# Tropical Protozoan Diversity: 80 Ciliate Species (Protozoa, Ciliophora) in a Soil Sample from a Tropical Dry Forest of Costa Rica, with Descriptions of four New Genera and seven New Species

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Summary: 80 ciliate species were found in a soil sample from a tropical dry forest of Costa Rica, Central America. Based on literature data, it is assumed that this site contains 200-300 species, i.e. three times more than commonly found in forest soils of Central Europe. Seven new species were discovered: Dileptus costaricanus nov. spec., D. similis nov. spec., Pedohymena australiense nov. gen., nov. spec., Condylostoma terricola nov. spec., Bicoronella costaricana nov. gen., nov. spec., Australothrix steineri nov. spec., and Cyrtohymena australis nov. spec. Their morphology and infraciliature were studied in live cells and in specimens impregnated with various silver methods. The following species, which were insufficiently known, are redescribed: Paracineta lauterborni, Pseudovorticella sphagni, Cyclidium muscicola, Colpodidium caudatum, Dapedophrya flexilis nov. gen., nov. comb., and Mykophagophrys terricola nov. gen., nov. comb. The genera Colpodidium and Pedohymena are united in a new family, Colpodidiidae nov. fam., which belongs to the order Nassulida and is characterized by a deep buccal cavity near mid-body containing one complete and two more or less distinctly reduced adoral organelles. Pseudokeronopsis ignea is transferred to the genus Uroleptopsis KAHL: Uroleptopsis ignea (MIHAILOWITSCH & WILBERT, 1990) nov. comb. Sixty-one ciliate species which are new for the fauna of Costa Rica are listed in the faunistic section.

**Key words:** Central America; Costa Rica; Tropical Soil Ciliates; Colpodidiidae nov. fam.; *Bicoronella* nov. gen.; *Dapedophrya* nov. gen.; *Mykophagophrys* nov. gen.; *Pedohymena* nov. gen.

# Introduction

During the last 15 years, I collected more than 1000 soil, moss and litter samples world-wide, and found them inhabited by a bewildering variety of ciliates. Some of the results have already been published [see reviews by AESCHT (1994) and FOISSNER (1987a, 1993) for references]; but most of the data, viz. about 300 new species and many new genera, are still unpublished, simply because I found the new taxa more quickly than I could describe them.

I started this programme at my own expense years before the UNED pushed forward an international convention for research and protection of biological diversity in June 1992. Very likely, we shall never come to know the real protozoan diversity, especially in the tropics, because the biotopes (e.g. rain forests) are destroyed more quickly than the few taxonomists can exploit them. In this paper I shall report on an outstanding sample from a tropical dry forest in Costa Rica,

containing 80 ciliate species, seven of which are new to science. Another new genus and species from this area, viz. *Pentahymena corticola*, lives in the bark of *Acacia* trees and has been described recently (Foissner 1994).

# Material, Methods, Type specimens

# Material

The sample investigated was collected on 13.02.1991 in the Santa Rosa National Park, Costa Rica, about 5 km east of the ranch house "La Casona", near a small path to the Pacific Ocean. This area harbours a tropical dry forest (1.600 mm annual rainfall, 6 months dry season) with an incredible wealth and variety of plants and wild life, viz. 240 species of trees and shrubs, 115 species of mammals, 253 of birds, 100 of amphibians and reptiles, over 10.000 of insects, including 3.410 species of moths and butterflies (Boza 1988). The upper 0–3 cm litter and soil layer was collected and air-dried for 14 days.

On 5. 08. 1991 the dry sample was saturated with distilled water according to the non-flooded petri dish method (FOISSNER 1993). The rewetted soil/litter-mixture had pH 6.6 and did not contain unusual amounts of salts. This sample was investigated 4 times during a period of one month.

Several species occurring in the Costa Rica sample and described in this paper have been found and studied previously in soil samples from other regions of the world, mostly from Australia and Africa. Thus, the type location of some of the new species is not the site described above. Short site descriptions for these species are provided in the respective ecology sections. The samples were processed as described for that from Costa Rica.

### Methods

All species were carefully studied in vivo using a high-power oil immersion objective and differential interference contrast. Extrusomes were stained with methyl green-pyronin (Foissner 1993). The following silver methods, which have been described in detail by Foissner (1993), were used to reveal the infraciliature and various cytological details: protargol (protocols 1, 2), dry and wet silver nitrate, silver carbonate. The loricae of *Paracineta lauter-borni* were air-dried on a coated SEM-stub and processed for scanning electron microscopy as described by Foissner (1993).

Counts and measurements on silvered specimens were performed at a magnification of  $\times 1,000$ . In vivo measurements were conducted at a magnification of  $\times 250-1,000$ . Although these provide only rough estimates, it is convenient to give such data as specimens usually shrink in preparations or may even contract during fixation. Standard deviation and coefficient of variation were calculated according to statistics textbooks. Drawings of live specimens are based on free-hand sketches, those of impregnated cells were made with a camera lucida.

# Type specimens deposited

Slides with type and voucher specimens have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria. Relevant specimens are marked by a black ink circle on the cover glass.

Dileptus costaricanus and D. similis: 1 holotype and 1 paratype slide each with protargol impregnated specimens. Paracineta lauterborni: 5 neotype slides with protargol impregnated specimens from Kenya (Africa) and Germany.

Pseudovorticella sphagni: 1 voucher slide with protargol impregnated specimens from Hungary.

Cyclidium muscicola: 1 neotype and 1 syntype slide with protargol impregnated specimens from Hawaii.

Colpodidium caudatum: 3 voucher slides with protargol and silver nitrate (dry method) impregnated specimens from Kenya (Africa).

*Pedohymena australiense:* 3 holotype slides with protargol and silver nitrate (dry and wet method, respectively) impregnated specimens and 2 paratype slides with silver nitrate (wet method) impregnated cells.

Condylostoma terricola, Bicoronella costaricana, Australothrix steineri: 1 holotype and 1 paratype slide each with protargol impregnated specimens.

Cyrtohymena australis: 1 holotype and 1 paratype slide with protargol impregnated specimens; 1 voucher slide with protargol impregnated cells from Costa Rica.

Dapedophrya flexilis: 3 neotype slides with protargol impregnated specimens.

# **Results**

# **Faunistics**

80 ciliate species were recorded during a 4-week-period of investigation. All identifications were checked by silver impregnation. The inventory is ordered alphabetically to facilitate comparison with similar lists from other sites (Foissner 1987a). Species marked with an asterisk are new for the fauna of Costa Rica.

\* Australothrix steineri nov. spec., \* Bicoronella costaricana nov. gen., nov. spec.; \* Blepharisma hyalinum Perty, 1849; \* Bresslauides terricola (Foissner, 1987) Foissner, 1993; \* Bryophyllum loxophylliforme Kahl., 1931; \* Bursaria truncatella Müller, 1773; \* Cinetochilum margaritaceum (Ehrenberg, 1830) Perty, 1852; \* Colpoda cucullus Müller, 1773; \* C. flavicans (Stokes, 1885) Foissner, 1993 (typical resting cysts also seen!); C. inflata (Stokes, 1884) Kahl., 1931; C. lucida Greeff, 1888; C. maupasi Enriques, 1908; C. tripartita Kahl., 1931; \* Condylostoma terricola nov. spec., Cyclidium muscicola Kahl., 1931; \* Cyrtolophosis mucicola Stokes, 1885; \* Cyrtohymena australis nov. spec., \* C. citrina (?) Berger & Foissner, 1987; \* C. candens (Kahl., 1932) Foissner, 1987; \* Dapedophrya flexilis

(PENARD, 1922) nov. gen., nov. comb., \* Dileptus costaricanus nov. spec., \* D. similis nov. spec.; \* Dimacrocaryon amphileptoides (KAHL, 1931) JANKOWSKI, 1967; Drepanomonas revoluta PENARD, 1922; \* D. muscicola Foissner, 1987; \* D. pauciciliata Foissner, 1987; \* Epispathidium terricola Foissner, 1987; \* Eschaneustyla terricola Foissner, 1982; \* Euplotes muscicola KAHL, 1932; Frontonia depressa (STOKES, 1886) KAHL, 1931; \* Fuscheria terricola Berger, Foissner & Adam, 1983; Gonostomum affine (STEIN, 1859) STERKI, 1878; \* G. kuehnelti Foissner, 1987; \* Grossglockneria hyalina Foissner, 1985; Halteria grandinella (Müller, 1773) DUJARDIN, 1841; \* Hausmanniella discoidea (GELLÉRT, 1956) Foissner, 1984; \* Hemiamphisiella terricola Foissner, 1988; \* Hemisincirra cf. gellerti (Foissner, 1982) Foissner, 1984; \* H. gracilis (Foissner, 1982) Foissner, 1984; H. inquieta Hemberger, 1985; \* H. similis (Foissner, 1982) Foissner 1984; \* Holosticha australis Blatterer & Foissner, 1988; \* Holosticha multistilata Kahl, 1928; \* H. sylvatica Foissner, 1982; \* Holostichides terricola Foissner, 1987; \* Homalogastra setosa Kahl, 1926; Kahlilembus fusiformis (Kahl, 1926) Groliere & Couteaux, 1984; Leptopharynx costatus Mermod, 1914; \* Litonotus muscorum (KAHL, 1931) Blatterer & Foissner, 1988; \* Metopus hasei Sondheim, 1929; \* Mykophagophrys terricola (Foiss-NER, 1985) nov. gen., nov. comb.; \* Nivaliella plana Foissner, 1980; \* Notoxoma parabryophryides Foiss-NER, 1993; \* Odontochlamys gouraudi CERTES, 1891; \* Oxytricha setigera Stokes, 1891; \* Paracineta lauterborni Sondheim, 1929; \* Paraenchelys terricola Foiss-NER, 1984; \* P. wenzeli Foissner, 1984; \* Paramphisiella caudata (Hemberger, 1985) Foissner, 1988; \* Pedohymena australiense nov. gen., nov. spec.; \* Platyophrya similis (Foissner, 1980) Foissner, 1987; P. vorax Kahl, 1926; \* Podophrya sp., \* Pseudochilodonopsis mutabilis Foissner, 1981; \* Pseudocyrtolophosis alpestris Foissner, 1980; \* Pseudoholophrya terricola BERGER, FOISSNER & ADAM, 1984; \* Pseudoplatyophrya saltans Foissner, 1988; \* Pseudourostyla franzi Foiss-NER, 1987; \* Pseudovorticella sphagni Foissner & SCHIFFMANN, 1974; \* Spathidium procerum KAHL, 1930; \* S. spathula (Müller, 1773) Moody, 1912; \* Stammeridium kahli (Wenzel, 1953) Wenzel, 1969; Tachysoma humicola GELLÉRT, 1957; \* Terricirra matsusakai BER-GER & FOISSNER, 1989; \* Tetrahymena rostrata (KAHL, 1926) CORLISS, 1952; \* Trachelophyllum apiculatum (PERTY, 1852) CLAPAREDE & LACHMANN, 1859; \* Urosoma macrostyla (Wrzésniowski, 1870) Kahl, 1932; Vorticella astyliformis Foissner, 1981; 2 species indet.

Very likely, this list is far from being complete because the non-flooded petri dish method requires repeated investigations of the same site at different seasons for a complete species inventory; 2–5 samples distributed over one year produced 50–80% of the species found in 10 samples investigated over two years (Foissner 1987a). Accordingly, the site in Costa Rica possibly contains 200–300 species! This is about three times more than found in lowland and forest soils of Central Europe, where AESCHT & FOISSNER (1993) and FOISSNER et al. (1985) enumerated 60–80 species on 10 sampling occasions during a period of 2–4 years.

# Description of species

Morphometric data shown in Tables 1–9 are not repeated in the descriptions.

# • Genus Dileptus DUJARDIN, 1841

Recent investigations showed that the genus *Dileptus* is polyphyletic: D. amphileptoides apparently lacks a usual pharyngeal apparatus (Foissner 1984) and D. monilatus lacks oblique preoral kineties (Foissner et al. 1995). In fact, years ago these species were chosen by JANKOWSKI (1967) as types for two new subgenera of *Dileptus* (with many macronuclear nodules), viz. Dimacrocaryon (with two macronuclear nodules) and Monilicaryon (with moniliforme macronucleus), using their macronuclear configurations as sole diagnostic character; an unfortunate action because the same macronuclear pattern very likely evolved independently in several evolutionary lines of Dileptus s. 1. Foissner (1984) thus amended JANKOWSKI's diagnosis of Dimacrocaryon and suggested uniting binucleate species with a normal oral apparatus in a new genus, Rimaleptus. However, he did not appreciate this genus for the reason mentioned above. Further studies are necessary to elucidate whether or not the macronuclear configuration can be used to split the genus according to its evolutionary history. For the present, it seems wise to keep all species which possess a usual infraciliature in the timehonoured genus Dileptus.

The somatic and oral infraciliature of most *Dileptus* species is very similar, except for the few species mentioned above and possibly some others. Thus, the classical species characters (size, shape, length of proboscis, nuclear apparatus, number and location of contractile vacuoles, biotope) used by Kahl (1931) and Dragesco (1963) are still valid. However, I would like to add another highly useful character, viz. the extrusomes which show a bewildering, yet hitherto unrecognized diversity in size, shape and arrangement (Song Weibo et al. 1988, present results and data from about 10 new terrestrial species not yet published). Usually, these organelles do not stain with protargol and their shape is more or less altered by various fixatives. Thus, size, shape and arrangement of the extrusomes must be studied in live cells.

• *Dileptus costaricanus* nov. spec. (Figs. 1–15, Tab. 1)

**Diagnosis:** In vivo about 230–330×40 μm, proboscis 30% of body length on average, posterior body end narrowly rounded to slightly pointed. Many macronuclear nodules. One row of contractile vacuoles each on dorsal and ventral side. Extrusomes conspicuous, thornshaped, not only in proboscis but also in single row around pharyngeal opening.

**Type location:** Upper soil layer near the ranch house "La Casona" in the Santa Rosa National Park, Costa Rica, W 85° 38', N 10° 50'.

**Derivatio nominis:** Named after the country (Costa Rica) where it was discovered.

**Description:** Shape blunt because proboscis rather wide and short and trunk not tailed; posterior end rounded in specimens collected from young raw culture, pointed in most cells found in old culture; postoral portion cylindroid, proboscis flattened leaf-like. Macronuclear nodules highly variable in shape and size, globular to ellipsoid, with few to many nucleoli, irregularly distributed throughout cell, difficult to count because narrowly spaced and of similar size as cytoplasmic inclusions; about 150–500 nodules seem common. Many globular micronuclei. Contractile vacuoles each with single excretory pore, dorsal row extends to anterior half of proboscis, ventral row commences near

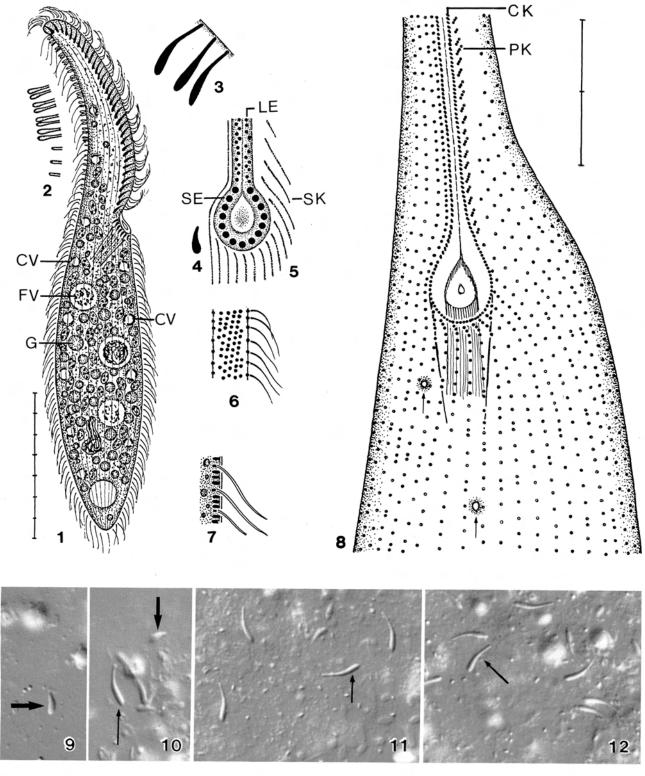
pharyngeal opening; pores not in single line but in narrow band in and between different kineties (Figs. 1, 8, 15). Extrusomes of proboscis 5–7×1 μm, distinctly curved, thorn- to club-shaped; those around inner pharyngeal wall 3×1 μm, only slightly curved, drop-shaped, oriented perpendicularly to pharynx surface with thick end distally producing very conspicuous ring (Figs. 3–5, 9–12); both size types occur also in cytoplasm and do not stain with protargol. Pellicle and cytoplasm colourless. About 5 rows each of 1×0.5 μm sized cortical granules between somatic kineties. Cytoplasm usually packed with 3–8 μm sized fat globules. Food vacuoles with indiscernible content, possibly ciliates.

