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REVIEW ARTICLE

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Soil ciliates (Protozoa: Ciliophora) from evergreen rain forests of Australia, South America and Costa Rica: diversity and description of new species

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Abstract This paper provides, for the first time, comprehensive data on alpha diversity of soil ciliates from evergreen tropical and temperate rain forests. Thirty-three samples were collected in Australia, Tasmania, Amazonia and Costa Rica and analysed with the non-flooded Petri dish method, which reactivates the ciliates' resting cysts from air-dried samples. The 175 taxa found contained 34 new species, 4 of which are described in this paper, viz. *Platyophrya paoletti* n. sp., *Lamtostyla abdita* n. sp., *L. granulifera* n. sp., and *Apoamphisiella tihanyiensis* (Gellért and Tamás 1958) n. gen., n. comb. Although this is a considerable number, it is much lower than one would expect. The data would be even more perplexing if the four rich samples (up to 90 species/sample) from the Manaus floodplain were excluded. We then would be confronted with about 90 taxa in 29 samples, of which 13 contained fewer than ten species. A hypothesis is put forward that the non-flooded Petri dish method is inappropriate for studying soil ciliate diversity in evergreen rain forests because most species have a reduced capacity to produce dry-resistant (protective) resting cysts due to the permanent wetness of their habitats. This view is supported by a comparative analysis of a fresh (containing 40 species) and air-dried/rewetted (2 species only) sample from a cloud rain forest near Merida (Venezuela), and the observation that the capacity of soil ciliates to produce resting cysts often dramatically decreases after prolonged laboratory cultivation in liquid media. Direct microscopy of fresh samples seems to be an appropriate alternative because specimens can be easily collected due to their considerable abundance (≥1000 individuals/g wet mass of litter).

Key words Biodiversity · Ecophysiology · Evergreen rain forests · Methodology · Soil protozoa

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Introduction

Evergreen rain forests are famous for their rich diversity of plants and animals and have become a central paradigm in biodiversity discussion and conservation (Beck et al. 1997; May 1992; World Conservation Monitoring Centre 1992). While all major groups of rain forest plants and animals have been studied to at least some extent, reliable data are extremely rare for single-celled soil organisms like bacteria and protozoa (Bamforth and Lousier 1995; Beck et al. 1997; Foissner 1987; Hawksworth and Colwell 1992; World Conservation Monitoring Centre 1992). Among soil protozoa, testate amoebae have been studied in some detail, mainly due to the prolific works of Bonnet, Jung and Hoogenraad (for literature and reviews, see Bamforth and Lousier 1995; Bovee 1957; Foissner 1987), while, apart from a few species descriptions (e.g. Foissner 1993) and abundance estimations (Bamforth and Lousier 1995), investigations on soil ciliates from evergreen rain forests are virtually lacking.

I thus commenced, in 1987, a taxonomic-faunistic project on soil ciliates from representative tropical and temperate rain forests. The present paper contains some of the results obtained in Australia, Tasmania, Costa Rica, and the famous Amazonian rain forest in South America. The data are a selection from many more samples which, however, show the same general trend, viz. a highly varying ciliate diversity in rain forest soils. It will be shown that this peculiar pattern is at least partially caused by methodological shortcomings, i.e. that the methods developed for studying soil ciliates in temperate and arid regions are of restricted value in evergreen rain forests.

