo* 65 - 88 x 28 - 43 µm, on average 73 x 30 µm (Table 1). On slides usually elongate ellipsoidal to slightly conical (Figs. 18, 20, 22, 23, 25), natural shape, however, like that shown in Figs. 19 and 24, that is, cylindroidal with distinctly broadened anterior region, which can be contracted, providing cells with obconical appearance; anterior end obliquely truncate to right and ventral side, posterior rounded. Macronucleus slightly underneath mid-body on average, globular to slightly ellipsoidal, contains many minute (< 1 µm) nucleoli; 1 - 3, usually 3, micronuclei attached to macronucleus (Figs. 18, 25, 29, 30; Table 1). Contractile vacuole in fourth fifth of body, with single excretory pore in midline of ventral side (Figs. 18, 22, 25). Cortex flexible, rather distinctly furrowed by ciliary rows, contains many tightly spaced, minute (< 0.5 µm), colourless granules (mucocysts? Fig. 26). Cytoplasm colourless, cells, however, appear greenish due to 18 - 64, on average 29 (Table 1), symbiotic algae (Fig. 24); symbionts irregularly distributed, about 5 x 4 µm, with cup-shaped chloroplast and without eye-spot (Figs. 18, 22, 23, 27, 30). Feeds on bacteria and algae (globular green algae, Scenedesmus, diatoms; Figs. 18, 22, 23, 25).

Paracondylostoma setigerum chlorelligerum lives in a mucous dwelling tube, which is very hyaline and thus difficult to recognize when not covered by organic particles (Fig. 24). The dwelling tube is left when the cell is transferred from the natural sample to the slide, and rebuilt within 12 h. When the cell is slightly disturbed and/or the elongated (tactile) cilia (see below) touch certain objects, it draws back into the tube, soon extending and assuming the obconical shape typical of the sessile, swirling organism (Fig. 24).

Normal somatic cilia *in vivo ca* 5 µm long and rather evenly spaced, except of anterior end, where each row commences with 4-8 narrowly spaced cilia, forming distinct ribbon. About 20-30 distinctly elongated (20 µm, Table 1) tactile cilia around anterior end, very likely originate from first and/or second dikinetid underneath circumoral ribbon (Figs. 18 - 20, 22 - 24, 26). Ciliary rows distinctly separate from paroral membrane, equidistant and rather distinctly spiralling, composed of dikinetids with, probably, only the posterior basal body ciliated (Figs. 18, 21, 22, 27-30).

Oral apparatus more conspicuous, but of same fine structure, than in *P. cavistoma oligostriatum* because occupying almost 50% of body length. Adoral zone composed of about 30-35 organelles. Paroral widely open ventrally, that is, surrounds vestibular opening by about 300° (Figs. 18, 20-23, 27-30).

Ecology and occurrence: as yet found only at type location, that is, a small (about 5 x 3 m, max. depth 1 m), acidic (pH 5.5- 6.0) brownwater pond at the grassy margin of a 100 m broad *Sphagnum* stripe with dwarfed pines (*Pinus* sp.). The pond surface was covered with water lilies (*Nymphaea* sp.), while on the bottom was a thick layer of mud, the upper zone of which contained a rich and diverse community of bacteria, algae, and protozoans, including *P. setigerum chlorelligerum*.

Comparison with related species: *P. setigerum chlorelligerum* is very similar, if not identical, to *P. setigerum setigerum* Foissner, 1980, except for the symbiotic algae, whose taxonomical value is controversial (for detailed discussion, see Foissner & Wölfl 1994). We find it appropriate to separate such populations at subspecies level, considering the distinctiveness of the character and the physiological and ecological differences they show.