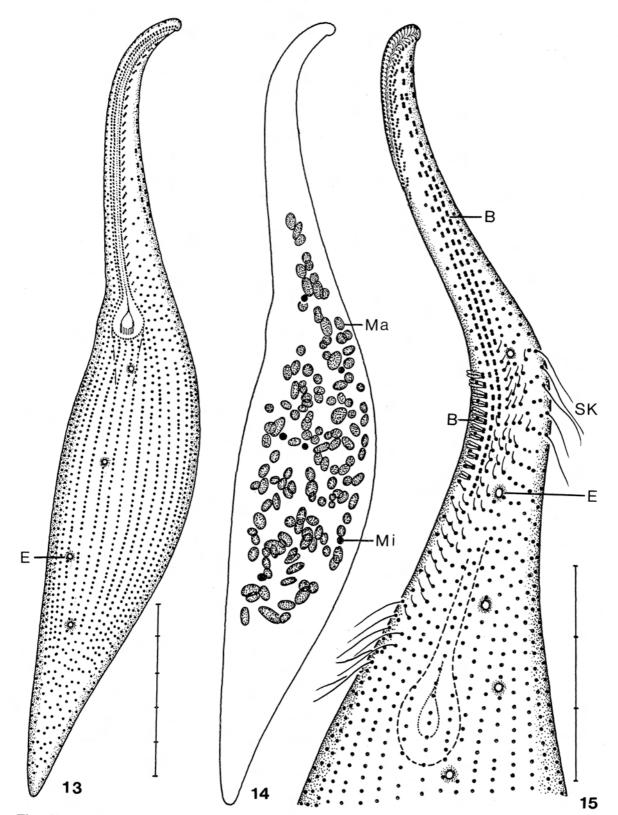
Somatic and oral infraciliature without peculiarities, i.e. as in other well-investigated, large-sized species of genus (Foissner 1984, 1989, Golinska 1971). However, the dorsal brush will be described at some length because few detailed data are available. Paired dorsal brush cilia 2-3 µm long and inflated, unpaired bristles 1–2 µm long and rod-shaped (Fig. 2). Brush formed by anterior portion of about 5 left lateral somatic kineties, except of those ending near pharyngeal opening and thus producing small, non-ciliated field along preoral kineties; brush kineties successively shortened forming remarkable pattern where 3 rows each of paired cilia extend for short distances in step-like manner side by side, giving impression of three-rowed dorsal brush (Fig. 15); some unpaired bristles posterior of each row of paired cilia, often some unpaired basal bodies at anterior end of brush kineties.

**Table 1.** Morphometric characteristics from *Dileptus costaricanus* (upper line) and *D. similis* (lower line)<sup>1</sup>).

Character	x	M	SD	$SE_{\bar{x}}$	CV	Min	Max	n
Body, length	247.1	245.0	37.3	10.8	15.1	185	310	12
	218.7	210.0	27.4	7.9	12.5	170	280	12
Body, width	38.8	37.5	6.1	1.8	25.7	44	55	12
	56.7	55.0	13.9	4.0	24.6	37	83	12
Anterior somatic end to proximal	76.4	75.0	12.9	3.9	16.8	60	95	11
vertex of circumoral kinety	104.3	102.5	19.2	5.5	18.4	80	140	12
Macronuclear nodules, length	4.8	5.0	1.1	0.3	23.1	3	7	12
, ,	36.8	39.0	7.1	2.1	19.3	22	45	12
Macronuclear nodules, width	2.9	3.0	0.2	0.06	7.9	2.5	3	12
	10.5	10.0	1.6	0.5	15.5	8	13	12
Micronucleus, diameter	2.0	2.0	0.1	0.03	5.7	1.8	2.2	12
	2.8	3.0	0.6	0.2	22.6	1.5	3.5	12
Somatic kineties, number	38.4	38.0	2.2	0.6	5.6	36	42	11
	28.7	28.0	2.6	1.0	9.2	25	32	7
Macronuclear nodules, number	about 150	) to 500						
, , , , , , , , , , , , , , , , , , , ,	2.0	2.0	0.0	0.0	0.0	2	2	12
Micronuclei, number	many							
	1.0	1.0	0.0	0.0	0.0	1	1	12

 $<sup>^{\</sup>scriptscriptstyle 1}$ ) Data based on randomly selected, protargol impregnated specimens from raw culture. Measurements in  $\mu$ m. CV– coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE $_{\bar{x}}$  – standard error of mean,  $\bar{x}$  – arithmetic mean.





Figs. 13–15. Dileptus costaricanus after protargol impregnation. – 13, 14. Infraciliature of ventral side and nuclear apparatus. – 15. Dorsal infraciliature of proboscis. Note that three types of cilia occur, viz. short paired brush cilia, short unpaired cilia, and long unpaired (normal somatic) cilia. B = brush, E = excretory pores, Ma = macronuclear nodules, Mi = micronuclei, SK = somatic kineties. Scale bar division  $10 \ \mu m$ .

Pharyngeal opening small compared to size of cell, about 10 µm in diameter; pharyngeal fibres inconspicuous.

Comparison with related species: *D. costaricanus* differs from all multinucleate congeners by the shape and arrangement of the massive extrusomes (toxicysts); however, these characters are difficult to rate because detailed data are lacking in most species. In *D. margaritifer* and *D. mucronatus*, two other large-sized species, the extrusomes are rod-shaped (Foissner 1984, Foissner et al. 1995); those of *D. beersi* are slightly thornshaped, but this information is based on mercuric chloride fixed specimens (Jones 1956). Possibly, most multinucleate *Dileptus* species have simple, i.e. rod-shaped extrusomes. A unique character of *D. costaricanus* is its ring of knotty extrusomes around the pharyngeal opening.

Only two other multinucleate *Dileptus* species possess ventral contractile vacuoles, viz. *D. anatinus* Golinska 1971 (length more than 500 µm; posterior end with short tail; extrusomes rod-shaped; Foissner et al. 1995) and *D. dubius* Vuxanovici, 1959 (described from single, 116 µm long specimen found in a lake in Romania; extrusomes short and delicate; only one contractile vacuole underneath pharyngeal opening).

**Ecology:** As yet found only at type location, where it occurred together with *Dileptus similis* (see next species). The population found was rather weak but present for 4 weeks.

• Dileptus similis nov. spec. (Figs. 16–23, Tab. 1)

**Diagnosis:** In vivo about 200–300×60 μm, proboscis 50% of body length on average, posterior body end broadly rounded. 2 macronuclear segments with micronucleus interposed. Single dorsal row of contractile vacuoles. Two size-types of rod-shaped extrusomes.

**Type location:** Upper soil layer near the ranch house "La Casona" in the Santa Rosa National Park, Costa Rica, W 85° 38', N 10° 50'.

**Derivatio nominis:** The epithet refers to its similarity with *D. mucronatus*.

**Description:** Shape blunt because length/width proportion rather narrow, viz. 3:1 to 5:1; postoral body portion cylindroid, proboscis very flexible, distinctly flattened, sickle-shaped, conspicuously widened near pharyngeal opening. Macronuclear segments in centre of trunk, sausage-shaped, often side by side or one upon the other, contain many small nucleoli. About 6–8 contractile vacuoles each with several excretory pores, upper-

most vacuole in proximal half of proboscis, posterior-most vacuole enlarged and slightly above cytopyge. Both types of extrusomes in proboscis and cytoplasm: large type  $8-10\times1$   $\mu m$  in size and slightly fusiform, small type about 3  $\mu m$  long, delicate and rod-shaped. Pellicle and cytoplasm colourless. About 6 rows each of 0.8  $\mu m$  sized cortical granules between somatic kineties. Feeds on other ciliates, e.g. *Frontonia depressa*, which are ingested whole and digested in large food vacuoles.

Somatic and oral infraciliature as described in *D. costaricanus* (see above) and *D. conspicuus* (FOISSNER 1989). However, both sides of proboscis have rather large field without cilia, that on left side larger than that on right. Paired dorsal brush cilia only 1–2 µm long, rod-shaped, arranged as described in *D. costaricanus* (Figs. 18, 20, 21).

Pharyngeal opening large, viz. about 25 µm in diameter; pharyngeal fibres delicate but numerous forming distinct outer and inner basket (Figs. 20, 23).

Comparison with related species: *D. similis* resembles several other species as concern size, nuclear apparatus and contractile vacuoles, viz. *D. robustus* VUXA-NOVICI, 1959 (a poorly described limnetic species with symbiotic algae), *D. orientalis* SONG WEIBO et al., 1988 (a terrestrial species with small, lemon-shaped extrusomes), and *D. mucronatus* PENARD, 1922 (a freshwater and soil species with distinct tail). The similarities between *D. similis* and *D. mucronatus* are obviously considerable, and it thus cannot be excluded that the new species is an untailed, blunt ecotype of *D. mucronatus*. On the other hand, *D. mucronatus*, as redescribed by FOISSNER (1984), is much more slender (9:1) than *D. similis* (4:1), whose shape and infraciliature thus resemble *D. conspicuus* (redescribed in FOISSNER 1989).

On superficial observation, *D. similis* is easily confused with *D. terrenus* Foissner, 1981 which, however, has a distinct tail and a single sausage-shaped macronucleus. Another, less similar terrestrial species is *D. americanus* Kahl, 1931 which is smaller (up to 200 µm) and has only 2 contractile vacuoles.

**Ecology:** As described in *D. costaricanus*. Recently found in a lowland soil from Namibia (Africa) with the typical characters mentioned; it is thus a reliable species.

 Paracineta lauterborni Sondheim, 1929 (Figs. 24–46, Tab. 2)

From this species I studied 4 populations occurring in Costa Rica, Kenya (grassland soil at exit of Amboseli National Park), Australia (coastal forest soil in the Royal National Park south of Sydney; BLATTERER &

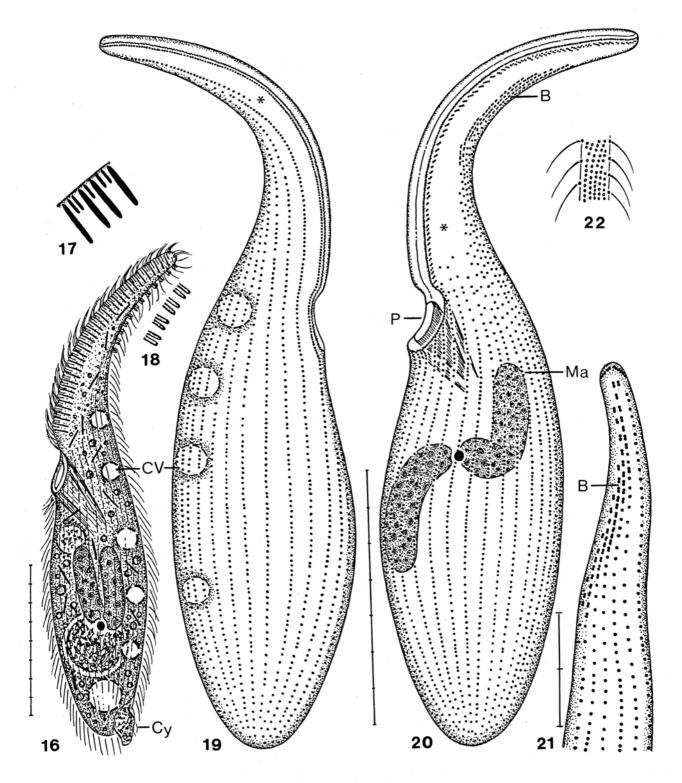


Fig. 16–22. Dileptus similis from life (Figs. 16–18, 22) and after protargol impregnation (Figs. 19–21). – 16. Left lateral view of typical specimen. – 17. Short and long extrusomes in proboscis. – 18. Brush cilia at higher magnification. – 19, 20. Infraciliature of right and left side. Note that this species has a rather wide non-ciliated field (\*) on both sides of the probosics. – 21. Dorsal infraciliature of proboscis. – 22. Cortical granules in surface view. B = brush, CV = contractile vacuoles, CV = contractile vacuoles,

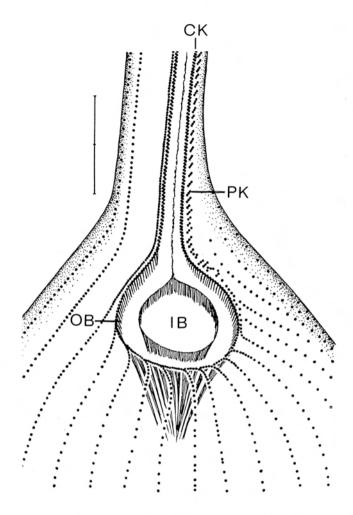


Fig. 23. Dileptus similis, oral infraciliature after protargol impregnation. CK = circumoral kinety, IB = inner basket, OB = outer basket, PK = preoral kineties. Scale bar division  $10 \ \mu m$ .

Foissner 1988), and Germany (soil of a deciduous forest near Munich). They were very similar and are thus treated together; however, morphometry is kept separate.

Generally, this species shows considerable variability in most characters. *Paracineta lauterborni* has never been reinvestigated since the short original description. I have thus prepared a complete redescription, including some data on swarmer formation.

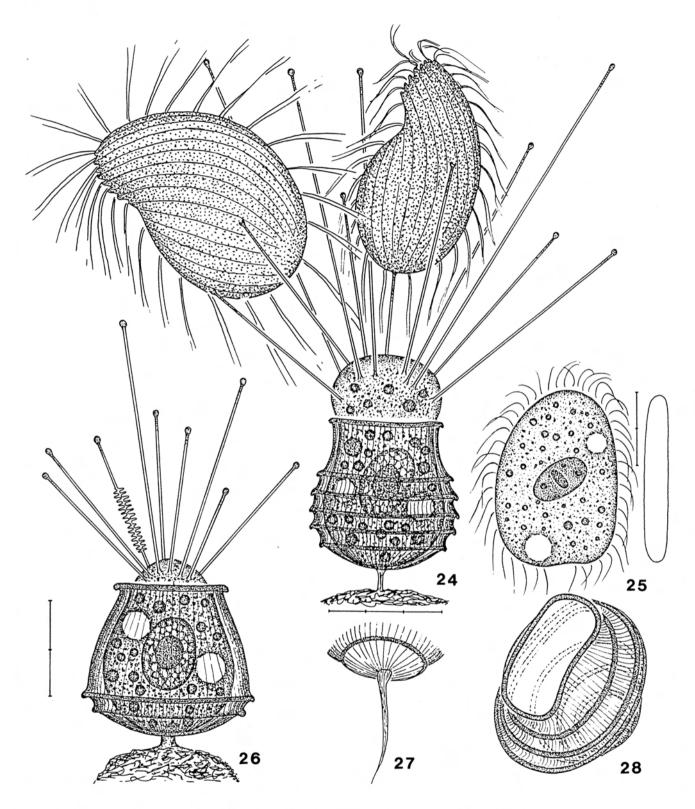
Adult cell (Figs. 24, 26, 29–31, 33–35, 41): Oviform to pyriform, anterior end in well-fed specimens usually hemispherically protruding from lorica opening. Posterior end with short, narrow or broad stalk-like elongation attached to centre of lorica base; elongation not recognizable in well-fed specimens which fill lorica completely; smaller individuals leave some space between

lorica and cell, especially in widened posterior half. Macronucleus in centre of cell, spherical to slightly ellipsoid, contains large central nucleolus. Single ellipsoid micronucleus with distinct membrane attached to macronucleus. 2 contractile vacuoles opposed or slightly diagonally opposed in or near mid-body. Up to 50 tentacles in single bunch on anterior surface of body, tentacles up to 50 µm long, distal end distinctly knobbed. One specimen occupied lorica in wrong direction, i.e. with tentacles directed to posterior end of lorica. Cytoplasm densely granulated by 1–2 µm sized lipoid droplets. Feeds on various ciliates (*Leptopharynx costatus, Cyrtolophosis mucicola*), especially on *Colpoda maupasi* of which up to 10 specimens are sometimes simultaneously attached to the tentacles of a single predator.

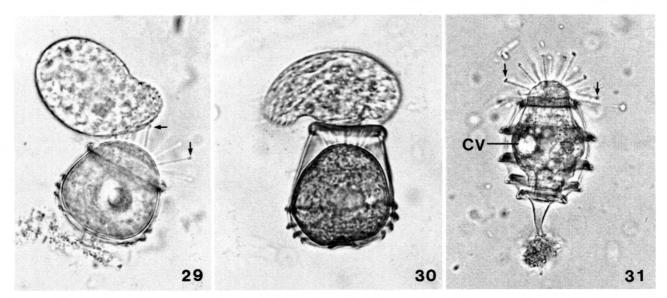
Lorica (Figs. 24, 26-40): Size and shape highly variable, truncated pyriform (Figs. 26, 30), ellipsoid (Figs. 31, 32) or cylindroid (Fig. 38), usually widest near base where it is fixed to soil particles by short cylindrical or posteriorly narrowing stalk rarely half as long as lorica; often distinctly asymmetrical because one side more vaulted than other and/or stalk slightly bent. Shape of lorica opening likewise highly variable, i.e. circular, ellipsoid or even almost rectangular, in side view often like a figure 8 because margins higher than centre. 2-8, on average 5 lorica corrugations, first corrugation forms border of lorica opening; corrugations slanted slightly backwards, sometimes incomplete forming indistinct spirals. Lorica material firm, colourless to brownish, distinctly striated longitudinally between corrugations.

**Budding and swarmer** (Figs. 25, 41–46): Budding commences on the anterior surface with the production of a short, narrow kinety band dividing the tentacle bundle. The macronucleus and the micronucleus elongate (Fig. 42). The kinety band consists of 9–11 ciliary rows (Tab. 2) and is passed to the oviform and leaf-like flattened swarmer which has a size of about 45×30 um; its posterior end is often slightly indented at the site of the contractile vacuole (Figs. 25, 44). Old swarmers become longer and narrower and have few to many short tentacles (Figs. 45, 46, Tab. 2). The macronucleus is irregularly ellipsoid, and there are at least 2 micronuclei often far away from the macronucleus. Like the adults, the swarmers have two contractile vacuoles, one in the anterior third between the ciliary rows and another near the posterior end.

**Ecology:** As mentioned above, I found this species in Kenya (Africa), Australia, Costa Rica and Germany, indicating that it occurs worldwide. It is, however, always rare, i.e. only few individuals develop with the culture method used.



Figs. 24–28. Paracineta lauterborni from life (Figs. 24–26 Kenyan population, Figs. 27, 28 Australian population). – 24. Well-fed specimen having captured two *Colpoda maupasi* cells. The anterior body portion protrudes hemispherically and the lorica has six corrugations. – 25. Broad and narrow side view of swarmer. – 26. Typical specimen with three lorica corrugations. Note that tentacles form single bunch at anterior end. – 27. Lorica with tapering stalk. – 28. Oblique anterior view of lorica. Scale bar division  $10 \, \mu m$ .