Materials and methods

Areas and sampling

Samples were collected in evergreen rain forests of Australia, Tasmania, Venezuela (north margin of the Amazonian rain forest), Brazil and Peru (centre of the Amazonian rain forest), and Costa Rica. Some

Table 1 Some basic data for the sites investigated. From various sources, especially Walter and Lieth (1967) (*ND* no data)

Variables	Australia		Amazonia			Costa Rica	
Station	Cairns	Mt. Fields NP	Puerto Ayacucho	Manaus	Iquitos	Braulio Carrillo NP	Monte Verde
Geographic coordinates	145°E17°S	147°E43°S	68°W5°N	60°W4°S	74°W4°S	83°50′W 10°12′N	85°49′W 10°20′N
Altitude (m)	5	~800	<100	45	106	ND	1500
Number of years of observation (temperature)	24	22	ND	11	1	ND	ND
Number of years of observation (precipitation)	49	37	32	25	1	ND	ND
Mean annual air temperature (°C)	24.7	7.8	27.0	26.7	24.8	ND	17.0
Mean annual sum-total of precipitation (mm)	2250	1460	2236	2180	2623	4500	3000

basic data on the location and climate of the sampling sites, as far as I could elicit them, have been compiled in Table 1. Unfortunately, detailed soil data are not available, but some information is included in the sample descriptions. For general characteristics of tropical rain forest soils, see Emmerich (1997) and Zech (1997).

All samplings are from the tropics and subtropics, except those from Tasmania. There is no general definition of a rain forest, many types of which have been distinguished (Odum 1980). However, there is some agreement that rain forests develop in regions having >2000 mm annual precipitation and >24°C mean annual temperature (Bick 1989; Lincoln et al. 1985; Odum 1980; Sedlag and Weinert 1987). The sites investigated match or are near to these characteristics (Table 1), except those in Tasmania, which are from a "temperate *Nothofagus* rain forest", according to the classifications by the National Parks and Wildlife Service (1976) and Bridgewater (1987).

The material collected usually included the litter from the soil surface, the humic layer, and mineral top soil (0–5 cm depth) with fine plant roots. Samples 1–4 and 5–9 are profiles up to 40 cm soil depth. Usually, about ten small subsamples were taken from an area of up to 100 m^2 and mixed to produce a composite sample. All samples were air-dried for at least 1 month and then sealed in plastic bags. Such samples can be stored for years without any significant loss of species (Foissner 1987, and unpublished results).

Sample description

Samples 1–9: Australia, Cairns, near sea level (collected on 5 February 1987, investigated in March 1988).

Samples 1–4: rain forest site 2; vertical profile from 0–10 cm. Sample 1: uppermost leaf litter layer; leaves almost complete, i.e. with few signs of decomposition; pH 5.9. Sample 2: leaf litter on root-carpet; leaves brown and with distinct signs of decomposition; pH 5.5. Sample 3: upper (0–2 cm) root-carpet; litter heavily decomposed and mixed with brownish, humic soil; pH 5.5. Sample 4: lower (2–10 cm) root layer; without recognizable litter but with rather a lot of roots; soil light yellow; pH 5.1.

Samples 5–9: rain forest site 4; vertical profile from 0–40 cm. Sample 5: uppermost litter layer; leaves almost complete, i.e. with few signs of decomposition; pH 6.1. Sample 6: upper (0–2 cm) leaf litter and soil layer; litter heavily decomposed and mixed with dark brown, humic soil; pH 6.0. Sample 7: upper (2–5 cm) root-carpet; litter heavily decomposed and mixed with brownish, humic soil; pH 5.7. Sample 8: lower (5–25 cm) soil layer; without recognizable litter, very few roots; soil grey; pH 5.9. Sample 9: lower (25–40 cm) soil layer; without recognizable litter and roots; soil yellow; pH 5.7.

Samples 10–16: Tasmania, Mt. Field National Park (collected on 22/23 January 1987, investigated in September/October 1988).

Sample 10: litter, roots, and some brown soil (0–5 cm) under *Nothofagus* trees at entrance to National Park; pH 4.1; about 150 m above sea level.

Sample 11: Russell Falls; litter, roots, and some blackish soil (0–5 cm) under Man Ferns; pH 3.8; about 150 m above sea level.

Sample 12: litter, roots, and some brown soil (0–5 cm) from a mixed deciduous rain forest (but without *Nothofagus*) with many ferns and mosses; pH 4.0; about 420 m above sea level.