Bursaridium pseudobursaria (Fauré-Fremiet, 1924) Kahl, 1927 (Figs. 31-37)

This species has been reinvestigated by Foissner (1993a) and is well-known, except for the paroral membrane, whose identity remained doubtful. Our investigations show that its location (close above the circumoral ribbon formed by the anterior end of the somatic kineties) and structure (single row of dikinetids) are very similar to that

Figs. 27 - 30. *Paracondylostoma setigerum chlorelligerum*, somatic and oral infraciliature after silver carbonate impregnation. Specimens were strongly squashed to reveal as many details as possible in the same focal plane. 27 - ventral view; 28 - lateral view; 29, 30 - lateral view of same specimen focused to surface and body centre. AO - adoral zone of organelles, MA - macronucleus, PM - paroral membrane, R - ciliary ribbon at anterior end of somatic kineties, SA - symbiotic algae
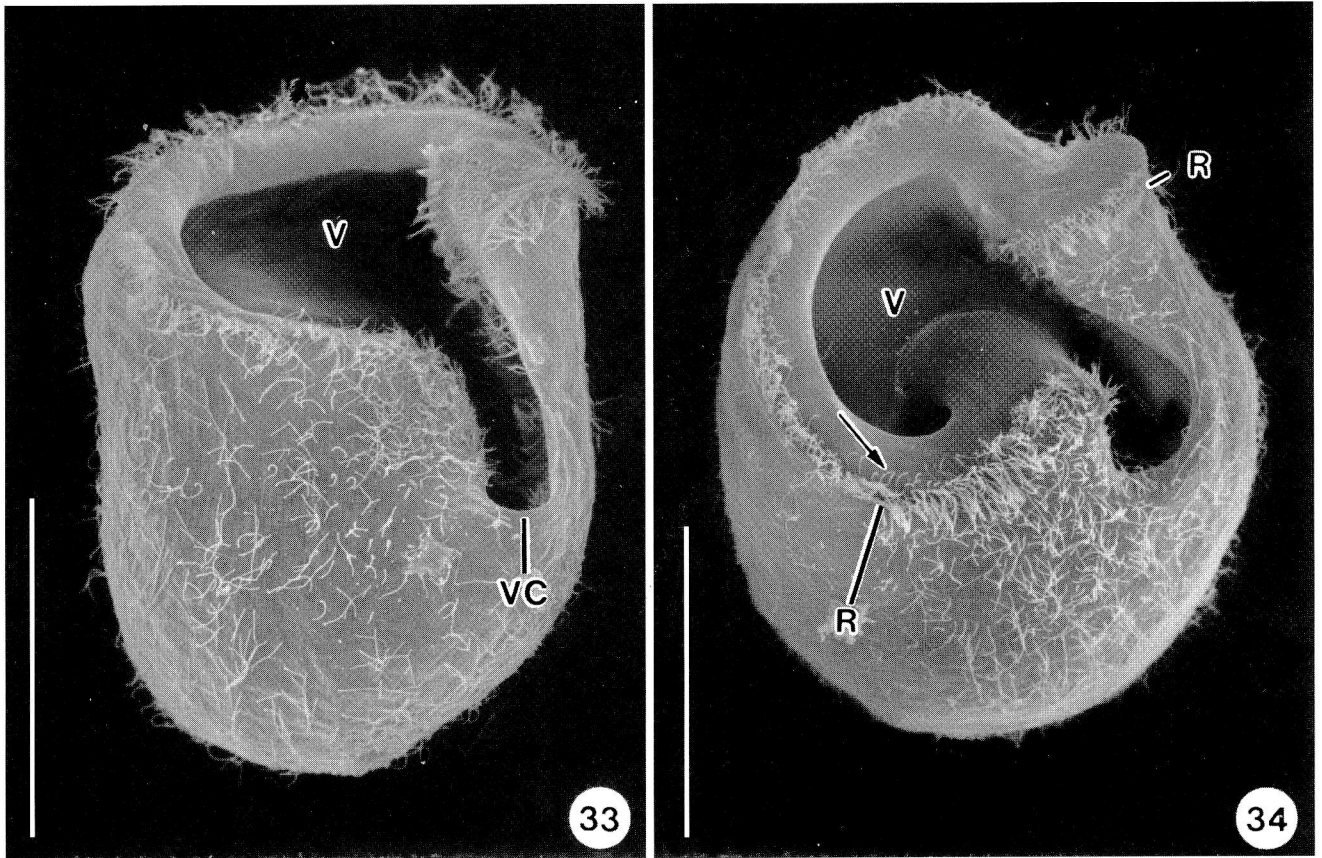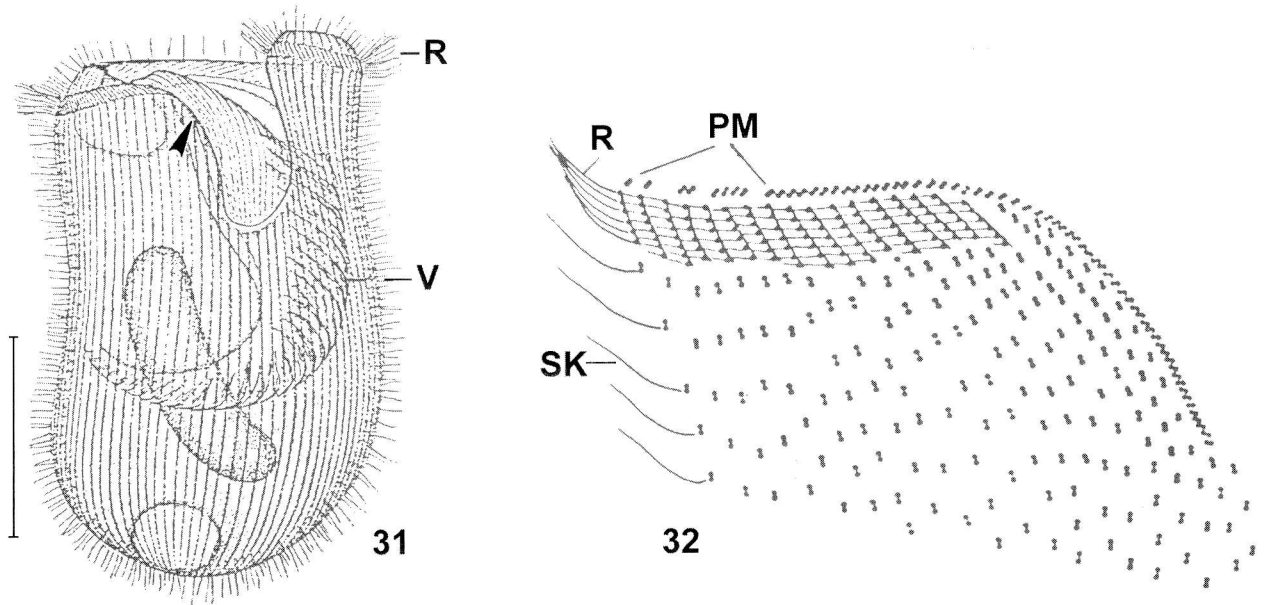
Figs. 31 - 34. *Bursaridium pseudobursaria* from life (31, from Fauré-Fremiet 1924), after silver carbonate impregnation (32, from Foissner 1993a), and in the scanning electron microscope (33, 34). 31 - ventral view of representative specimen, with arrowhead marking area shown in Fig. 32 after silver impregnation; 32 - infraciliature of outer surface of right vestibular wall, marked by arrowhead in Fig. 31; 33, 34 - ventrolateral and oblique frontal view showing general organization and huge vestibulum, which has a distinct ventral cleft. Arrow marks loosely ciliated paroral, shown at higher magnification in Fig. 37. PM - paroral membrane, R - circumoral ciliary ribbon formed by the anterior end of the somatic kineties, SK - somatic kineties, V - vestibulum, VC - vestibular cleft. Scale bars - 50 µm