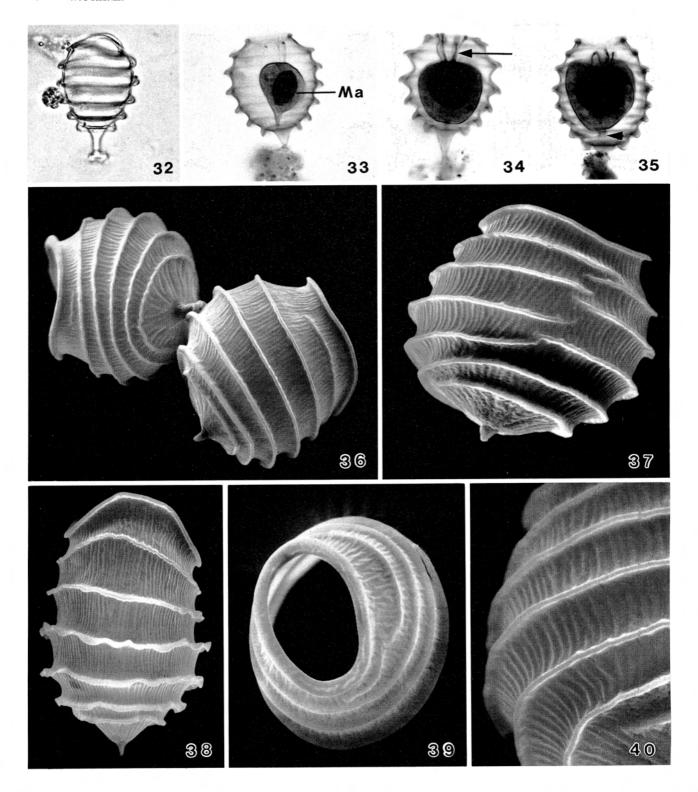


**Figs. 29–31.** Paracineta lauterborni, bright field light micrographs of live cells from Kenya, Austria and Germany. Note high variability of lorica and cell shape which, however, occurs not only among but also within populations (Figs. 24, 26; 36–38). The specimens from Kenya and Austria each have captured a *Colpoda maupasi*. Arrows mark tentacles with distinctly knobbed distal end. CV = contractile vacuole.

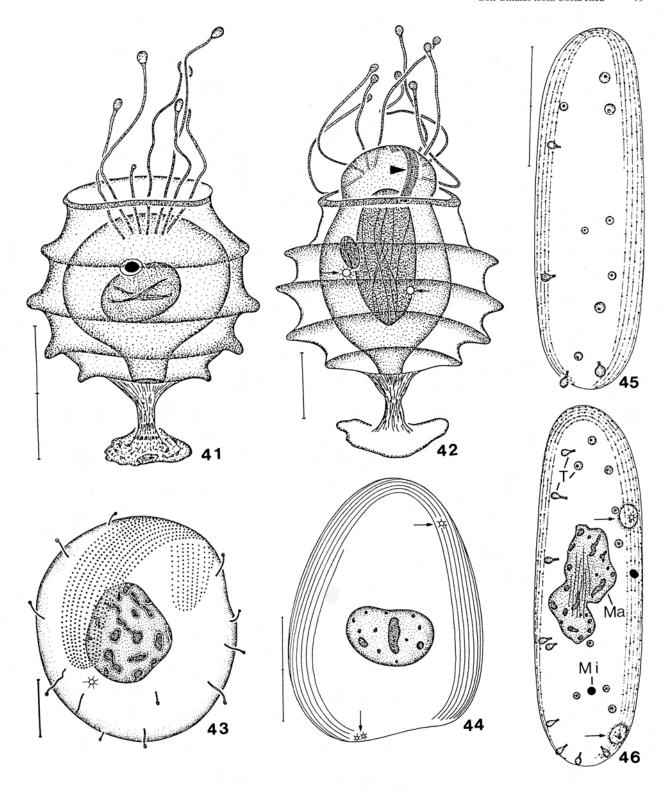
**Table 2.** Morphometric characteristics from *Paracineta lauterborni* populations of Costa Rica (Cr), Australia (Au), Kenya (Ke), and Germany (Ge)<sup>1</sup>).

Character		$\bar{\mathbf{x}}$	M	SD	$SE_{\bar{x}}$	CV	Min	Max	n
Lorica, length without	Cr	36.2	36.0	4.0	1.2	11.0	29	41	11
stalk	Au	35.0	35.0	4.2	1.3	11.9	27	41	10
	Ge	29.7	28.0	8.1	2.2	27.2	20	45	14
Lorica, maximum	Cr	35.8	35.0	3.2	1.0	9.0	30	40	11
width	Au	31.4	30.0	2.5	0.8	7.9	30	38	10
	Ge	32.1	31.5	7.8	2.1	24.2	22	47	14
Lorica, length of	Cr	9.9	9.0	1.7	0.5	17.2	8	13	11
stalk	Au	7.0	3.5	6.8	2.2	97.6	2	21	10
	Ge	9.4	7.0	6.1	1.6	65.3	2 5	25	14
Lorica, number of	Cr	6.6	7.0	0.7	0.2	10.2	6	8	11
corrugations	Au	5.9	6.0	1.4	0.5	24.6	3	8	10
8	Ke	3.8	3.5	1.2	0.3	31.4	2	6	12
	Ge	5.2	5.0	0.6	0.2	11.1	4	6	14
Adult, number of	Cr	13.5	12.0	7.7	2.3	56.9	3	25	11
tentacles	Ge	11.6	10.0	5.0	1.3	42.9	6	20	14
All populations, length of lorica with stalk		42.5	39.5	10.6	1.8	24.9	25	70	36
All populations, width of lorica		33.1	32.0	5.5	0.9	16.7	22	47	36
All populations, number of lorica corrugations		5.2	5.0	1.5	0.2	28.5	2	8	49
Swarmer, length	Ke	64.2	64.5	5.6	1.8	8.7	55	72	10
Swarmer, width	Ke	20.4	20.5	2.6	0.8	12.7	17	24	10
Swarmer, macronucleus length	Ke	15.8	15.0	2.9	0.9	18.6	11	21	10
Swarmer, macronucleus width	Ke	11.5	11.0	2.3	0.7	19.8	10	17	10
Swarmer, number of ciliary rows	Ke	9.5	9.0	0.8	0.2	8.6	9	11	11
Swarmer, number of excretory pores		2.1	2.0	-	-	-	2	3	10

¹) Data based on randomly selected, protargol impregnated (Cr, Ke, Ge) or live (Au) specimens from raw cultures. Measurements in  $\mu$ m. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation,  $SE_{\bar{x}}$  – standard error of mean,  $\bar{x}$  – arithmetic mean.



**Figs. 32–40.** *Paracineta lauterborni* from life (Fig. 32, Costa Rica population), after protargol impregnation (Figs. 33–35, Costa Rica population), and in the scanning electron microscope (Figs. 36–40, Australian population). – **32, 36-38.** Variability of lorica shape. – **33.** Small specimen which does not fill up its lorica. – **34, 35.** Typical specimens with single tentacle bunch (arrow) at anterior end. The cell is anchored by a cylindroid elongation (arrowhead) to the lorica bottom, whereas the lorica is anchored to soil particles by a cone-shaped stalk. – **39.** Oblique anterior view of lorica. – **40.** Fine structure of lorica. Ma = macronucleus.



Figs. 41–46. Paracineta lauterborni after protargol impregnation (Figs. 41, 42 German population, Figs. 43-46 Kenyan population). – 41. Morphostatic specimen. – 42. Swarmer production. A ciliary ribbon develops between the tentacle bunch (arrowhead). – 43. Infraciliature of a young swarmer with tentacle remnants. – 44. Infraciliature of a typical, fully developed swarmer. – 45, 46. Infraciliature of an old, oblong swarmer with many short, distinctly knobbed tentacles. Arrows in Figs. 42, 44, 46 mark excretory pores of contractile vacuoles. Ma = macronucleus, Mi = micronucleus, T = tentacles. Scale bar division 10 μm.

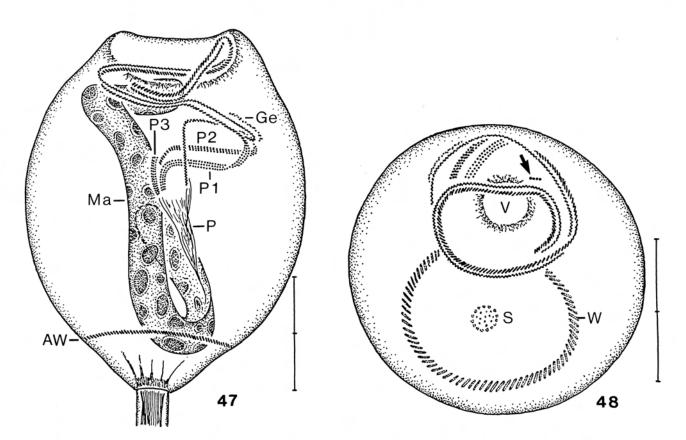
**Identification and synonymy:** My observations agree perfectly with those of SONDHEIM (1929), who discovered P. lauterborni in a dried and rewetted mud sample from Madagascar. A previously unrecognized synonym is Thecacineta edmondsoni KING (1931), which was transferred to the genus Loricophrya by MATTHES (1956). King (1931) discovered this species in a mixed culture of tap water and garden soil in Iowa City, USA. His population had only 3–4 corrugations in the posterior half of the lorica. However, this character is highly variable (Tab. 2) and thus can not be used to distinguish species. Furthermore, KING (1931) did not compare his new taxon with P. lauterborni. Thecacineta caepula PENARD, 1920, a moss inhabitant, could be a further synonym, viz. a poorly developed P. lauterborni without lorica corrugations. Jankowski (1978) erected the genus Heliotheka for this species, without new evidences however, while MATTHES (1956) transferred it to *Loricophrya*.

**Systematic position:** Sondheim's and my observations show that *Paracineta lauterborni* belongs to the suborder Podophryina because the swarmer is produced by

pseudotransverse fission, as defined by BATISSE (1994). Within the Podophryina, *P. lauterborni* fits into the family Paracinetidae JANKOWSKI, 1978 and possibly to the genus *Paracineta*. However, JANKOWSKI (1978) erected, again without new evidences, the genus *Paraloricophrya* for SONDHEIM's species, giving as sole distinguishing character "with stalk". Likewise, the combination with *Loricophrya*, as suggested by MATTHES (1956, 1988), is uncertain because the type of swarmer production is unknown in the type species, *L. parva* (SCHULZ). All these genera are still poorly defined and it seems thus wise to keep the present species in the genus it was placed originally.

 Pseudovorticella sphagni Foissner & Schiffmann, 1974 (Figs. 47, 48)

The population from Costa Rica is very similar to those described by Foissner & Schiffmann (1974) and Foissner (1979), i.e. it has 2 contractile vacuoles at opposite sites of the vestibulum and the posterior third of the macronucleus is bent anteriorly. I thus add only a



**Figs. 47, 48.** *Pseudovorticella sphagni*, somatic and oral infraciliature after protargol impregnation. – **47.** Morphostatic specimen. – **48.** Telotroch (swarmer) with epistom membrane (arrow). Note that only the distal portion of the oral infraciliature is depicted. AW = anlage of aboral ciliary wreath, Ge = germinal kinety, Ma = macronucleus, P = pharynx, P1–P3 = peniculi (adoral membranelles), S = scopula, W = aboral ciliary wreath, V = vestibular opening.

few in vivo measurements from a population of a bottom land soil in Austria (Foissner et al. 1985) and provide a couple of drawings of the oral infraciliature from another population which I found in a grassland soil near Hortobagy, Hungary.

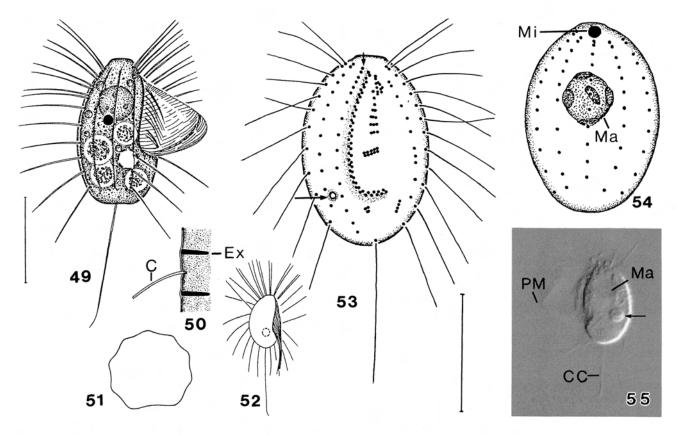
Length of zooids 53–70  $\mu$ m ( $\bar{x}$  = 59.2, n = 6), width at peristomial collar 46–60  $\mu$ m ( $\bar{x}$  = 50.5, n = 6), maximum postperistomial width 38–48  $\mu$ m ( $\bar{x}$  = 43.7, n = 6), length of stalk 125–279  $\mu$ m ( $\bar{x}$  = 186  $\mu$ m, n = 3), width of stalk 5.3  $\mu$ m (n = 1). Oral infraciliature as in other members of genus and in *Vorticella* spp. All peniculi consist of 3 rows of closely spaced basal bodies. Epistom membrane of swarmer rather distant from anterior end of oral polykinetid (Fig. 48).

 Cyclidium muscicola KAHL, 1931 (Figs. 49–55, Tab. 3)

Improved diagnosis: Size in vivo  $14-20\times9-13~\mu m$ . Usually 1 macronucleus and 1 micronucleus. Contrac-

tile vacuole distinctly subterminal, viz. right of peristomial vertex with excretory pore between kineties 1 and 2. 9–10 somatic kineties, anterior end of kinety 1 polymerized. Adoral membranelle 2 small, laterally attached to membranelle 1.

Redescription: The populations investigated were found in meadow soils near the town of Salzburg and in Hawaii. They are very similar, at least in vivo, to those observed in Costa Rica and in other soils world-wide. Size in vivo 14–20×9–13 μm. Shape slenderly to broadly ellipsoid, frontal plate distinct, laterally sometimes inconspicuously flattened. Nuclear apparatus in anterior body half, usually 1 globular macronucleus disintegrated into as many as 6 smaller spheres in about 20% of specimens. Micronucleus globular, attached to macronucleus in Salzburg population, often distant from macronucleus and in anterior end of cell in Hawaii population, difficult to recognize in living cells. Contractile vacuole on average exactly right of peristomial



Figs. 49–55. Cyclidium muscicola from life (Figs. 49–52, 55) and after protargol impregnation (Figs. 53, 54). – 49, 55. Right and left lateral views of feeding cells. Arrow marks compact food vacuole. – 50. Side view of cortex with extrusomes attached. – 51. Transverse view. – 52. Resting cell. – 53, 54. Infraciliature of ventral and dorsal side (Hawaiian population). The micronucleus of this population is usually far away from the macronucleus, viz. in the anterior end of the cell. Furthermore, the anterior end of the somatic kineties bears only one dikinetid. Long arrow marks excretory pore of contractile vacuole which is between kineties 1 and 2; small arrow points to condensed cilia (basal bodies) at anterior end of kintey 1. C = cilium, CC = caudal cilium, Ex = extrusomes, Ma = macronucleus, Mi = micronucleus, PM = paroral membrane. Scale bars 10  $\mu$ m.

**Table 3.** Morphometric characteristics from *Cyclidium muscicola*. Upper line: population from Salzburg (Austria); lower line: population from Hawaii <sup>1</sup>).

Character	$\bar{\mathbf{x}}$	M	SD	$SE_{\bar{x}} \\$	CV	Min	Max	n
Body, length	14.9	15.0	1.0	0.3	6.7	13	17	10
	16.5	16.0	0.8	0.2	4.7	15	18	13
Body, width	8.8	8.5	0.9	0.3	9.8	8	10	10
	11.2	11.0	1.0	0.3	8.8	10	13	13
Anterior somatic end	1.9	2.0	0.6	0.2	30.7	1	3	10
to macronucleus	3.3	4.0	1.2	0.3	35.8	2	5	13
Anterior somatic end	9.4	10.0	1.1	0.4	11.6	8	11	10
to excretory pore	12.2	12.0	0.8	0.2	6.6	11	13	13
Anterior somatic end	10.0	10.0	0.8	0.3	8.2	9	11	10
to vertex of paroral membrane	12.3	12.0	0.8	0.2	6.1	11	13	13
Macronucleus, length <sup>2</sup> )	4.3	4.2	0.4	0.1	8.5	4	5	10
, , , , , , , , , , , , , , , , , , , ,	5.0	5.0	0.6	0.2	12.2	4	6	13
Macronucleus, width2)	4.1	4.2	0.1	0.04	3.4	3.8	4.2	10
	3.9	4.0	0.6	0.2	16.9	3	5	13
Micronucleus, largest diameter	1.3	1.2	0.1	0.04	11.3	1	1.5	10
	1.4	1.3	0.2	0.1	15.6	1.2	2	13
Somatic kineties, number	9.0	9.0	0.0	0.0	0.0	9	9	10
	10.0	10.0	_	_	_	9	10	13
Basal bodies in a dorsal kinety,	11.9	12.0	0.6	0.2	4.8	11	13	10
number <sup>3</sup> )	10.8	11.0	1.2	0.3	11.2	9	13	13
Paroral dikinetids, number	_	_	_	_	_	_	_	_
	25.8	25.0	1.1	0.3	4.4	24	27	13
Macronuclei, number	1.2	1.0	_	-	_	1	2	10
	1.2	1.0	_	_	_	1	2	13
Micronuclei, number	1.0	1.0	0.0	0.0	0.0	1	1	10
	1.0	1.0	_	_	_	1	2	13

<sup>&</sup>lt;sup>1</sup>) Data based on randomly selected, silver nitrate (Salzburg population) or protargol (Hawaii population) impregnated specimens from raw cultures. Measurements in  $\mu m$ . CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation,  $SE_{\bar{x}}$  – standard error of mean,  $\bar{x}$  – arithmetic mean.

vertex, i.e. distinctly subterminal (Tab. 3), with single excretory pore located between kineties 1 and 2, connected to kinety 2 with faint silverline (Figs. 49, 53). Extrusomes about 3 μm long, cuneate with thicker end anchored in cortex (Fig. 50), often difficult to recognize in living cells, probably absent in some cells or populations. Cortex distinctly furrowed (Fig. 51). Cytoplasm colourless, contains some small fat droplets and usually many 2–5 μm sized food vacuoles with bacterial residues. Movement as in *C. glaucoma*, i.e. jumping and resting; when resting and feeding cilia of anterior third directed anteriorly, those behind posteriorly. Rarely, populations have been observed which, although resting, did not distinctly jump.