Sample 13: litter, roots, and some pale soil (0–5 cm) under *Nothofagus* trees; pH 4.0; about 580 m above sea level.

Sample 14: litter, roots, and brown soil (0–5 cm) under large *Eucalyptus* trees; pH 4.9; about 680 m above sea level.

Sample 15: litter, roots, and some soil under large *Nothofagus* trees; pH 4.4; about 680 m above sea level.

Sample 16: litter, roots, and some soil under small *Nothofagus* trees; pH 4.3; about 1140 m above sea level.

Samples 17–20: Venezuela, vicinity of Puerto Ayacucho, north edge of Amazonian rain forest (collected in February 1996, investigated between April and July 1996).

Sample 17: about 10 km north of Puerto Ayacucho at Pozo Azul, a holiday site; Gallery forest soil 0–10 cm, loosely packed fresh and decaying, dark brown leaf litter mixed with many fine roots, arthropod excrement, and some soil; pH 4.9.

Sample 18: about 20 km north of Puerto Ayacucho at Pavoni, an Indian village; evergreen, seasonal rain forest, 0–10 cm, fresh and decaying leaf litter mixed with many fine roots and brown, sandy soil, which consisted mainly of old earthworm casts; pH 5.2.

Sample 19: about 20 km south of Puerto Ayacucho at Caño Tigre, an Indian village; evergreen, seasonal rain forest, 0–5 cm, fresh and decaying leaf litter mixed with many roots and brown, humic soil, which consisted mainly of old earthworm casts; pH 4.9.

Sample 20: about 30 km south of Puerto Ayacucho at Tobogán de la Selva, an Indian village; secondary, evergreen, seasonal rain forest, 0–5 cm, fresh and decaying leaf litter mixed with many fine roots and brown, very sandy and humic soil; formerly used as crop field (conuco); pH 5.5.

Samples 21–25: Brazil, vicinity of Manaus, centre of Amazonian rain forest (collected in November 1996, investigated in December 1996).

Sample 21: outskirts of Manaus, surroundings of Tropical Hotel Manaus; terra firma secondary rain forest about 300 m off the Rio Negro, not flooded during high water periods of the river; collection of litter, soil and roots from 0–5 cm: litter layer less than 2 cm thick, under which was a root-carpet mixed with brown, humic soil about 3 cm thick; mineral soil under root-carpet loamy, brownish; pH 5.1.

Sample 22: about 20 km east of Manaus, Janauari region; floodplain primary (?) rain forest on one of the many small islands in the region where the yellow Rio Solimões units with the black Rio Negro to form the Rio Amazonas, flooded by the Rio Solimões during high water periods; collection of litter, soil and roots from 0–5 cm: litter layer up to 2 cm thick, followed by a relatively conspicuous root-carpet mixed with brown, humic soil; mineral soil under root-carpet loamy, brownish; pH 5.1.

Sample 23: about 40 km west of Manaus, Anavilhanas archipelago in the Rio Negro, vicinity of Ariau lodge; blackwater inundation primary (?) rain forest on one of the many small islands of the region, flooded by the Rio Negro during high water periods; collection of litter, soil and roots from 0–8 cm; litter layer up to 5 cm thick, followed by a 3–5 cm thick root-carpet mixed with brown, humic soil; mineral soil under root-carpet loamy, brown; pH 5.1.

Sample 24: about 40 km west of Manaus, Anavilhanas archipelago in the Rio Negro; terra firma primary (?) rain forest on one of the many small islands of the region, about 10 m above low water level and thus not flooded during high water periods of the river; collection of litter,

roots and soil from 0–10 cm; litter layer 2–5 cm thick and with many fungal hyphae, followed by an about 5 cm thick, very dense root-carpet mixed with brown, humic soil; mineral soil under root-carpet loamy-sandy and brownish, yellowish down to 10 cm; pH 5.1.