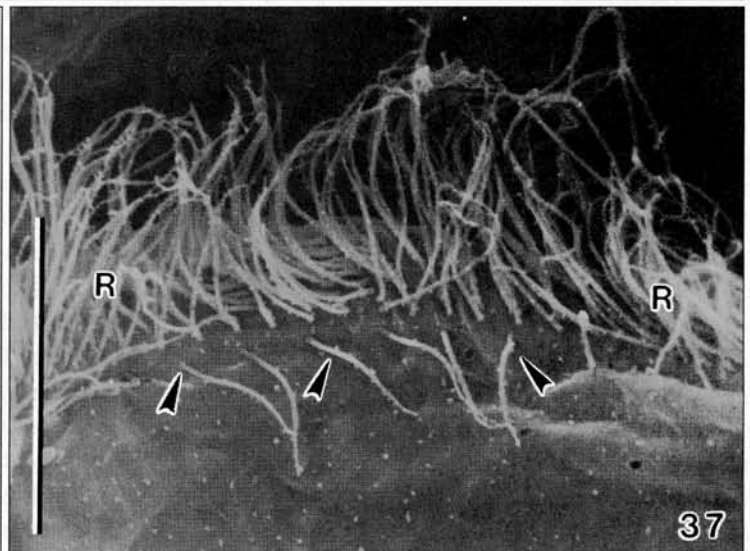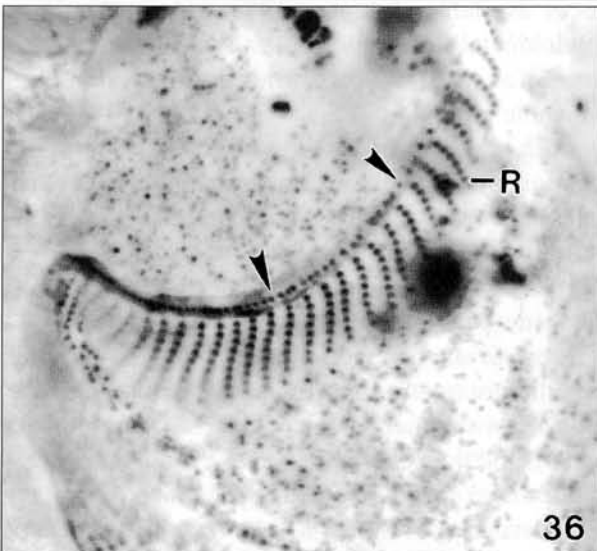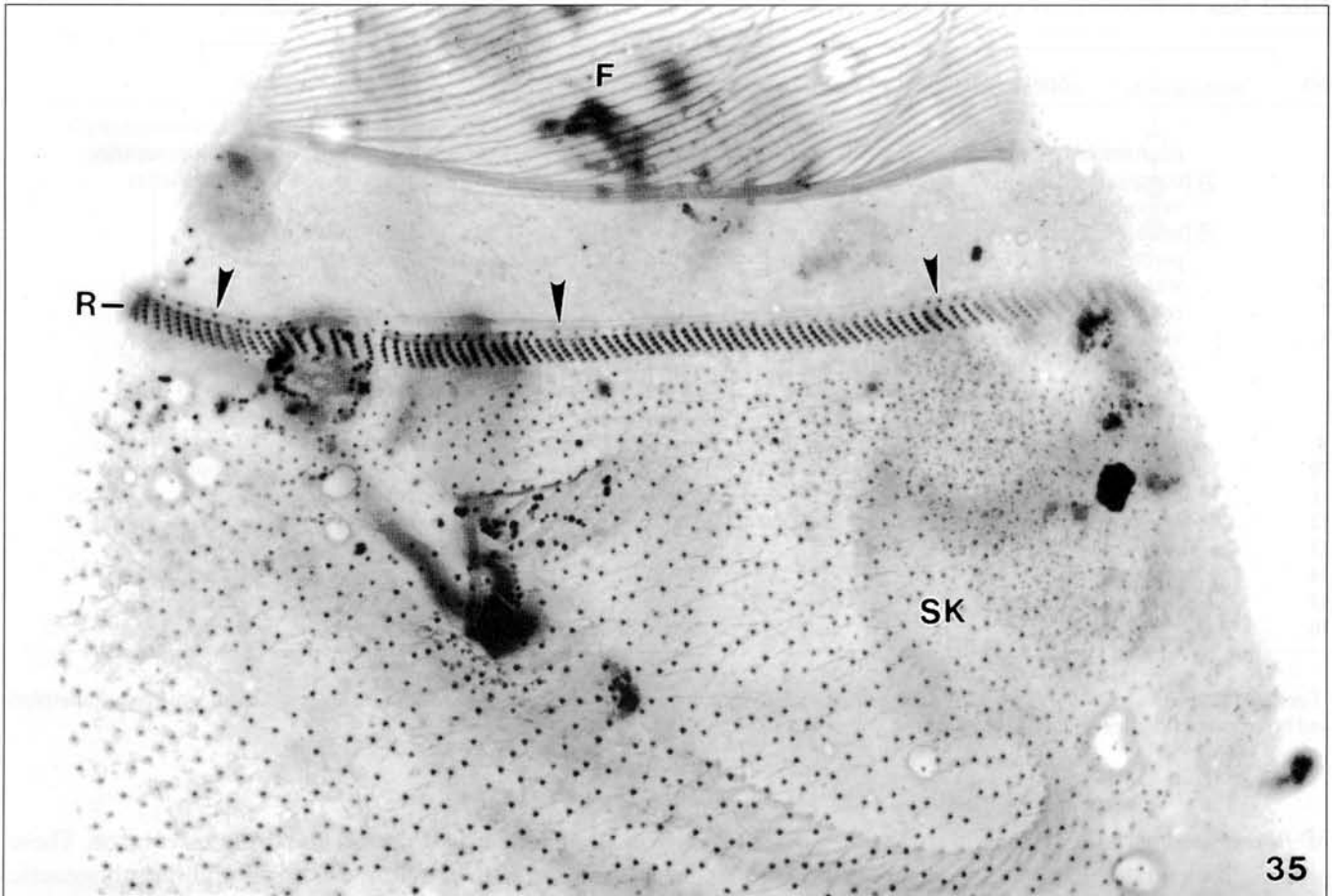
Figs. 35 - 37. *Bursaridium pseudobursaria*, somatic and oral infraciliature after silver carbonate impregnation (35, 36) and in the scanning electron microscope (37). The silver carbonate impregnated specimens were strongly squashed to reveal as many details as possible in the same focal plane. 35, 37 - anterior dorsal portion showing fibres lining the vestibular wall and the paroral membrane (arrowheads), which is composed of very loosely spaced kinetids, close above the conspicuous circumoral ciliary ribbon, which is distinctly separate from the somatic kineties; 36 - left end of paroral membrane (arrowheads) and circumoral ciliary ribbon. F - fibres, R - ciliary ribbon at anterior end of somatic kineties, SK - somatic kineties. Scale bar - 10 μm