Somatic infraciliature and silverline system similar to other members of genus. Cilia  $8{\text -}10~\mu m$  long, rather stiff,  $4{\text -}7$  cilia very closely spaced in anterior portion of first kinety right of paroral membrane. Somatic kineties

regularly spaced, of four populations analyzed two had mostly 9 and two mostly 10 kineties (Tab. 3); each kinety commences with 1–4 dikinetids, depending on population. Caudal cilium at least as long as cell, inclined to ventral side, proximal portion very fine and curved.

Oral apparatus extends from anterior end to second third of cell. Adoral membranelles inconspicuous, membranelle 2 distinctly smaller than in *C. glaucoma*, i.e. composed of about 12 basal bodies only and indistinctly separate from membranelle 1. Cilia of undulating membrane 8–10  $\mu m$  long, form conspicuous velum during feeding, directed backwards in swimming and resting cells.

**Identification:** The populations studied perfectly match the short but appropriate original description. *Cyclidium muscicola* is easily recognized by its small

<sup>&</sup>lt;sup>2</sup>) From specimens with single nucleus.

<sup>&</sup>lt;sup>3</sup>) Dikinetids counted as single basal body.

size and the unusual location of the contractile vacuole, also emphasized by KAHL (1931). Superficially observed, it could be confused with the similarly sized C. glaucoma, which, however, occurs very rarely in terrestrial biotopes (Foissner 1987 a, b) and differs from C. muscicola not only by the terminal location of the contractile vacuole but also by the higher number (10-11) of somatic kineties and the larger adoral membranelle 2 (Berger & Thompson 1960, Didier & Wil-BERT 1981, FOISSNER et al. 1994). However, another Cyclidium species occurs in many soils, possibly C. terricola KAHL, 1931, which resembles C. muscicola, especially in the subterminal location of the contractile vacuole. This species is larger (30-35 µm), distinctly flattened and has 12 somatic kineties (Foissner, unpubl.); it is apparently rather similar to C. bonneti GROLIERE, 1980. Cyclidium muscicola has also been redescribed by SONG WEIBO & WILBERT (1989). This population differs distinctly from my specimens by its larger membranelle 2, which is not attached to membranelle 1, and the contractile vacuole pore which is located more distally and not beside but at end of kinety 2. Furthermore, it is larger (20-30×12-17 µm) and the cilia are very widely spaced in the anterior end of somatic kinety 1. SONG WEIBO & WILBERT (1989) found this population in an eutrophic pond in Germany, while KAHL (1931) discovered C. muscicola in terrestrial mosses. I thus suggest considering my soil population as the species described by KAHL (1931). The population studied by SONG WEIBO & WILBERT (1989) is possibly a new species or an ecoform of C. bonneti Gro-LIERE, 1980.

**Ecology:** Cyclidium muscicola occurs, according to my experience (Foissner 1987a and newer data), in many soils world-wide. It is obviously restricted to terrestrial biotopes where it has often been confused with *C. glaucoma* (Foissner 1987a, b). Very likely, it does not prefer any certain type of soil or humus.

Colpodidiidae nov. fam.

**Diagnosis:** Medium-sized Nassulida with conspicuous buccal cavity in middle ventral third of cell containing 1 complete and 2 more or less distinctly reduced adoral organelles.

Type genus: Colpodidium WILBERT, 1982.

**Discussion:** PUYTORAC et al. (1983) also suggested a new family for *Colpodidium*. However, they did not provide any characterization for their "? Colpodidiidae fam. nov.", which is thus invalidated by the Int. Code of Zool. Nomenclature.

WILBERT (1982) assigned *Colpodidium* to the family Colpodidae (class Colpodea) because of its paired cilia and the rather deep vestibulum near mid-body, containing an upper and lower ciliary field. Foissner (1985) followed WILBERT (1982). However, a reinvestigation of the type species showed that WILBERT's description contains serious mistakes and misinterpretations (Foissner 1990 and below).

The reinvestigation of *C. caudatum* and observations on a new genus, Pedohymena, related to Colpodidium and described below, showed that both are near the family Furgasoniidae within the order Nasssulida. The evidence for this new classification can be summarized as follows (for details see species descriptions): (1) The somatic ciliature consists of monokinetids except of a few postoral dikinetids (Figs. 62, 63, 67, 84); (2) The oral ciliature is composed of a dikinetidal paroral membrane at the right margin of the buccal cavity and of 1-3 triple-rowed adoral organelles on the bottom of the buccal cavity (Figs. 56-59, 63, 69, 72, 80, 84); (3) The contractile vacuole pore and the cytopyge have the same spatial relationship as in many nassulids, i.e. are on the postoral ventral surface (Figs. 62, 65, 69, 82, 85); (4) The cortex is thick and inflexible and contains a tightly and irregularly meshed silverline system as, e.g., in Parafurgasonia (FOISSNER & ADAM 1981; Figs. 70, 71); (5) Division occurs in free-swimming condition (Figs. 56-59); (6) The few ontogenetic stages observed (Figs. 56-59) are highly reminiscent of those described by EISLER & BARDELE (1986) in Furgasonia and Nassula.

The general organization of *Colpodidium* and *Pedohymena* suggests that their nearest relatives are *Parafurgasonia* (1 adoral organelle, paroral membrane conspicuous) and *Furgasonia* (3 adoral organelles, paroral membrane inconspicuous). However, these genera and all other nassulids s. str., e.g. *Nassula* and *Obertrumia*, have a conspicuous cytopharyngeal basket and the oral apparatus located subapically on the cell surface, i.e. do not have the distinct buccal cavity so characteristic of *Colpodidium* and *Pedohymena*. These characters of *Colpodidium* and *Pedohymena* are highly reminiscent of microthoracid nassulids, which, however, have a reduced somatic ciliature (KAHL 1931). It is thus reasonable to separate *Colpodidium* and *Pedohymena* at family level.

• Genus Colpodidium WILBERT, 1982

**Improved diagnosis:** Colpodidiidae with short, slightly curved paroral membrane, 1 large adoral organelle and two postoral kineties with dikinetids anteriorly.

**Type species:** Colpodidium caudatum WILBERT, 1982 (by monotypy).

 Colpodidium caudatum WILBERT, 1982 (Figs. 56, 57, 60–72, Tab. 4)

**Redescription:** Size in vivo about  $55-70\times25-35 \mu m$ , lateral view reniform to Dexiostoma (Colpidium)shaped, ventral view fusiform with both ends rounded, laterally slightly to distinctly (2:1) flattened. Macronucleus globular, in posterior half to quarter of cell, contains roundish nucleoli. Micronucleus globular, in indentation of macronucleus. Contractile vacuole subequatorial, with single excretory pore underneath buccal cavity. Cytopyge in median of cell between excretory pore of contractile vacuole and posterior end of cell, often underlain by bright, seemingly empty vacuole. Cortex thick, glassy, distinctly furrowed by ciliary rows, in one population colonized by epibiontic bacteria. Extrusomes recognizable neither in vivo nor in silver carbonate or protargol stained cells. Cytoplasm colourless, contains many 1-2 µm sized, brightly shining fat droplets, mainly in posterior half of body; no crystals. Food vacuoles 5-10 µm in diameter, usually containing only few bacteria and/or food residues. Swims rapidly by rotation about longitudinal body axis.

Somatic cilia about 10 µm long and rather stiff, single except for few pairs at anterior end of postoral kineties 2, 3, 4. Silver carbonate impregnations show each kinetid composed of a large granule, which bears the cilium and a short kinetodesmal fibre extending obliquely anteriad, and of a small granule, possibly a parasomal sac or an alveolocyst (Figs. 67-69). Distances of kinetids increase within kineties from anterior to posterior, those of first kinety right of oral apparatus especially closely spaced in anterior portion. Ciliary rows bipolar on dorsal side, those on ventral surface form long and narrow preoral suture, because anterior left kineties abut obliquely on anterior right kineties which gradually shorten from anterior end of cell to oral apparatus. Four postoral kineties: first kinety commences very close to anterior end of paroral membrane, second in buccal cavity very near pharyngeal opening, third at distal end of adoral organelle, fourth left of excretory pore of contractile vacuole. No elongated caudal cilia. Oral apparatus slightly above mid-body, with conspicuous tube-shaped buccal cavity containing single, large adoral organelle and anterior end of postoral kinety 2. Adoral organelle in posterior vertex of buccal cavity, slightly curved, composed of 3 rows of ciliated basal bodies. Paroral membrane at right margin of buccal cavity, slightly curved, composed of distinctly inclined dikinetids having only anterior basal bodies ciliated; distances between dikinetids increase from anterior to posterior. Cytopharyngeal basket large but delicate, thus not recognizable in vivo and also faintly stained with protargol, composed of about 10 thin nematodesmal bundles; commences in upper vertex of buccal

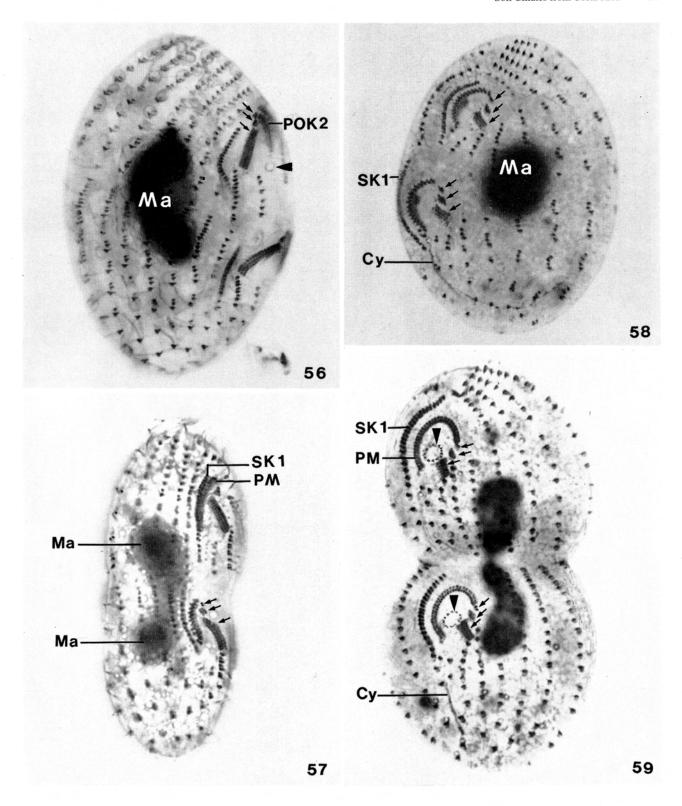
cavity, which appears more intensely stained at this site, and extends as wide, somewhat irregular tube almost to anterior end of cell where it curves dorsally and posteriorly.

Silverline system tightly and irregularly meshed in somatic and oral cortex, meshes within ciliary rows often filled with argyophilic substance (Figs. 70, 71).

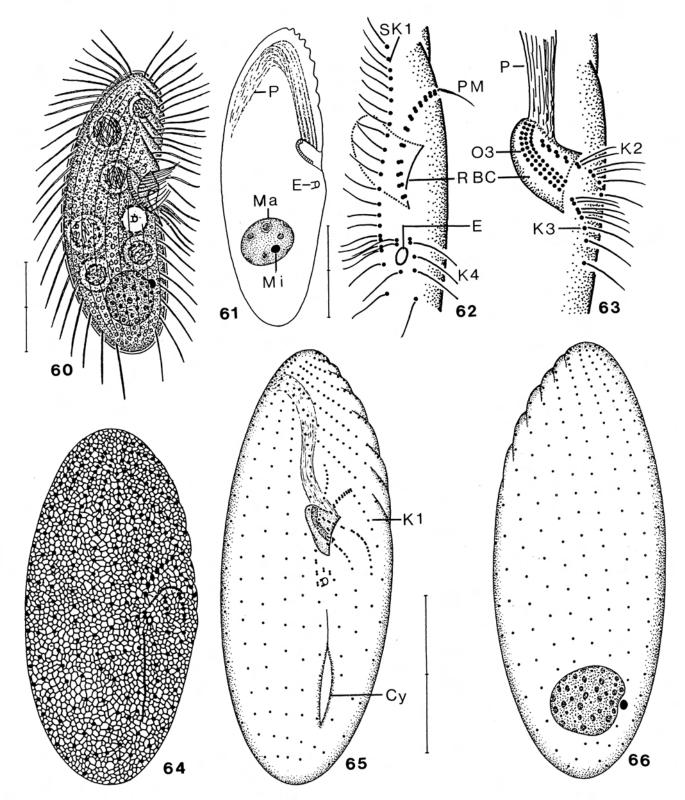
**Morphogenesis:** A few middle (Fig. 56), late (Fig. 57) and very late dividers were found in the preparations. The middle and late stages show 2 very small adoral organelles ahead of the large adoral organelle and reorganization of the parental paroral membrane and cytopharyngeal basket. In very late dividers a small ( $5\times2.5$   $\mu$ m), distinctly stained cytopharyngeal basket is apparent in both proter and opisthe; the 2 small adoral organelles disappear or are at least no more recognizable.

**Ecology:** The type population was found in a prairie soil at Ningerhar, Afghanistan (WILBERT 1982). The population described here is from Africa, viz. from soil of a coastal rain forest near Mombasa, Kenya. In fact, *C. caudatum* is not very rare, because I have records also from Australia, Japan, Tibet and Costa Rica, but not from Central Europe.

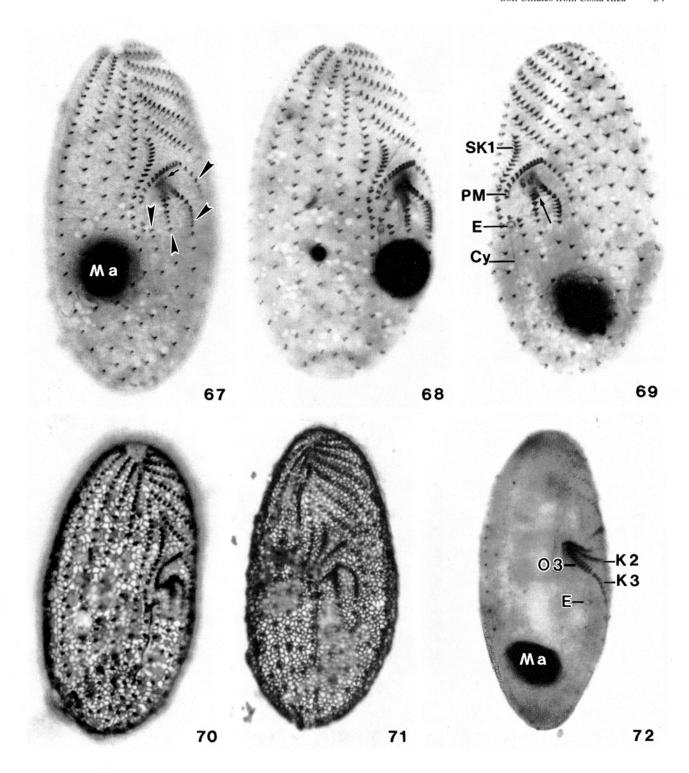
**Discussion:** I have no doubt about the identification, although my observations differ in many significant details from those of WILBERT (1982), who obviously observed superficially, at least the living cells, and misinterpreted the silver nitrate preparations. These show paired granules (cilia according to WILBERT) which are not recognizable in his micrographs from protargol impregnated specimens. Obviously, one of the two granules is a parasomal sac or an alveolocyst. I checked very carefully the absence of paired cilia in vivo, in silver carbonate preparations, and in protargol slides. Furthermore, WILBERT (1982) described an "upper ciliary field" (membranelle) deep in the buccal cavity. Such a field is lacking in my specimens. Very likely, WILBERT (1982) misinterpreted the pharyngeal fibres (entrance) as a membranelle, because he figured this structure exactly at the site where the pharyngeal basket commences in my specimens (Figs. 61, 63, 67). A third difference concerns the location of the contractile vacuole, which WILBERT drew rather far to the rear in his Figure 1 (living aspect), while it is located subequatorially in my specimens and in WIL-BERT's Figure 3a, which shows a silver nitrate impregnated cell. Obviously, WILBERT (1982) drew the oral apparatus and the contractile vacuole too near to the posterior end in Figure 1. Next, WILBERT (1982) stated that C. caudatum lacks a silverline system. In fact, I was also unable to impregnate it with the CHATTON-LWOFF technique, but it stains well with KLEIN's dry silver method (Figs. 70, 71). Finally, WILBERT (1982) claimed



**Figs. 56–59.** Middle and late dividers of *Colpodidium caudatum* (Figs. 56, 57) and *Pedohymena australiense* (Figs. 58, 59) after silver carbonate impregnation. Arrows mark adoral organelles, arrowheads denote developing pharyngeal baskets. Note that adoral organelle 1 is very near to distal end of paroral membrane (*P. australiense*) and postoral kinety 2 (*C. caudatum*), respectively. Cy = cytopyge, Ma = macronucleus, PM = paroral membrane, POK2 = postoral kinety 2, SK1 = somatic kinety 1.