Sample 25: as for sample 24 but on top of island about 25 m above low water level.

Samples 26–29: Peru, Amazonian rain forest in the vicinity of Iquitos (collected in spring 1989, investigated in August 1989 and May 1990).

Sample 26: light brown soil mixed with much leaf litter; pH 6.2. Sample 27: a small amount of dark brown soil mixed with much leaf litter; pH 7.1. Sample 28: material similar to sample 27. Sample 29: bark from trees mixed with some leaf litter, roots and soil.

Samples 30–33: Costa Rica, Central America (collected in February 1991, investigated between April 1991 and May 1992).

Sample 30: cloud rain forest near summit of Monteverde Preserve, Quetzal trail near research station; soil and roots from 0–3 cm; pH 4.7.

Sample 31: cloud rain forest near summit of Monteverde Preserve, way to river (Sendero Rio) near research station; litter and soil from 0–5 cm; pH 4.7.

Sample 32: Braulio Carrillo National Park; soil from trees with epiphytes; pH 4.8.

Sample 33: cloud rain forest in Braulio Carrillo National Park; litter, roots and soil from 0–5 cm; pH 4.5.

Sample processing and faunistic methods

All samples were analysed with the non-flooded Petri dish method as described by Foissner (1987, 1992), which reactivates the ciliates' resting cysts from air-dried samples. Briefly, this simple method involves placing 10–50 g air-dried moss, litter and/or soil in a Petri dish (15 cm diameter) and saturating but not flooding it with distilled water. Such cultures were analysed for ciliates by inspecting about 2 ml of the run-off on days 2, 7, 14, 21, and 28.

Identification, nomenclature and terminology of species are according to the literature cited in Foissner (1987, 1997b). Most of the species found were described or redescribed by me and my students. Thus, determinations were done mainly on live specimens using a high-power (×100; N.A. 1.32) oil immersion objective and differential interference contrast. However, all "difficult", new, or supposedly new species were checked with the silver-staining techniques described in Foissner (1991).

Species similarity between individual samples was analysed with Jaccard's (1902) coefficient, followed by UPGM clustering. Analysis of functional groups was based on Foissner's (1997b) compilation.

Cytological methods

The species described were studied in vivo using a high-power (×100, N.A. 1.32) oil immersion objective and differential interference contrast. The ciliary pattern (infraciliature) was revealed by protargol impregnation as described in Foissner (1991). The descriptions are based on material obtained with the non-flooded Petri dish method mentioned above, i.e. no clonal cultures were set up.

Counts and measurements on silvered specimens were performed at a magnification of ×1000. In vivo measurements were made at magnifications of ×40–1000. While the latter measurements provide only rough estimates, it is worth giving such data as specimens usually shrink in preparations or contract during fixation. Standard deviation and coefficient of variation were calculated according to statistics textbooks. Illustrations of live specimens are based on freehand sketches and micrographs; those of impregnated cells were made with a camera lucida. All figures are oriented with the anterior end of the organism directed to the top of the page.

Type slides

Two to four type slides (1–2 holotypes and 1–2 syntypes, depending on the variety of methods used) of each of the new species described, and two voucher slides of the species redescribed, have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria. The slides usually contain many silver-impregnated cells with relevant specimens marked by a black ink circle on the cover glass.

Results and discussion

Alpha diversity of soil ciliates in evergreen rain forests: a methodological problem

The presentation of the data only make sense with the prior knowledge that the isolation technique used (non-flooded Petri dish method) was very likely inappropriate, because soil ciliates from evergreen rain forests have obviously a reduced capacity to make dry-resistant (protective) resting cysts.