Table 2. State for the characters shown in Figure 38. See Foissner (1993a) for detailed explanation of characters.

No.	Apomorphic ●	Plesiomorphic ○
1	micronucleus in perinuclear space of macronucleus	macronucleus and micronucleus separate
2	conspicuous zone of adoral organelles	small, brick-shaped adoral organelles
3	ventral cleft	without ventral cleft
4	apical oral opening	ventral oral opening
5	paroral composed of many dikinetidal rows	paroral a single row of dikinetids
6	with conjugation (sex)	without sex
7	resting cyst with emergence pore	resting cyst without emergence pore
8	vestibulum obconical or cornute and curved to right. Adoral organelles each composed of two long rows and one short row of basal bodies in zigzag pattern*	vestibulum cornute and curved to left. Adoral organelles each composed of three rows of same length with basal bodies not in zigzag pattern*
9	LKM fibre reduced (V-shaped pattern)	LKM fibre typical
10	supraepiplasmic microtubules	no supraepiplasmic microtubules
11	circumoral somatic ciliary ribbon	without ciliary ribbon
12	loss of ventral cleft and ventralization of oral apparatus	with ventral cleft and apical oral opening
13	paroral within vestibulum	paroral at margin of oral opening
14	vestibulum obconical	vestibulum cornute
15	paroral kinetids loosen	paroral kinetids evenly spaced
16	euplanktonic	benthic, semi-sessile

*For details, see Foissner (1993a), Perez-Paniagua et al. (1980), and Wirnsberger et al. (1985). Generally, the adoral ciliature of bursariomorphid and bryometopid ciliates is insufficiently known.

of *Paracondylostoma*. The sole difference is that the paroral dikinetids, which have only one basal body ciliated (Fig. 37), are more loosely spaced laterally and dorsally than ventrally (Figs. 32, 35, 36).