Figs. 60–66. Colpodidium caudatum from life (Fig. 60) and after protargol (Figs. 61–63, 65, 66) and dry silver nitrate impregnation (Fig. 64). – 60, 61. Right lateral views showing main cell organelles. – 62, 63. Oral infraciliature at two focus levels. – 64. Silverline system. – 65, 66. Infraciliature of ventral and dorsal side. BC = buccal cavity, Cy = cytopyge, E = excretory pore, K1-4 = postoral kineties, Ma = macronucleus, Mi = micronucleus, O3 = adoral organelle 3, P = pharyngeal basket, PM = paroral membrane, R = roof of buccal cavity, SK1 = somatic kinety 1. Scale bar division  $10 \, \mu m$ .



**Figs. 67–72.** Colpodidium caudatum after silver carbonate (Figs. 67-69), dry silver nitrate (Figs. 70, 71) and protargol impregnation (Fig. 72). - **67.** Infraciliature of ventral side. Arrow marks pharyngeal opening, arrowheads denote postoral kineties. - **68, 69.** Infraciliature of right and left side. Arrow marks distal end of adoral organelle 3. - **70, 71.** Silverline system. - **72.** Right lateral view showing main cell organelles. Cy = cytopyge, E = excretory pore of contractile vacuole, K2, 3 = postoral kineties, Ma = macronucleus, O3 = adoral organelle 3, PM = paroral membrane, SK1 = somatic kinety 1.

**Table 4.** Morphometric characteristics from *Colpodidium caudatum* (upper line) and *Pedohymena australiense* (lower line) 1).

Character	$\bar{\mathbf{x}}$	M	SD	$SE_{\bar{x}}$	CV	Min	Max	n
Body, length	55.2	55.0	4.0	1.1	7.2	49	64	13
	48.9	49.5	3.4	1.0	7.1	41	53	12
Body, width	22.6	22.0	2.7	0.7	11.9	16	26	13
	19.3	19.5	1.9	0.5	9.7	17	23	12
Anterior somatic end to	18.0	18.0	1.9	0.5	10.6	14	22	13
paroral membran, distance	11.6	11.5	1.1	0.3	9.4	10	13	12
Anterior somatic end	29.5	29.0	2.3	0.6	7.8	25	34	13
to excretory pore, distance	24.9	25.0	1.5	0.4	6.0	23	28	12
Anterior somatic end	37.7	38.0	2.9	0.8	7.6	32	42	13
to macronucleus, distance	18.7	20.0	3.4	1.0	18.4	11	23	12
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1	1	13
	1.0	1.0	0.0	0.0	0.0	1	1	12
Macronucleus, length	10.5	10.0	1.2	0.3	11.4	9	13	13
, 0	7.2	7.0	1.1	0.3	15.6	5	9	12
Macronucleus, width	8.6	8.0	0.9	0.2	10.1	8	10	13
	6.2	7.0	1.1	0.3	16.9	4	7	12
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1	1	13
	1.0	1.0	0.0	0.0	0.0	1	1	12
Micronucleus, largest diameter	1.8	1.8	0.2	0.1	10.3	1.5	2	13
	about 2 μ	ım						12
Somatic kineties, number	17.6	18	0.9	0.2	4.9	16	19	13
	16.2	16	0.6	0.2	3.6	15	17	12
Basal bodies in a dorsal kinety,	26.9	27	2.7	0.7	10.0	23	32	13
number	17.9	18	1.7	0.5	9.4	14	20	12
Paroral dikinetids, number	12.8	13	0.8	0.2	6.2	12	14	13
	32.4	32	1.5	0.4	4.6	31	36	12

¹) Data based on randomly selected, protargol (C. caudatum) and Chatton-Lwoff silver nitrate (P. australiense) impregnated specimens from raw cultures. Measurements in  $\mu$ m. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation,  $SE_{\bar{x}}$  – standard error of mean,  $\bar{x}$  – arithmetic mean.

that *C. caudatum* divides in cysts. This is obviously not the case (Figs. 56, 57).

Colpodidium caudatum was also redescribed by DRAGESCO & DRAGESCO-KERNÉIS (1986). However, their species differs greatly from the populations investigated by WILBERT (1986) and myself, especially in the size of the paroral membrane. In fact and as the authors suppose, it is a new species which I also found recently in several African soils. It has not only a much larger paroral membrane but also very peculiar extrusomes, which were overlooked by DRAGESCO & DRAGESCO-KERNÉIS (1986), who apparently did not study the species in vivo.

### · Pedohymena nov. gen.

**Diagnosis:** Colpodidiidae with long, loop-shaped paroral membrane and 1 large and 2 small adoral organelles.

**Type species:** Pedohymena australiense nov. spec.

**Derivatio nominis:** Composite of the Greek words "pedon" (soil) and "hymen" (membrane), referring to its occurrence in soil and the conspicuous paroral membrane. Feminine.

Comparison with related genera: There is no doubt that *Pedohymena* is closely related to *Colpodidium*. The main difference is the long, loop-shaped paroral membrane which extends not only along the right and anterior margin of the oral apparatus, as in *Colpodidium*, but curves back along the left margin of the buccal cavity. Very likely, this tail is a young acquisition (apomorphy) because middle stomatogenic stages of *Pedohymena* closely resemble morphostatic cells of *Colpodidium*, as concerns the shape of the paroral membrane and the number of dikinetids composing it (Fig. 58). Further-

more, *Pedohymena* has 3 adoral organelles throughout the life cycle, whereas *Colpodidium* very likely reduces the very small organelles 1 and 2 during cytokinesis.

• *Pedohymena australiense* nov. spec. (Figs. 73–85, Tab. 4)

**Diagnosis:** In vivo 45–65×20–25 μm, slightly reniform to distinctly *Dexiostoma*-shaped. Extrusomes fusiform, 5–7 μm long. 16 somatic kineties with 18 cilia each on average. Buccal cavity conspicuous, cone-shaped, contains 1 large and 2 small adoral organelles. Paroral membrane composed of 32 dikinetids on average.

**Type location:** Coastal soil at Darwin, Australia (Northern Territory), E 131°, S 13°.

**Derivatio nominis:** "australiense" refers to the occurrence in the southern hemisphere.

**Description:** Laterally slightly flattened, ventral view fusiform with both ends rounded. Macronucleus slightly ellipsoid, usually close above centre of cell, i.e. opposite buccal cavity, contains some comparatively large nucleoli sometimes connected by narrow bridges. Micronucleus slightly ellipsoid, in indentation of macronucleus. Contractile vacuole in mid-body, with single excretory pore underneath buccal cavity. Cytopyge in median of cell between excretory pore of contractile vacuole and posterior end of cell. Cortex thick, glassy, distinctly furrowed by ciliary rows, especially preorally. Extrusomes (trichocysts) conspicuous, fusiform, obliquely attached to pellicle and close to somatic basal bodies (Figs. 73, 74, 79, 85); extruded trichocysts up to 35 µm long, needle-shaped (Fig. 75). Cytoplasm colourless, with many food vacuoles often containing only few bacteria and/or food residues. Swims slowly and crawls on soil particles.

Somatic cilia about 10 µm long and rather stiff, single throughout, rarely does a dikinetid occur at anterior end of postoral kineties. Silver carbonate preparations show each kinetid composed of a small granule, possibly a parasomal sac or an alveolocyst, and of a large granule which bears the cilium, a short kinetodesmal fibre extending obliquely anteriad, and a short transverse fibre (Figs. 84, 85). In Chatton-Lwoff silver nitrate impregnated specimens kinetids likewise composed of two components, viz. a dark granule bearing the cilium, and a relatively large circle having a dark dot (trichocyst?) in its upper half (Fig. 76). Distances of kinetids increase within kineties from anterior to posterior, those in first kinety right of oral apparatus so closely spaced in upper portion that they are easily mistaken for the paroral membrane. Ciliary rows bipolar on dorsal side, those on ventral surface form short but wide preoral suture, because anterior left kineties abut obliquely on anterior right

kineties which gradually shorten from anterior end of cell to oral apparatus. Four postoral ciliary rows, first kinety commences left of distal end of paroral membrane, other kineties originate slightly underneath adoral organelles. No elongated caudal cilia.

Oral apparatus in second quarter of cell, with conspicuous cone- shaped buccal cavity containing adoral organelles. Adoral organelle 1 very near distal end of paroral membrane, tiny, i.e. composed of 2-4 cilia only; organelle 2 likewise small, i.e. composed of 2–3 rows with about 4 cilia each, near posterior vertex of buccal cavity close above organelle 3, which is comparatively large and composed of 3 rows with about 6 cilia each (Figs. 80, 84, 85). Paroral membrane curved loop-like along right, upper and left margin of buccal cavity, composed of distinctly inclined dikinetids having only anterior basal bodies ciliated. Cytopharyngeal basket large but very delicate, thus not recognizable in vivo and so faintly stained with protargol that individual nematodesmal bundles cannot be counted; commences in upper vertex of buccal cavity and extends as wide tube near to anterior end of cell, where it curves dorsally and posteriorly (Fig. 79).

Silverline system as in *Colpodidium caudatum*, i.e. tightly and irregularly meshed throughout (Fig. 77); sometimes a similar or even identical structure impregnates with silver carbonate (Fig. 85).

**Morphogenesis:** A few middle (Fig. 58), late (Fig. 59) and very late dividers were found in the preparations. They look very similar to those described for *C. caudatum*, except for the paroral membrane in which the number of dikinetids is doubled during the late division stages.

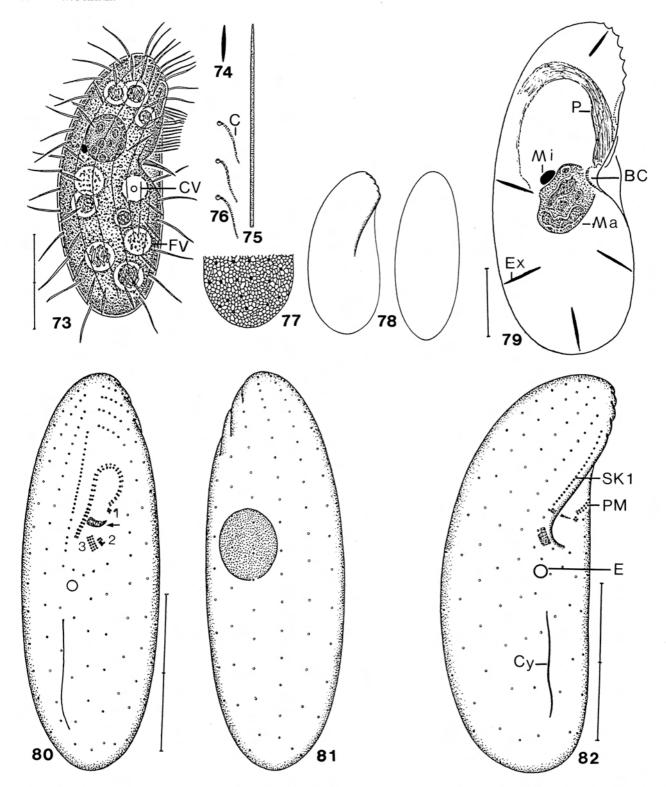
**Ecology:** Less frequent than *Colpodidium caudatum*. As yet found in a non-saline coastal soil in Australia (see type location) and in Costa Rica.

**Comparison with related species:** At low magnification easily confused with *Colpodidium caudatum*; under oil immersion easily separated from this species, even live, by the prominent trichocysts.

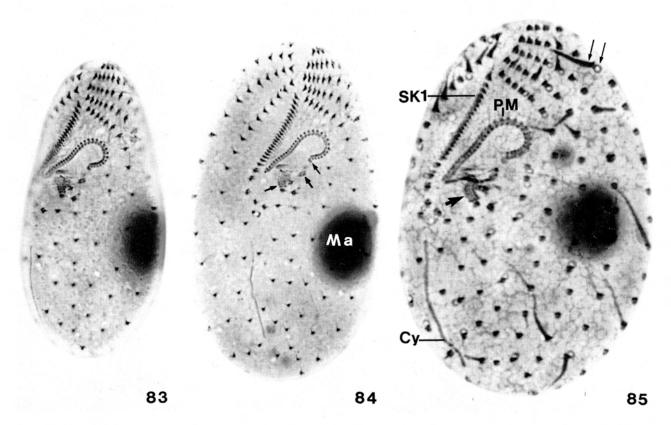
• *Condylostoma terricola* nov. spec. (Figs. 86–97, Tab. 5)

**Diagnosis:** In vivo 90–140×30–60  $\mu$ m. Cortical granules conspicuously bright, yellowish, 0,7×0,5  $\mu$ m in size, arranged in loose rows with small clusters interspersed. On average 7 macronuclear beads, 17 somatic kineties and 36 adoral membranelles.

**Type location:** Upper soil layer near the ranch house "La Casona" in the Santa Rosa National Park, Costa Rica, W 85° 38', N 10° 50'.



Figs. 73–82. *Pedohymena australiense* from life (Figs. 73–75, 78), after wet (Figs. 76, 80–82) and dry (Fig. 77) silver nitrate impregnation, and protargol staining (Fig. 79). -73. Right lateral view. -74, 75. Resting and discharged extrusome. -76. Somatic kinety. -77. Silverline system. -78. Right lateral and dorsal view of *Colpoda maupasi* shaped specimen. -79. Main cell organelles. -80–82. Infraciliature of ventral, dorsal, and right side. Arrow marks pharyngeal opening. BC = buccal cavity, C = cilium, CV = contractile vacuole, Cy = cytopyge, E = excretory pore, Ex = extrusome, FV = food vacuole, Ma = macronucleus, Mi = micronucleus, P = pharyngeal basket, PM = paroral membrane, SK1 = somatic kinety 1, 1, 2, 3 = adoral organelles. Scale bar division 10  $\mu$ m.

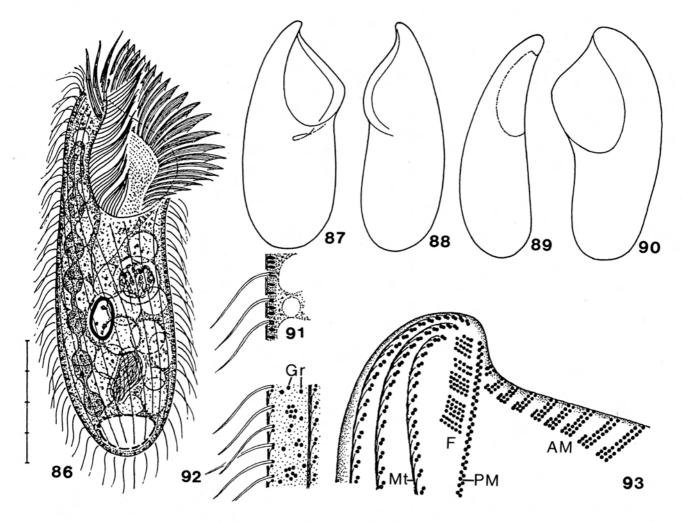


Figs. 83-85. Pedohymena australiense, somatic and oral infraciliature after silver carbonate impregnation. -83, 84. Ventral views. Arrows mark adoral organelles. -85. Ventral view of heavily squashed specimen. Thick arrow denotes adoral organelle 3, thin arrows mark extrusome and its pellicular discharge opening. Note a faintly impregnated lattice in the cortex, possibly the silverline system or pellicular alveoli. Cy = cytopyge, Ma = macronucleus, PM = paroral membrane, SK1 = somatic kinety 1.

**Table 5.** Morphometric characteristics from *Condylostoma terricola*<sup>1</sup>).

x	M	SD	$SE_{\bar{x}}$	CV	Min	Max	n	-
100.8	100.0	11.9	3.3	11.8	85	130	13	_
31.9	30.0	4.5	1.2	14.0	26	43	13	
37.7	35.0	10.4	2.9	27.5	23	58	13	
34.5	35.0	2.7	0.7	7.7	30	38	13	
63.9	63.0	12.3	3.4	19.2	38	85	13	
9.8	10.0	1.8	0.5	18.8	7	13	13	
5.9	6.0	0.9	0.2	14.6	5	7	13	
6.5	7.0	1.3	0.4	20.3	4	8	13	
16.8	17.0	0.9	0.2	5.5	15	18	13	
61.5	58.0	11.7	3.2	19.0	46	93	13	
35.9	36.0	1.6	0.4	4.5	33	40	13	
	100.8 31.9 37.7 34.5 63.9 9.8 5.9 6.5 16.8 61.5	100.8  100.0    31.9  30.0    37.7  35.0    34.5  35.0    63.9  63.0    9.8  10.0    5.9  6.0    6.5  7.0    16.8  17.0    61.5  58.0	100.8  100.0  11.9    31.9  30.0  4.5    37.7  35.0  10.4    34.5  35.0  2.7    63.9  63.0  12.3    9.8  10.0  1.8    5.9  6.0  0.9    6.5  7.0  1.3    16.8  17.0  0.9    61.5  58.0  11.7	100.8      100.0      11.9      3.3        31.9      30.0      4.5      1.2        37.7      35.0      10.4      2.9        34.5      35.0      2.7      0.7        63.9      63.0      12.3      3.4        9.8      10.0      1.8      0.5        5.9      6.0      0.9      0.2        6.5      7.0      1.3      0.4        16.8      17.0      0.9      0.2        61.5      58.0      11.7      3.2	100.8      100.0      11.9      3.3      11.8        31.9      30.0      4.5      1.2      14.0        37.7      35.0      10.4      2.9      27.5        34.5      35.0      2.7      0.7      7.7        63.9      63.0      12.3      3.4      19.2        9.8      10.0      1.8      0.5      18.8        5.9      6.0      0.9      0.2      14.6        6.5      7.0      1.3      0.4      20.3        16.8      17.0      0.9      0.2      5.5        61.5      58.0      11.7      3.2      19.0	100.8      100.0      11.9      3.3      11.8      85        31.9      30.0      4.5      1.2      14.0      26        37.7      35.0      10.4      2.9      27.5      23        34.5      35.0      2.7      0.7      7.7      30        63.9      63.0      12.3      3.4      19.2      38        9.8      10.0      1.8      0.5      18.8      7        5.9      6.0      0.9      0.2      14.6      5        6.5      7.0      1.3      0.4      20.3      4        16.8      17.0      0.9      0.2      5.5      15        61.5      58.0      11.7      3.2      19.0      46	100.8      100.0      11.9      3.3      11.8      85      130        31.9      30.0      4.5      1.2      14.0      26      43        37.7      35.0      10.4      2.9      27.5      23      58        34.5      35.0      2.7      0.7      7.7      30      38        63.9      63.0      12.3      3.4      19.2      38      85        9.8      10.0      1.8      0.5      18.8      7      13        5.9      6.0      0.9      0.2      14.6      5      7        6.5      7.0      1.3      0.4      20.3      4      8        16.8      17.0      0.9      0.2      5.5      15      18        61.5      58.0      11.7      3.2      19.0      46      93	100.8      100.0      11.9      3.3      11.8      85      130      13        31.9      30.0      4.5      1.2      14.0      26      43      13        37.7      35.0      10.4      2.9      27.5      23      58      13        34.5      35.0      2.7      0.7      7.7      30      38      13        63.9      63.0      12.3      3.4      19.2      38      85      13        9.8      10.0      1.8      0.5      18.8      7      13      13        5.9      6.0      0.9      0.2      14.6      5      7      13        6.5      7.0      1.3      0.4      20.3      4      8      13        16.8      17.0      0.9      0.2      5.5      15      18      13        61.5      58.0      11.7      3.2      19.0      46      93      13

¹) Data based on randomly selected, protargol impregnated specimens from raw culture. Measurements in  $\mu m$ . CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation,  $SE_{\bar{x}}$  – standard error of mean,  $\bar{x}$  – arithmetic mean.