175 ciliate taxa were found in the 33 samples investigated, 34 species were very likely new (Table 2). Although this is a considerable number, it is much lower than one would expect given that a single sample from a tropical dry forest in Costa Rica contained 80 species (Foissner 1995), and taking into account the high diversity exhibited by plants and animals in general in rain forests (Beck et al. 1997; World Conservation Monitoring Centre 1992). The data would be even more perplexing if the four rich samples from the Manaus floodplain were excluded, since we would then be confronted with about 90 taxa in 29 samples, of which 13 contained less than ten species (Table 2). Such data hardly look reliable, although it is well-known that some groups of animals and plants have a higher diversity in temperate deciduous forests than in tropical evergreen rain forests, for instance mosses, of which more species live in the Schwarzwald (a small forest region in Germany) than in the large Amazonian lowland rain forest. Frahm and Kürschner (1992) showed that this strange pattern is caused by the ecophysiological properties of mosses in general, i.e. their adaptation to cool-temperate climates. Under the warm, wet conditions of lowland tropical rain forests, especially above 25°C, they respire more energy than they can produce during the light periods. Likewise, earthworm richness is slightly larger in temperate than in tropical soils, although functional diversity increases towards the tropics, i.e. earthworms become able to use organic resources of increasingly lower quality (Lavelle et al. 1995). As for ciliates, I shall argue below that the depauperate fauna is very likely a methodological artifact, although it nonetheless reveals remarkable insights in the ecophysiological properties of soil ciliates in evergreen rain forests.

I have been perplexed by the paucity of the soil ciliate fauna in evergreen rain forests since I commenced studying such habitats a decade ago. Usually I found more species in neighbouring cultivated soils and arid deserts. At first I assumed that I simply had bad luck in choosing good sampling sites. Later, when I recognized that it is a world-wide phenomenon, I supposed that ciliates could be very patchily distributed, as are many rain forest animals and plants (e.g. Bridgewater 1987; Greenslade and Rusek 1996), or that specific soil attributes, especially their low

Table 2 List of species recorded in evergreen rain forests from Australia (samples 1–9), Tasmania (10–16), Amazonia (17–20 Venezuela; 21–25 Brazil; 26–29 Peru) and Costa Rica (30–33) (+ found, – not found)

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Amphisiella terricola Gellért 1955	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Amphisiella vitiphila (Foissner 1987)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
Amphisiella (?) sp.[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	+	–	–	–	–	–	–	–	–
Apoamphisiella tihanyiensis (Géllert & Tamás 1958) n. comb.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–
Arcuospathidium atypicum (Wenzel, 1953)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	–	–	–	–	–	–	–	–	–
Arcuospathidium japonicum Foissner 1988	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–
Arcuospathidium lionotiforme (Kahl 1930)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	–	–	–	–	–	–	–
A. muscorum (Dragesco & Dragesco-Kernéis 1979)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	+	–
Arcuospathidium sp.[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–
Australocirrus octonucleatus Foissner 1987	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	+	–	–	–	–	–	–
Australocirrus oscitans Blatterer & Foissner 1988	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	–	–	–	–	–	–	–	–
Australothrix steineri Foissner 1995	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Birojimia muscorum (Kahl 1932)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Blepharisma bimicronucleatum Villeneuve-Brachon 1940	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Blepharisma hyalinum Perty 1849	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	+	–	–	+	–	–	–
Blepharisma steini Kahl 1932	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–
Blepharisma sp.[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Brachonella cydonia (Kahl 1927)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–
Bresslaua sicaria Claff, Dewey & Kidder 1941	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–
Bryometopus pseudochilodon Kahl 1932	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	+	–	–	–	–	+	–	–	–
Bryometopus triquetus Foissner 1993	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	+	–	–	–	–	–	–	–	–	–
Bryophyllum loxophylliforme Kahl 1931	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–
Bryophyllum sp.[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Chilodonella uncinata (Ehrenberg 1838)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
Cinetochilum margaritaceum (Ehrenberg 1830)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–
Colpoda aspera Kahl 1926	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	+	–	+
Colpoda cavicola Kahl 1935	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Colpoda cucullus Müller 1773	+	+	–	–	+	+	–	+	–	–	–	+	–	+	–	–	–	–	–	–	+	+	+	+	+	–	+	+	–	+	+	–	–
Colpoda ecaudata (Liebmann 1936)	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–
Colpoda edaphoni Foissner 1980	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Colpoda henneguyi Fabre-Domergue 1889	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–
Colpoda inflata (Stokes 1885)	+	+	+	–	+	+	+	–	+	+	+	+	+	+	+	+	–	–	–	–	+	+	+	+	+	–	+	+	+	+	+	+	+
Colpoda lucida Greeff 1888	–	–	–	–	–	–	–	–	–	+	–	+	–	+	+	–	–	–	–	–	+	+	+	+	+	+	–	+	–	–	+	–	–
Colpoda maupasi Enriques 1908	+	+	–	+	+	+	+	–	+	–	–	+	+	+	+	+	–	–	–	–	+	+	+	+	+	+	+	–	+	+	–	+	–