DISCUSSION

Recent molecular data showed that *Bursaria* and *Bryometopus* are rather closely related (Lynn et al. 1998), that is, did not confirm Foissner (1993a), who assigned *Bursaria/Bursaridium/Paracondylostoma* and *Bryometopus/Thylakidium* to different subclasses, viz. the Colpodia and Bryometopia. Foissner (1993a) over-interpreted details of the silverline system and somatic cortical microtubular pattern; furthermore, the detailed structure of the oral apparatus was not known in *Bursaridium* and *Paracondylostoma*.

The present investigation shows some new aspects, which will be discussed in the following paragraphs using a Hennigian scheme of argumentation (Fig. 38; Table 2). We shall demonstrate that the relationships of the genera in question are now fairly clear. The scheme is based on the new molecular data mentioned above, which show a rather close relationship of *Bursaria* and *Bryometopus*

and indicate that cyrtolophosids are the sister taxon. These data agree with the morphological and morphogenetic evidences available (Foissner 1993a). Accordingly, a pleurotelokinetal stomatogenesis and a "simple" paroral composed of a single row of dikinetids, are the apomorphies for the whole group.

(1) *Bursaridium*, *Paracondylostoma*, *Thylakidium*, *Bryometopus*, and *Bursaria* have a unique character constellation not found in any other colpodid, viz. an apical oral opening, a ventral cleft, and a conspicuous "heterotrich" zone of adoral organelles. Thus, they are very likely monophyletic.

(2) *Bursaria* is separated from the other genera by the paroral ciliature (many short rows), the structure of the resting cyst (with emergence pore; lacking in all other colpodids), and the occurrence of sex (conjugation; unknown in other colpodids). This suggests not only a rather separate (derived) position of *Bursaria* within the group, but also maintenance of the ordinal rank (Foissner 1993a, Lynn and Small 1997).