Figs. 86-93. Condylostoma terricola from life (Figs. 86-92) and after protargol impregnation (Fig. 93). – 86. Ventral view of slender specimen. – 87–89. Ventral, dorsolateral and right lateral view of broad specimen. – 90. Dorsal view of specimen with contracted oral area. – 91, 92. Side and surface view of cortex. – 93. Anterior portion of oral infraciliature. AM = adoral membranelles, F = frontal membranelles, F = cortical granules, F = protal membranelles, F = protal membrane. Scale bar division 10  $\mu$ m.

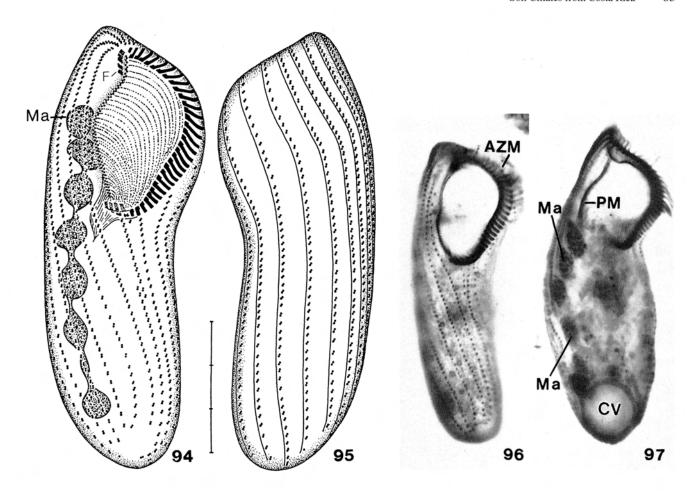
**Derivatio nominis:** "terricola" refers to the occurrence in soil.

Description: Narrowly to broadly sac-shaped, oral portion often distinctly widened and slightly contractile, posterior end invariably broadly rounded. Very flexible, oral area distinctly flattened. Macronucleus moniliform, along dorsal side of cell, beads connected by rather broad bridges; nucleoli variable, in some specimens tiny, in others rather large. Micronuclei not observed, do not impregnate with the protargol method used. Contractile vacuole at posterior end. Cortex thick, gelatinous. Cells appear greyish at low magnification because colour of cortical granules is very light. Cytoplasm strongly vacuolated due to many large, almost empty vacuoles. Feeds on fungal spores, heterotrophic flagel-

lates (*Peranema* sp.) ciliates (hypotrichs, *Sathrophilus muscorum*) and even on brownish soil particles. Swims slowly, often crawling around soil particles.

Somatic and oral infraciliature as in other members of genus (Figs. 93–97). Right of kineties distinct (postciliary) fibre recognizable also in live specimens. Basal bodies paired throughout. Adoral organelles each composed of 2 long rows and 1 short row of basal bodies. Paroral membrane conspicuous, cilia 30 µm (!) long, at right anterior end 3–4 more or less distinctly separated cirri forming conspicuous tuft. Buccal cavity large, deep, underlain by thick fibres. Pharynx and pharyngeal fibres indistinct.

Comparison with related species and ecology: This is the first reliable record of a *Condylostoma* species in



Figs. 94–97. Condylostoma terricola, somatic and oral infraciliature after protargol impregnation. – 94, 96, 97. Ventral views. – 95. Dorsal view. AZM = adoral zone of membranelles, CV = contractile vacuole, F = frontal membranelles, Ma = macronucleus, PM = paroral membrane. Scale bar division 10  $\mu$ m.

soil. Most members of this genus live in marine biotopes and have a distinct tail. Five species are known from saline inland waters or from freshwater: Condylostoma tardum Penard, 1922 is larger (>180 µm) than C. terricola and has only 3 macronuclear beads (FAURÉ-Fremiet 1958, Kahl 1932, Penard 1922); C. nigra DRAGESCO, 1960 is also larger (180–300  $\mu$ m) than C. terricola and has blue cortical granules (like Stentor coeruleus), 40 somatic kineties and several contractile vacuoles along the dorsal and ventral side; C. vorax VILLENEUVE-BRACHON, 1940 is poorly described, but is distinctly larger (250–400 µm) than C. terricola, has 30–40 somatic kineties and apparently lacks coloured cortical granules; C. kasymovi ALEKPEROV, 1984 is also poorly described (according to silver nitrate impregnated cells only), but is distinctly larger (240–280 μm) than C. terricola and has 65-70 somatic kineties, 70-75 adoral membranelles, and 15-17 macronuclear beads; C. luteum KAHL, 1932 is a sapropelic species

whose shape, size and cortical granulation are very similar to those of *C. terricola*. It has, however, only 2 macronuclear beads, curious rods (extrusomes?) around the pharynx, and a different arrangement of the cortical granules, which form short, transverse rows.

# • Bicoronella nov. gen.

**Diagnosis:** Pseudokeronopsidae (?) with transverse and caudal cirri and 2 arched rows of frontal cirri along anterior body margin. 2 frontoterminal cirri.

Type species: Bicoronella costaricana nov. spec.

**Derivatio nominis:** Composite of the Greek words "bi" (two) and "corone" (arch, latinized to "coronella"). Feminine.

Comparison with related genera: Bicoronella is similar to Tricoronella Blatterer & Foissner, 1988 (3 arched rows of frontal cirri), *Pseudokeronopsis* Bor-ROR & WICKLOW, 1983 (without caudal cirri), Uroleptopsis Kahl, 1932 (without transverse cirri), Keronella WIACKOWSKI, 1985 (many frontoterminal cirri forming a row, tailed midventral rows; now in subfamily Bakuellinae [EIGNER, in press]), and Holosticha WRZEŠNIO-WSKI, 1877 (with 3-4 frontal cirri only). An almost unique feature of B. costaricana is the cirral row extending from the first frontal cirrus to the undulating membranes. Such a row is present also in Holosticha sylvatica Foissner, 1982, which, however, has 3 distinct frontal cirri only and is thus a typical *Holosticha* species (Ber-GER & FOISSNER 1989). Whether Bicoronella belongs to the Pseudokeronopsidae or to another family (e.g. Holostichidae) is uncertain, because morphogenetic data are lacking and the Pseudokeronopsidae are still insufficiently defined (WIRNSBERGER 1987).

BORROR & WICKLOW (1983) rejected the genus *Uroleptopsis* Kahl, 1932 because of the lack of transverse cirri in some marine clones of *Pseudokeronopsis*. However, no evidence was given, and more recent ontogenetic investigations prove the existence of populations with and without transverse cirri (MIHAILOWITSCH & WILBERT 1990, WIRNSBERGER 1987, WIRNSBERGER et al. 1987). I thus re-establish *Uroleptopsis* Kahl, 1932 and combine *Pseudokeronopsis ignea* MIHAILOWITSCH & WILBERT, 1990 with this genus: *Uroleptopsis ignea* (MIHAILOWITSCH & WILBERT, 1990) nov. comb.

 Bicoronella costaricana nov. spec. (Figs. 98–102, Tab. 6)

**Diagnosis:** Size in vivo about 150–200×50–60 μm. Cortical granules in rows, yellowish, 0.5–1 μm in diameter. On average 65 macronuclear nodules, 53 adoral membranelles, 7 cirri in upper and 5 cirri in lower frontal row, 6 cirri in row extending from first frontal cirrus to buccal cavity, 19 midventral pairs terminating distinctly above transverse cirri, 10 transverse cirri, 4 caudal cirri, and 5 dorsal kineties.

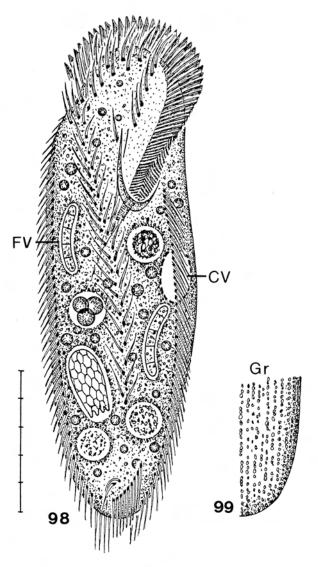
**Type location:** Upper soil layer near the ranch house "La Casona" in the Santa Rosa National Park, Costa Rica, W 85° 38′, N 10° 50′.

**Derivatio nominis:** Named after the country (Costa Rica) where it was discovered.

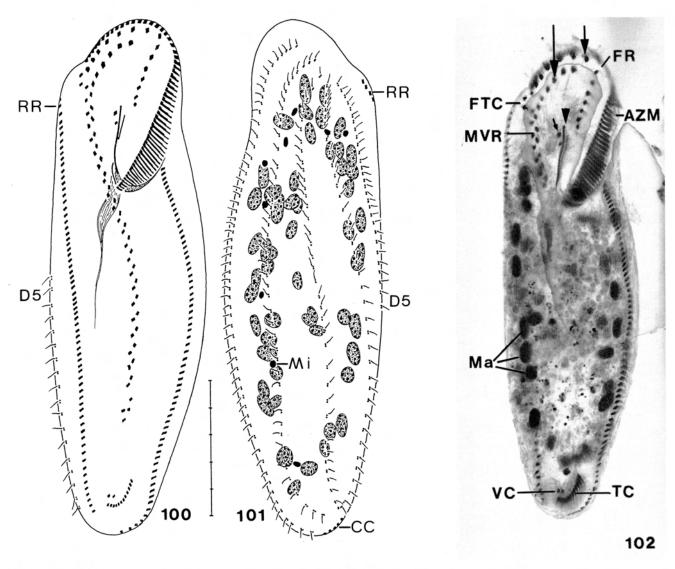
**Description:** Slender, slightly sigmoidal and narrowed to posterior end, left margin distinctly convex, right slightly convex, straight or even slightly concave, both ends broadly rounded. Very flexible and dorsoventrally flattened up to 2:1. Macronuclear nodules and

micronuclei ellipsoid, located mainly along body margins. Contractile vacuole at left margin in mid-body, with two collecting canals extending anteriorly and posteriorly. Cells appear yellowish to yellowbrown at low magnification due to cortical granules and food inclusions. Feeds on coccal cyanobacteria, fungal spores, testate amoebae (Euglyphya rotunda) and possibly also on ciliates.

Cirri 15–20 µm long, marginal rows open at posterior end, gap occupied by caudal cirri. Distance between marginal cirri only slightly increasing from anterior to posterior end of rows. Midventral cirri closely spaced, form slightly sigmoid rows in median of cell, continue



**Figs. 98, 99.** *Bicoronella costaricana* from life. – **98.** Ventral view of well-fed specimen with many food vacuoles containing fungal spores, algae, and testate amoebae. – **99.** Cortical granulation. CV = contractile vacuole, FV = food vacuole, Gr = cortical granules. Scale bar division 10 μm.



Figs. 100 -102. *Bicoronella costaricana*, somatic and oral infraciliature after protargol impregnation. – 100, 102. Ventral views. Large arrows mark upper and lower arch of frontal cirri which are continuous with the midventral cirri. Small arrow points to buccal cirri. Arrowhead marks undulating membranes. – 101. Dorsal infraciliature and nuclear apparatus. AZM = adoral zone of membranelles, CC = caudal cirri, D5 = dorsal kinety 5, FR = frontal row, FTC = frontoterminal cirri, Ma = macronuclear nodules, Mi = micronucleus, MVR = midventral row, RR = right marginal row, TC = transverse cirri, VC = ventral cirri ahead of transverse cirri. Scale bar division 10 μm.

anteriorly as arched, distinctly separate rows of slightly enlarged frontal cirri having rhomboid and pentagonal bases. Frontoterminal cirri inconspicuous, closely underneath distal end of adoral zone of membranelles. Buccal cirrus near anterior end of paroral membrane. Transverse cirri slightly projecting above posterior end of body, minute, form J-shaped row. Dorsal cilia about 5 µm long, arranged in 5 (rarely 6) meridional rows almost as long as cell.

Adoral zone of membranelles about 35% of body length, bases of largest membranelles about 10  $\mu m$  wide. Buccal cavity short and flat, but rather wide.

Undulating membranes short as compared with length of adoral zone of membranelles, almost straight, intersect in posterior third. Pharyngeal fibres indistinct.

Comparison with related species: Bicoronella costaricana is easily recognized in protargol slides by its unique frontal ciliature. In vivo it is easily confused with Holosticha sylvatica, Eschaneustyla bachytona and Keronella gracilis, which have a similar size, shape and cortical granulation.

**Ecology:** As yet found only in Costa Rica.

**Table 6.** Morphometric characteristics from *Bicoronella costaricana* 1).

Character	$\bar{\mathbf{x}}$	M	SD	$SE_{\tilde{x}}$	CV	Min	Max	n
Body, length	165.8	172.0	17.6	5.9	10.6	140	187	9
Body, width	52.6	55.0	4.4	1.5	8.5	43	58	9
Anterior somatic end to proximal end of adoral zone, distance	59.1	62.0	6.0	2.0	10.1	50	65	9
Anterior somatic end to proximal end of midventral row, distance	124.9	133.0	17.0	5.7	13.6	98	147	9
Posterior somatic end to transverse cirri, distance	10.7	11.0	1.6	0.5	14.8	8	12	9
Macronuclear nodules, length	8.6	8.0	1.5	0.5	17.6	6	11	9
Macronuclear nodules, width	4.0	4.0	0.7	0.2	16.5	3	5	9
Micronuclei, length	3.0	3.0	0.4	0.1	12.6	2.2	3.5	9
Micronuclei, width	2.6	2.5	0.3	0.1	11.1	2.2	3.0	9
Adoral membranelles, number	51.6	53.0	5.3	1.8	10.3	43	57	9
Midventral pairs, number	19.0	19.0	3.3	1.1	17.5	15	24	9
Upper cirral arch, no. of cirri	6.6	7.0	0.9	0.3	13.4	5	8	9
Lower cirral arch, no. of cirri	4.9	5.0	0.9	0.3	18.9	4	6	9
Frontal row, number of cirri	6.2	6.0	0.8	0.3	13.4	5	7	9
Frontoterminal cirri, number	2.0	2.0	0.0	0.0	0.0	2	2	9
Buccal cirri, number	1.3	1.0	-	_	_	1	2	9
Right marginal cirri, number	57.0	54.0	7.6	2.5	13.4	49	71	9
Left marginal cirri, number	52.7	51.0	8.4	2.8	16.0	42	64	9
Ventral cirri near transverse cirri, number	2.4	2.0	-	-	-	2	3	9
Transverse cirri, number	10.0	10.0	1.8	0.6	18.0	8	12	9
Caudal cirri, number	4.1	4.0	1.1	0.4	25.7	3	6	9
Macronuclear nodules, number	75.4	65.0	20.4	6.8	27.1	52	115	9
Micronuclei, number	8.2	8.0	2.4	0.8	29.7	5	11	9
Dorsal kineties, number	5.1	5.0	_	-	-	5	6	9

 $<sup>^{1}</sup>$ ) Data based on randomly selected, protargol impregnated specimens from raw culture. Measurements in  $\mu m$ . CV-coefficient of variation in %, M-median, Max-maximum, Min-minimum, n-number of individuals investigated, no. – number, SD- standard deviation,  $SE_{\bar{x}}-$  standard error of mean,  $\bar{x}-$  arithmetic mean.

• Australothrix steineri nov. spec. (Figs. 103–109, Tab. 7)

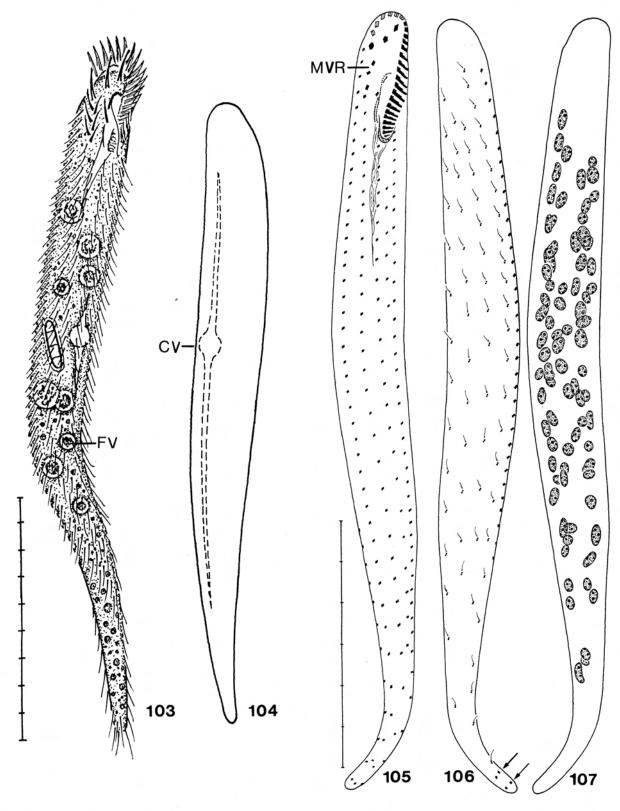
**Diagnosis:** Size in vivo 160–320×20–30 μm. Many macronuclear nodules. 25 adoral membranelles, 5 ventral cirral rows and 4 dorsal kineties on average. Midventral row slightly shorter than adoral zone of membranelles, consists of 2–3 cirral pairs, continues as ventral cirral row.