Table 2 (continued)

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Colpoda steinii Maupas 1883	–	+	+	+	+	+	+	+	+	+	–	+	+	+	+	+	–	–	–	–	+	–	+	+	+	–	–	+	+	+	+	+	–
Colpoda tripartita Kahl 1931	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Colpoda variabilis Foissner 1980	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Coriplites terricola Foissner 1988	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
Cyclidium glaucoma Müller 1773	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
Cyclidium muscicola Kahl 1931	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	+	+	+	+	+	–	–	+	–
Cyrtohymena australis Foissner 1995	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Cyrtohymena candens (Kahl 1932)	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cyrtohymena citrina (Berger & Foissner 1987)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	–	–	–
Cyrtohymena quadrinucleata (Dragesco & Njine 1971)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–	–	–	–	–	–	–	–	–
Cyrtolophosis acuta Kahl 1926	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cyrtolophosis elongata (Schewiakoff 1892)	–	–	–	–	–	+	–	+	+	–	–	–	–	–	–	–	+	+	–	–	–	–	+	–	–	–	–	–	+	–	–	–	–
Cyrtolophosis minor Vuxanovici 1963	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–
Cyrtolophosis mucicola Stokes 1885	+	+	+	+	+	+	–	+	–	–	–	–	–	–	–	–	–	+	+	–	+	+	+	+	+	+	+	+	+	–	+	+	+
Dileptus alpinus Kahl 1932	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Dileptus anguillula Kahl 1931	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	+	–	–	–	+	+	+	–	–	–
Dileptus costaricanus Foissner 1995	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Dileptus terrenus Foissner 1981	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Dileptus sp.1 [a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	+	–	–	–	–	–	–	–	–
Dileptus sp.2 [a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–
Dileptus sp.3 [a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Dileptus sp.4 [a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Dimacrocaryon amphileptoides (Kahl 1931)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–
Dimacrocaryon sp.1 [a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–
Dimacrocaryon sp.2 [a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–
Drepanomonas dentata Fresenius 1858	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Drepanomonas exigua Penard 1922	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Drepanomonas muscicola Foissner 1987	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	–	–	–	–	–	–	–	–
Drepanomonas pauciciliata Foissner 1987	–	+	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	+	+	+	–	+	–	–	–
Drepanomonas revoluta Penard 1922	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Drepanomonas sphagni Kahl 1931	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–
Enchelyodon longinucleatus Foissner 1984	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Enchelyodon sp.1 [a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Enchelyodon sp.2 [a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Enchelyotricha sp. [a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Epispathidium amphoriforme (Greeff 1888)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–	+	–	–	–	–	–	–	–	–
Epispathidium ascendens (Wenzel 1955)	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	+	–	–
Epispathidium terricola Foissner 1987	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–	+	–	–	–	–	+	–	–	–

Table 2 (continued)