(3) We were unsuccessful in finding a strong synapomorphy uniting the genera *Bursaridium*, *Paracondylostoma*, *Thylakidium*, and *Bryometopus*, indicating underinvestigation and/or misclassification. The details of the oral apparatus mentioned in Table 2 are
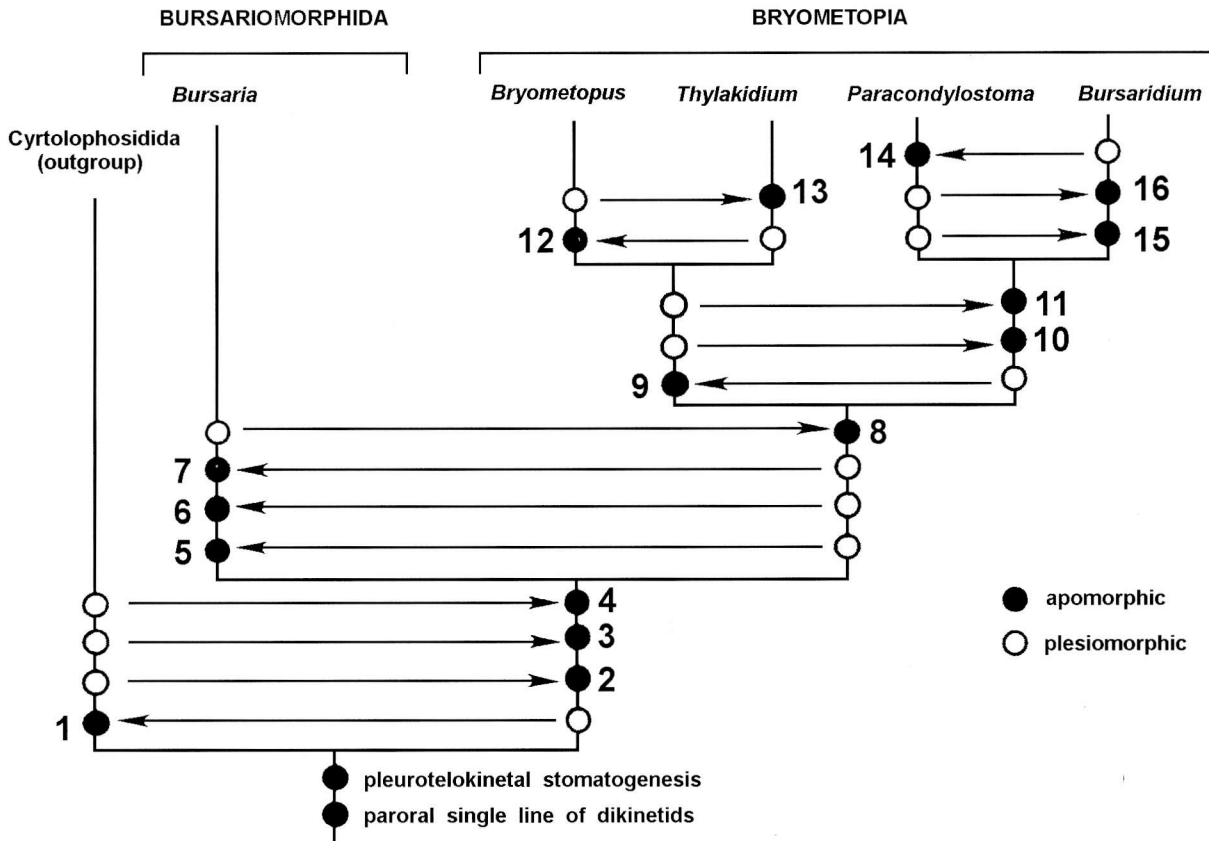
Fig. 38. Hennigian phylogeny of the genera *Bursaria*, *Bryometopus*, *Thylakidium*, *Paracondylostoma*, and *Bursaridium*. For character states, see Table 2

weak. However, the general appearance of these genera is more similar to each other than to *Bursaria*. Furthermore, several ultrastructural details argue against considering any of these genera to be very closely related to *Bursaria*: *Bursaridium* (and very likely also *Paracondylostoma*) has supraepiplasmic microtubules (Foissner 1993a), which are lacking in *Bursaria* (Lynn 1980, Perez-Paniagua *et al.* 1980) and *Bryometopus* (Wirnsberger *et al.* 1985; re-checked in the original material); and *Bryometopus* (very likely also *Thylakidium*) has short, non-overlapping transverse microtubule ribbons (Wirnsberger *et al.* 1985), while those of *Bursaria* are very long and overlapping (Lynn 1980, Perez-Paniagua *et al.* 1980).

(4) *Paracondylostoma* and *Bursaridium* have two strong synapomorphies, namely, the supraepiplasmic microtubules (as yet, definitely shown only in *Bursaridium*; Foissner 1993a) and the circumoral ciliary ribbon, which

is composed of narrowly spaced somatic kinetids having a particular fine structure (Foissner 1993a), at the anterior end of the somatic kineties (Figs. 7, 13, 21, 29, 32, 35). No other colpodid has such a pattern. Thus, even the generic separation could be questioned. However, the slightly different structure of the paroral membrane (kinetids loosen in mid-portion of *Bursaridium*; Figs. 27, 32, 35-37), the large, cornute vestibulum (Figs. 31, 33, 34), and the euplanktonic mode of life of *Bursaridium* are rather different from the simple, obconical vestibulum (Figs. 1, 12, 18, 20, 23) and the semi-sessile life strategy of *Paracondylostoma*. Thus, generic separation still seems appropriate.

(5) *Bryometopus* and *Thylakidium* are linked by the short transverse microtubule ribbons forming a V-shaped pattern (Wirnsberger *et al.* 1985, Foissner 1993a). *Bryometopus* differs from the other genera in the argumentation scheme by the ventralization of the oral appa-

ratus. Possibly, the vestibulum has flattened and driven the oral structures into the ventral cleft during the evolution of the genus.

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