**Type location:** Upper soil layer of bank of Rio Corobici at the hacienda "La Pacifica" (Centre Ecologia La Pacifica) near town Canas in Costa Rica (Central America), W 85° 08′, N 10° 27′.

**Dedication:** This species is named in honour of my friend Prof. ERICH STEINER (Vienna), president of the "Mikrographische Gesellschaft Wien", a great lover of microscopy.

**Description:** Very slender and flexible, often slightly sigmoidal and contorted along major body axis; widest in oral area, postorally gradually narrowed with posterior end pointed or even elongated tail-like; slightly flattened dorsoventrally. About 70-150 macronuclear nodules, exact number difficult to ascertain because of similar sized and stained food vacuoles and irregular distribution in postoral body portion. Several compact micronuclei, 4×2.5 μm in vivo, weakly stained by protargol. Contractile vacuole in mid-body at left margin, with two long collecting canals extending to anterior and posterior end of cell. Cortex and cytoplasm colourless, no cortical granules or cytoplasmic crystals; posterior end often containing shiny fat droplets 1-3 µm in diameter. Food vacuoles 5-10 µm in diameter, contain fungal spores and, possibly, bacteria and heterotrophic flagellates.

All cirri 8–10 µm long, frontal cirri distinctly, midventral cirri slightly enlarged. Both marginal rows extend to pointed posterior end of cell. Rightmost ventral cirral row

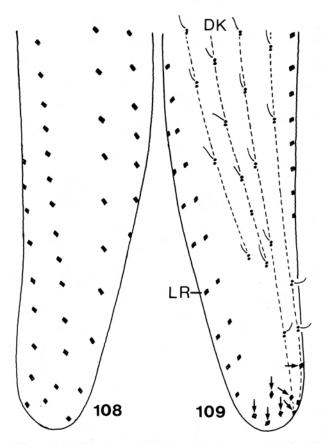


Figs. 103–107. Australothrix steineri from life (Figs. 103, 104) and after protargol impregnation (Figs. 105–107). – 103. Ventral view of typical, slightly spiralized specimen. – 104. Dorsal view of broad specimen. – 105–107. Infraciliature of ventral and dorsal side, and nuclear apparatus. Arrows mark caudal cirri. CV = contractile vacuole, FV = food vacuole,  $MVR = midventral row consisting of two cirral pairs only. Scale bar division <math>10 \, \mu m$ .

Table 7. Morphometric characteristics from Australothrix steineri 1).

Character	$\bar{\mathbf{x}}$	M	SD	$SE_{\bar{x}}$	CV	Min	Max	n
Body, length	236.1	240.0	53.3	17.8	22.6	145	315	9
Body, width	22.7	24.0	4.6	1.5	20.2	16	31	9
Anterior somatic end to proximal end of adoral zone, distance	31.6	32.0	2.2	0.7	7.1	28	35	9
Anterior somatic end to proximal end of midventral row, distance	24.3	25.0	3.1	1.2	12.7	31	30	7
Macronuclear nodules, length	5.3	5.0	0.7	0.2	13.3	4	6	9
Macronuclear nodules, width	2.6	3.0	0.5	0.2	20.6	2	3	9
Adoral membranelles, number	25.2	25.0	1.1	0.4	4.3	24	27	9
Midventral pairs, number	2.3	2.0	_	_	_	2	3	7
Ventral cirral rows, number	4.8	5.0	0.9	0.3	18.1	4	6	11
Right marginal cirri, number	63.3	75.0	20.7	7.8	32.7	35	85	7
Left marginal cirri, number	58.0	56.5	19.7	7.0	34.0	36	82	8
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3	3	8
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1	1	7
Dorsal kineties, number	4.0	4.0	0.0	0.0	0.0	4	4	9

<sup>1)</sup> Data based on randomly selected, protargol impregnated specimens from raw culture. Measurements in  $\mu m$ . CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation,  $SE_{\bar{x}}$  – standard error of mean,  $\bar{x}$  – arithmetic mean.



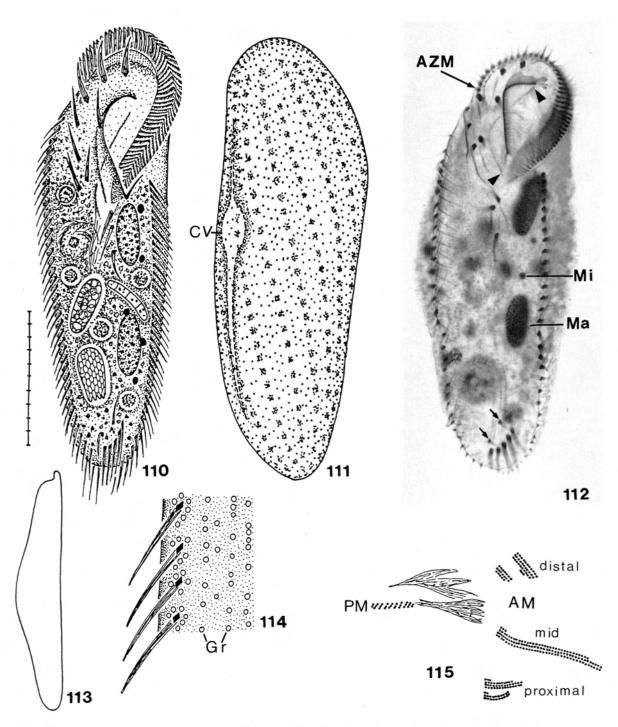
**Figs. 108, 109.** Australothrix steineri, somatic infraciliature of posterior ventral and dorsal side after protargol impregnation. Arrows mark caudal cirri. DK = dorsal kineties, LR = left marginal row.

as long as right marginal row, other ventral rows commence underneath very short midventral row and postorally; leftmost row distinctly shortened, does not extend into posterior half of cell. About 4–8 caudal cirri, exact number difficult to recognize because located at pointed posterior end. No transverse cirri. Dorsal kineties slightly shortened anteriorly and posteriorly, cilia 3 µm long.

Adoral zone of membranelles only about 13% of body length, bases of largest membranelles about 5 µm wide. Buccal area flat, narrow and short, oral lip inconspicuous. Undulating membranes one upon the other, paroral membrane distinctly bent anteriorly. Pharyngeal fibres distinct after protargol impregnation.

Comparison with related species: So far, four species have been assigned to the genus *Australothrix* BLATTERER & FOISSNER, 1988: *A. australis* BLATTERER & FOISSNER, 1988 (type), *A. alwinae* BLATTERER & FOISSNER, 1988, *A. zignis* (ENTZ, 1884), *A. gibba* (CLAPAREDE & LACHMANN, 1859). The first two species, which were found in terrestrial biotopes of Australia, are distinctly wider, have conspicuous cortical granules, and possess a higher number of ventral cirral rows and midventral pairs. *Australothrix zignis* resembles *A. steineri* in size, shape and cirral pattern, but is highly contractile, reddishly pigmented and lives in marine environments. *Australothrix gibba* has, like *A. steineri*, 4 ventral cirral rows, but is much smaller (100–130 µm), less slender and lives in freshwater.

**Ecology:** As yet found only in Costa Rica. The type location is in the flood area of the river Corobici and



Figs. 110–115. Cyrtohymena australis from life (Figs. 110, 111, 113, 114) and after protargol impregnation (Figs. 112, 115). – 110, 112. Ventral views. The cytoplasm is filled with food vacuoles containing bacteria, fungal spores, testate amoebae, and ciliates. Long arrow denotes distal end of adoral zone of membranelles which is very near to third frontal cirrus. Small arrows mark two inconspicuous ventral cirri above of five thick transverse cirri. Arrowheads mark distal and proximal end of endoral membrane. – 111. Dorsal view of broad specimen showing pattern produced by cortical granules. – 113. Lateral view. – 114. Surface view showing arrangement of cortical granules on ventral side. – 115. Details of oral structures. The anterior portion of the paroral membrane consists of short kineties and has fan-shaped fibres attached. The adoral membranelles are of different size and their fine structure varies depending on the location within the membranellar zone. AM = adoral membranelles, AZM = adoral zone of membranelles, CV = contractile vacuole, Gr = cortical granules, Ma = macronuclear nodule, Mi = micronucleus, PM = paroral membrane. Scale bar division 10 μm.

thus it cannot be excluded that *A. steineri* is a limnetic species whose resting cysts excysted in the soil cultures. However, the record from the Santa Rosa National Park and the very slender shape indicate that *A. steineri* is a true soil inhabitant.

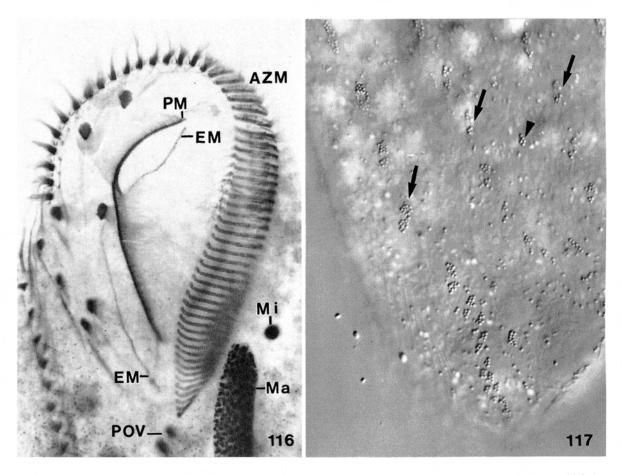
• Cyrtohymena australis nov. spec. (Figs. 110–119, Tab.8)

**Diagnosis:** Size in vivo 250–400×60–100 μm. Cortical granules citrine, 0.4–1 μm in diameter, mainly around cirral bases and dorsal bristles. On average 57 adoral membranelles, 37 right marginal cirri, 39 left marginal cirri, and 8 dorsal kineties. Transverse cirri displaced considerably anteriorly.

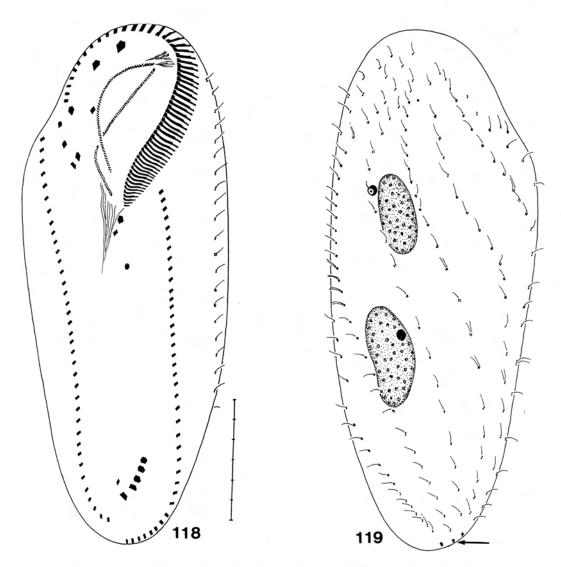
**Type location:** Amazonian rain forest near the town of Iquitos, Peru, W 74°, S 4°.

**Derivatio nominis:** "australis" refers to the occurrence in the southern hemisphere.

**Description:** Lanceolate, right margin usually slightly concave, left more or less convex, widest in buccal area, gradually narrowed and broadly rounded at both ends. Very flexible and dorsoventrally flattened up to 2:1. Macronuclear nodules distinctly ellipsoid, in vivo about 45×20 µm, in middle third of cell left of median, with many tiny nucleoli. Micronuclei almost spherical, often distant from macronuclear nodules. Contractile vacuole slightly above mid-body at left margin, with two long collecting canals extending anteriorly and posteriorly. Cells yellow at low magnification due to brilliant citrine colour of cortical granules arranged mainly around cirral bases and dorsal bristles, but also in loose rows between cirri and bristles (Figs. 111, 114, 117); granules do not impregnate with protargol. Cytoplasm colourless, with some fat globules 2-4 µm in dia-



Figs. 116, 117. Cyrtohymena australis after protargol impregnation (Fig. 116) and from life (Fig. 117). – 116. Somatic and oral infraciliature in anterior ventral third. – 117. Posterior portion of dorsal side showing arrangement of cortical granules within (arrows) and between (arrowhead) dorsal kineties. AZM = adoral zone of membranelles, EM = endoral membrane, EM = macronucleus, EM = micronucleus, EM = paroral membrane, EM = postoral ventral cirri.



Figs. 118, 119. Cyrtohymena australis, somatic and oral infraciliature of ventral and dorsal side after protargol impregnation. Arrow marks caudal cirri. Scale bar division 10 μm.

meter and many small and large food vacuoles containing fungal spores, testate amoebae (*Trinema lineare*, *Euglypha* spp.), ciliates (*Leptopharynx costatus*, *Drepanomonas pauciciliata*), and cysts of *Polytoma* sp. Moves rapidly to and fro.

Marginal and anterior frontal cirri  $20-25~\mu m$ , transverse cirri  $30~\mu m$  long. Marginal rows open at posterior end, gap occupied by caudal cirri right of cell median. Marginal, transverse and caudal cirri form conspicuous fringe at posterior end. Ventral cirral pattern as in other members of genus, but unusually variable, especially in population from Costa Rica (Tab. 8). Dorsal cilia about  $5~\mu m$  long, arranged in 5-7 rows almost as long as body and few shortened rows at margins of anterior body half. Bristle complexes composed of 2-6 basal bodies, only one or two of which are, however, ciliated.

Oral apparatus and adoral zone of membranelles very conspicuous, occupy about 34% of body length, bases of largest membranelles about 20  $\mu m$  wide. Buccal cavity large and deep.

Paroral membrane almost semicircular with two fanlike bundles of fibres at anterior end, in large specimens composed of oblique rows having 4–6 cilia each in anterior and dikinetids in posterior half. Endoral membrane hook-like, extends diagonally across buccal cavity and crosses (optically) paroral membrane in posterior third, very likely composed of dikinetids. Pharyngeal fibres inconspicuous.

An early divider (Costa Rica population) showed that morphogenesis commences with the proliferation of basal bodies at the postoral ventral cirri and the uppermost two transverse cirri.

**Table 8.** Morphometric characteristics from *Cyrtohymena australis*. Upper line: type population from Peru; lower line: population from Costa Rica<sup>1</sup>).

Character	$\bar{\mathbf{X}}$	M	SD	$SE_{\bar{x}} \\$	CV	Min	Max	n
Body, length	285.3	280.0	38.7	10.0	13.6	245	370	15
	179.1	183.0	22.6	5.8	12.6	145	230	15
Body, width	97.3	95.0	10.3	2.7	10.6	80	120	15
	67.6	70.0	10.7	2.8	15.9	50	83	15
Anterior somatic end to proximal	91.7	95.0	9.9	2.5	10.8	75	105	15
end of adoral zone, distance	63.1	62.0	8.0	2.1	12.7	55	80	15
Posterior somatic end to posterior-	22.2	20.0	7.3	1.9	33.0	11	35	15
most transverse cirrus, distance	13.2	14.0	3.2	0.8	24.5	7	18	15
Macronuclear nodules, length	43.3	42.0	5.9	1.5	13.7	33	54	15
	20.9	21.0	2.5	0.6	11.9	17	26	15
Macronuclear nodules, width	16.1	16.0	2.9	0.7	17.8	11	22	15
	13.3	13.0	1.9	0.5	14.1	11	18	15
Micronuclei, length	4.9	5.0	0.4	0.1	8.5	4	6	15
	3.1	3.0	0.2	0.1	5.5	3	3.5	15
Micronuclei, width	4.5	4.5	0.4	0.1	9.9	4	5	15
	3.0	3.0	0.2	0.1	6.4	2.7	3.5	15
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2	2	15
	2.0	2.0	0.0	0.0	0.0	2	2	15
Micronuclei, number	4.1	4.0	0.9	0.2	22.1	2	6	15
,	5.2	5.0	1.6	0.4	31.0	3	8	15
Adoral membranelles, number	57.3	57.0	4.8	1.2	8.4	50	64	15
	48.1	45.0	5.5	1.4	11.4	43	58	15
Right marginal cirri, number	36.1	37.0	3.6	0.9	10.1	29	41	15
	33.8	33.0	3.9	1.0	11.7	27	40	15
Left marginal cirri, number	38.1	39.0	3.7	1.0	9.7	31	42	15
8	35.8	34.0	4.2	1.1	11.8	31	45	15
Anterior frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3	3	15
	3.0	3.0	0.0	0.0	0.0	3	3	15
Posterior frontal cirri, number	4.0	4.0	0.0	0.0	0.0	4	4	15
	3.8	4.0	0.4	0.1	10.9	3	4	15
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1	1	15
,	1.0	1.0	_	_	_	0	1	15
Postoral cirri, number	3.0	3.0	_	_	_	2	3	15
	3.0	3.0	_	_	_	2	3	15
Ventral cirri ahead of transverse	2.0	2.0	_	_	_	1	2	15
cirri, number	2.0	2.0	_	_	_	1	2	15
Transverse cirri, number	5.1	5.0	_	_	_	5	7	15
	5.0	5.0	0.0	0.0	0.0	5	5	15
Caudal cirri, number	3.0	3.0	_	_	_	2	3	15
	2.9	3.0	0.5	0.1	18.0	$\frac{2}{2}$	4	15
Dorsal kineties, number	about 7–9 about 7–10	5.0	0.0	0.1	10.0	-	·	

 $<sup>^{\</sup>text{I}})$  Data based on randomly selected, protargol impregnated specimens from raw cultures. Measurements in  $\mu m$ . CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation,  $SE_{\bar{x}}$  – standard error of mean,  $\bar{x}$  – arithmetic mean.

Comparison with related species: This large, beautiful species resembles *C. citrina* BERGER & FOISSNER, 1987 and *C. primicirrata* BERGER & FOISSNER, 1987 as concerns the yellow cortical granules, body shape and general plane of the somatic and oral infraciliature.

However, it is much larger than these species and has thus many more adoral membranelles and right and left marginal cirri. However, the *C. australis* population from Costa Rica is considerably smaller than that from the type location (Tab. 8), indicating a close relationship

with the above mentioned Laurasian species. These three yellowly granulated species obviously form a special complex within the genus.

**Ecology:** Two other populations have been found, one in Costa Rica and another at Curaçao, a small island at the north coast of Venezuela. At this site it occurred in a rather saline sample collected in a garden in the town of Salina. These records indicate that *C. australis* is probably widespread in soils of South America.

· Dapedophrya nov. gen.

**Diagnosis:** Medium-sized Jaroschiidae (?) with three differently shaped oral ciliary fields and short, almost straight preoral suture containing few brick-shaped adoral organelles. Left (second) oral ciliary field almost circular, gradually narrowing from left to right.

**Type species:** Dapedophrya flexilis (PENARD, 1922) nov. comb. (basionyms: Glaucoma flexilis PENARD, 1922 and Bryophrya flexilis FOISSNER, 1993).

**Derivatio nominis:** Composite of "dapedo" (soil) and "phrya" (hair); both Greek. Feminine. The name refers to its occurrence in soil.

Comparison with related genera: Like Jaroschia FOISSNER, 1993 and Pentahymena FOISSNER, 1994, Dapedophrya either belongs to the colpodid subclass Colpodia or Bryometopia (FOISSNER, 1993). Even its family classification is uncertain, because D. flexilis has characters of *Bryophrya* (rather simple oral structures) and Jaroschia (shape of left oral polykinetid like ciliary field 4, silverline system irregularly reticulate). In fact, Dapedophrya looks like a highly simplified Jaroschia or a slightly modified Bryophrya. I thus asked Prof. J. GRAIN (Univ. Clermont-Ferrand) for the original material of their redescription (GRAIN et al. 1979) of B. bavariensis, type of the genus. The micrographs sent from protargol impregnated specimens indeed show the large right oral ciliary field described by these authors. Thus, Bryophrya differs significantly from Dapedophrya, which has an enlarged left oral ciliary field. Generally, the differences between the Bryophryidae

Generally, the differences between the Bryophryidae and Jaroschiidae, as defined by Foissner (1993), have become less distinct by the discovery of *Dapedophrya* and *Pentahymena* Foissner, 1994. Possibly, the main difference concerns the oral ciliary fields: the right field is more developed in the Bryophryidae than in the Jaroschiidae, the left vestibular slope of which not only bears small brick-shaped adoral organelles, as in *Bryophrya*, but also a heavy ciliary field (polykinetid).

• Dapedophrya flexilis (PENARD, 1922) nov. comb. (Figs. 120–131, Tab. 9)

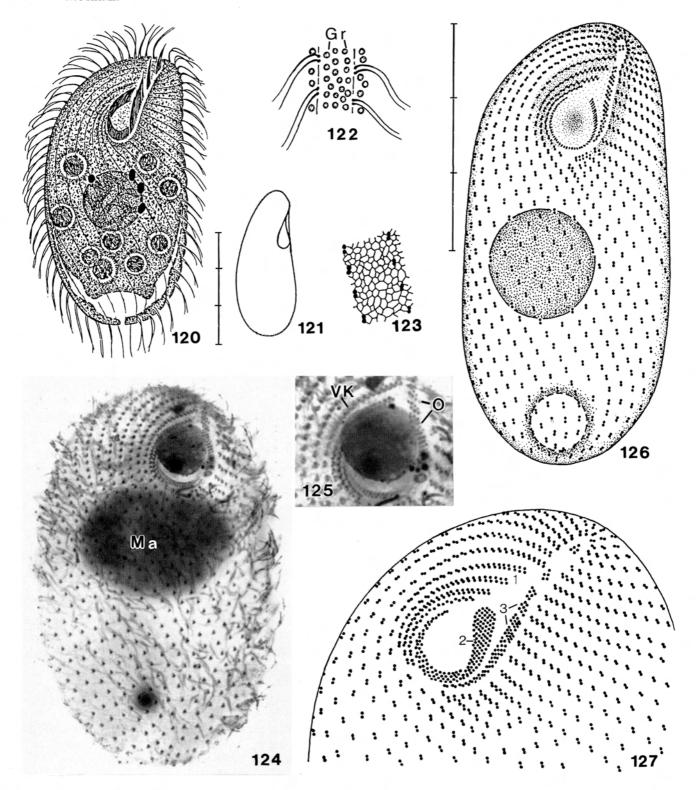
**Redescription:** Only few well-impregnated specimens were found in the protargol slides (Fig. 126). Morphometry is thus incomplete.

In vivo 60-80 µm long, ellipsoid to slightly reniform, right and dorsal side convex, left and ventral side slightly indented at oral apparatus, both ends broadly rounded, right anterior portion slanted. Very flexible and slightly flattened dorsoventrally. Macronucleus usually globular, rarely slightly ellipsoid, near centre of cell; nucleolus reticulate. Usually 3-4 micronuclei, about 3×2 µm in size, attached to macronucleus; one of the specimen observed possibly had 1 micronucleus only. Contractile vacuole with 2 collecting canals each having ampulla-like dilation near distal end, discharges via tubular excretory pore near centre of posterior pole. Cortex slightly furrowed by somatic kineties, very flexible and fragile, contains many silvery shining, about 1 µm sized granules, possibly mitochondria, which do not stain with methyl green-pyronin and protargol. No extrusomes recognizable in vivo and with the staining methods applied. Cytoplasm colourless, postorally with few to many globular (not fusiform as in Parabryophrya; Foissner 1993), 4-8 µm sized, conspicuously compact food vacuoles possibly containing bacteria and fungal spores. Moves slowly by rotating about main body axis, never rests.

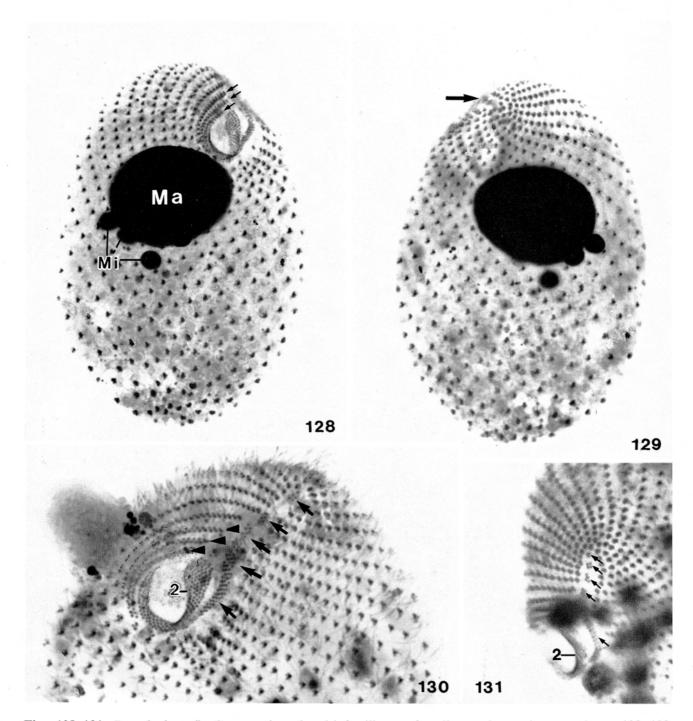
31 somatic kineties on average, consist of slightly inclined dikinetids having cilia about 8 µm long. Kineties evenly spaced, commence around vestibular opening and along preoral suture, most extend to posterior end of organism (Figs. 124, 126, 128, 129).

Oral apparatus in anterior ventral third. Vestibular opening oval to almost circular, somewhat obliquely orientated to longitudinal body axis; vestibulum deep, bowllike, contains oral ciliary field 2. First (rightmost) oral ciliary field composed of 3 vestibular kineties on right slope of vestibulum, consists of narrowly spaced, zigzaglike arranged dikinetids, producing dense ciliary plate. Second oral ciliary field on inner and lateral wall of vestibulum, almost circular, i.e. interrupted only anteriorly, orientated perpendicularly to cell surface and thus appearing as thin line if cell is viewed ventrally (Figs. 124-126); consists of many oblique, short kineties whose length decreases from left to right. Third (leftmost) oral ciliary field on left slope of vestibulum and in preoral suture, consists of about 5 brick-shaped adoral organelles extending from proximal vertex of vestibular opening to anterior pole of cell; individual organelles composed of 2–3 kineties with 2–4 basal bodies each, proximal (two) organelle(s) tail-like (Figs. 124-128, 130, 131).

Silverline system tightly and irregularly meshed (Fig. 123).



Figs. 120–127. Dapedophrya flexilis from life (Figs. 120-122) and after dry silver nitrate (Fig. 123), protargol (Fig. 126) and silver carbonate (Figs. 124, 125, 127) impregnation. – 120, 121. Ventral and right lateral view of typical specimens. – 122. Surface view showing cortical granules. – 123. Silverline system. – 124–127. Somatic and oral infraciliature of ventral side. Numbers in Fig. 127 designate oral structures (cp. Figs. 125, 130, 131). The dark blister in the vestibulum of the specimen shown in Figs. 124, 125 is a preparation artifact. Gr = cortical granules, Ma = macronucleus, O = adoral organelles, VK = vestibular kineties. Scale bar division 10 μm.



Figs. 128–131. Dapedophrya flexilis, somatic and oral infraciliature after silver carbonate impregnation. – 128, 129. Ventrolateral and dorsolateral view of same specimen. Small arrows mark vestibular kineties, large arrow points to preoral suture. – 130. The oral infraciliature is composed of three differently shaped ciliary fields: vestibular kineties (arrowheads), a curved and tailed polykinetid (marked number 2), and about five brick-shaped adoral organelles (arrows) which extend along left vestibular wall and in preoral suture. – 131. Anterior polar view showing adoral organelles (arrows) in preoral suture and along left vestibular wall. Number 2 designates ciliary field 2 (cp. Fig. 130). Ma = macronucleus, Mi = micronuclei.

Table 9. Morphometric characteristics from Dapedophrya flexilis1).

Character	Σ̄	M	SD	$SE_{\bar{x}}$	CV	Min	Max	n
Body, length	59.8	61.5	3.3	1.0	5.4	54	63	10
Body, width	30.9	30.0	3.8	1.2	12.2	27	40	10
Anterior somatic end to vertex of vestibular opening, distance	16.7	16.0	2.0	0.6	12.0	15	20	10
Anterior somatic end to macronucleus, distance	24.1	24.5	3.5	1.1	14.4	18	29	10
Vestibular opening, width	7.4	7.0	0.9	0.4	12.1	7	9	5
Macronucleus, length	15.9	16.0	1.2	0.4	7.5	14	18	10
Macronucleus, width	14.8	15.0	1.5	0.5	10.0	12	17	10
Somatic kineties, number	31.1	31.0	1.3	0.4	4.1	29	33	9

¹) Data based on protargol impregnated specimens from raw culture. Measurements in  $\mu m$ . CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation,  $SE_{\bar{x}}$  – standard error of mean,  $\bar{x}$  – arithmetic mean.

Identification: Penard's (1922) description is not very detailed and Kahl (1931) even suggested synonymy with *Bryophrya bavariensis*. However, this can be excluded if my identification is accepted [see genus discussion and Foissner (1993) for a detailed review of all species concerned]. There are three characters mentioned in the original description which forced me to identify my population as *G. flexilis* Penard, 1922, viz. the straight preoral suture (although drawn by Penard at right edge of oral apparatus), the conspicuous cortical granules which are not extruded when chemicals are applied, and the circular oral apparatus which appears very similar in my and Penard's drawing. Furthermore, size, shape and nuclear apparatus match rather well.

### · Mykophagophrys nov. gen.

**Diagnosis:** Very small to small Grossglockneriidae with inflexible body and slightly spirally coursing somatic kineties, some of which distinctly shortened on both sides of cell. Discharged extrusomes nail-like, i.e. long and thin with conical distal end.

**Type species:** *Mykophagophrys terricola* (Foissner, 1985) nov. comb. (basionym: *Pseudoplatyophrya terricola* Foissner, 1985).

**Derivatio nominis:** Composite of the Greek words "myko" (derived from mykes = fungus, mushroom), "phag" (derived from phagein = to eat) and "ophrys" (eyelash, cilia). Refers to the special feeding strategy of grossglockneriid ciliates, viz. on fungal hyphae and spores. Feminine.

**Discussion:** Foissner (1993) already mentioned that a new genus is required for *Pseudoplatyophrya terricola* 

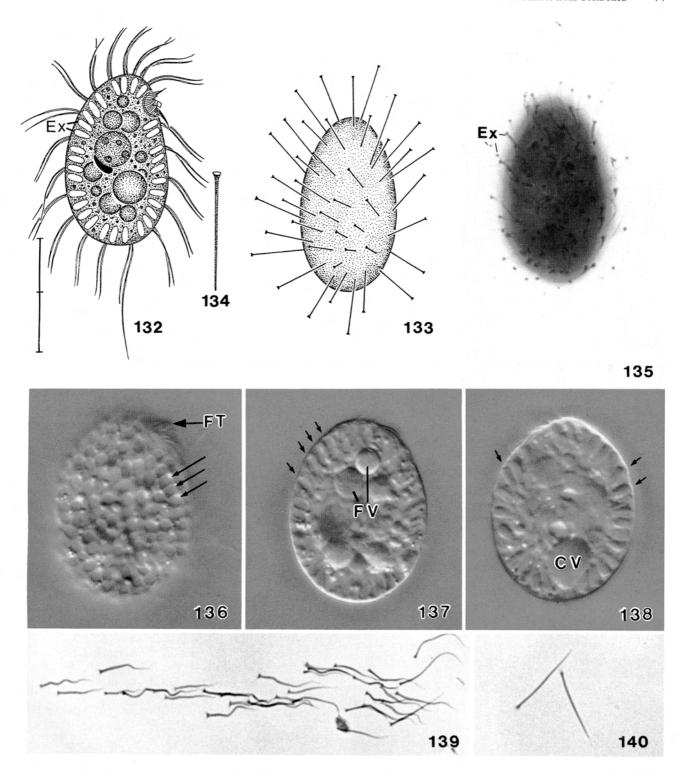
and *Platyophrya armata* KAHL, 1926, because of their unique extrusomes; however, the preparation of the book was too advanced to include all the changes needed.

Extrusomes were noted in the original description of *P. terricola*, but their peculiar shape in discharged condition was not observed. I am indebted to my co-worker, Mag. ALINE BERTHOLD, for recognizing this peculiarity, which I have since been able to confirm on 12 populations found in soils worldwide. Furthermore, I reinvestigated the other members of the Grossglockneriidae, i.e. *Nivaliella plana, Pseudoplatyophrya nana, P. saltans, Grossglockneria acuta* and *G. hyalina;* their extrusomes are granular and not nail-shaped when extruded.

Two species need to be transferred to the new genus, viz. *Pseudoplatyophrya terricola* Foissner, 1985 and *Platyophrya armata* Kahl, 1926. Both are rather similar and the few differences described, viz. the slightly larger size (32–40 µm), the more distinctly furrowed cortex and the less conspicuous caudal cilium of *P. armata*, might be caused by some natural variability and/or incomplete observations. However, *P. armata* has been recorded only from freshwater, whereas *P. terricola* is very likely confined to terrestrial biotopes. Thus, I keep them separate.

# • *Mykophagophrys terricola* (Foissner, 1985) nov. comb. (Figs. 132–140)

The population figured is from a subalpine meadow soil in Tyrol near Brixlegg. It matches the original description and the population from Costa Rica very well. Thus, only observations relating to the extrusomes are described. The inactive extrusomes of *M. terricola* are hardly recognizable in normal live cells, even if oil



Figs. 132–140. Mykophagophrys terricola from life (Figs. 132, 136–138) and after methyl green-pyronin staining (Figs. 133–135, 139, 140). – 132. Left lateral view of disturbed specimen with extrusomes ready to be discharged. Scale bar division  $10 \ \mu m.$  – 133–135, 139, 140. Specimens with discharged extrusomes which appear nail-like due to the conical anterior end. – 136–138. Surface and lateral views of slightly pressed specimens. The extrusomes (arrows) become blister-like before extrusion and cause a characteristic vacuolation of the cortex. CV = contractile vacuole, Ex = extrusomes, FT = feeding tube, FV = food vacuoles.

immersion and interference contrast are applied. However, the cortex of *M. terricola* always appears thick and bright, obviously due to the narrowly spaced extrusomes (Foissner 1993). Only if the cell is heavily disturbed, e.g. by being slightly pressed between the slide and the cover glass, many conspicuous, cylindroid blisters become apparent underneath the pellicle (Figs. 136–138). The content of these blisters is extruded and stained red when methyl green-pyronin is applied (Figs. 133, 135). It elongates to a 15–20 µm long thread with a thickened distal end, thereby producing the nail-like appearance of the discharged extrusomes (Fig. 135). More detailed analysis shows, however, that the nailhead is in fact a small, wide cone (Figs. 134, 140).

• Mykophagophrys armata (KAHL, 1926) nov. comb.

This species is critically reviewed in Foissner (1993) under its original name, *Platyophrya armata*.

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