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Frontonia depressa (Stokes 1886)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	+	–	–	–	–	–	–	–	–
Fuscheria terricola Berger, Foissner & Adam 1983	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	+	–	–	–	–	–
Gonostomum affine (Stein 1859)	–	–	–	–	–	–	+	–	–	+	–	+	+	–	–	–	–	–	–	–	+	+	+	+	+	+	+	+	+	+	+	+	+
Grossglockneria acuta Foissner 1980	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	–	–	–	–	+	+	+	–	–
Halteria grandinella (Müller 1773)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	+	+	–	–	–	–	–	–
Hausmanniella discoidea (Gellért 1956)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	+	–	–	–	–	–	–	–	–
Hausmanniella patella (Kahl 1931)	+	+	–	–	+	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	+	–	+	–	–	–	+	–	–	–	–	–
Hausmanniella (?) sp.[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Hemisincirra gellerti (Foissner 1982)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Hemisincirra inquieta Hemberger 1985	–	+	+	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	+	–	–	–	–	+	–	–	–
Hemisincirra wenzeli Foissner 1987	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Holosticha australis Blatterer & Foissner 1988	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–
Holosticha multistilata Kahl 1928	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	+	–	–	–	–	–	–	–	–
Holosticha muscorum (Kahl 1932)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Holosticha sigmoidea Foissner 1982	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	+	–	–	–	–	–	–	–	–
Holosticha sylvatica Foissner 1982	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	+	+	–	–	–	–	–	–	–	–
Holosticha tetracirrata Buitkamp & Wilbert 1974	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	+	–	–	–	–	–	–	–	–	–
Holostichides terricola Foissner 1988	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Homalogastra setosa Kahl 1926	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–	–	–	–	–	+	–	–	–
Kahlilembus attenuatus (Smith 1897)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	+	–	–	+	–	–	–
Lamtostyla abdita sp. nov.	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lamtostyla granulifera sp. nov.	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Lamtostyla islandica Berger & Foissner 1988	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–
Lamtostyla sp.[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	+	–	–	–	–	–	–	–	–
Lepidotrachelophyllum sp.[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–
Leptopharynx costatus Mermod 1914	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	+	+	+	+	+	+	+	+	–
Metopus contractus Penard 1922	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Metopus es (Müller 1776)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Metopus hasei Sondheim 1929	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	+	–	–	–	–	–	–
Metopus ovalis Kahl 1927	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–
Metopus palaeformis Kahl 1927	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–
Metopus setosus Kahl 1927	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–
Metopus setosus minor Kahl 1927	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–
Metopus sp.1[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Metopus sp.2[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Metopus sp.3[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Microdiaphanosoma arcuatum (Grandori & Grandori 1934)	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	+	–	–	+	+

Table 2 (continued)

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Microdiaphanosoma terricola Foissner 1993	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	–	–	–	–	–	–	–	–	–	–
Mykophagophrys terricola (Foissner 1985)	+	–	–	–	+	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	+	+	+	+	–	–	+	–	+	+	–	–
Nivaliella plana Foissner 1980	+	+	–	–	+	+	–	–	–	+	–	+	+	+	+	–	–	–	–	–	–	+	+	–	+	–	–	–	–	+	+	+	+
Nivaliella sp.[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	+	+	–	–	–	–	–	–	–
Notoxoma parabryophryides Foissner 1993	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Opisthonecta minima Foissner 1975	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Orthoamphisiella stramenticola Eigner & Foissner 1991	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–
Oxytricha auripunctata Blatterer & Foissner 1988	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–
Oxytricha granulifera Foissner & Adam 1983	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	+	+	–	+
O. granulifera quadricirrata Blatterer & Foissner 1988	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–
Oxytricha lanceolata Shibuya 1930	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–
Oxytricha longigranulosa Berger & Foissner 1989	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	–	–	–	–	–	–	–	–
Oxytricha nauplia Berger & Foissner 1987	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–
Oxytricha opisthomuscorum Foissner et al. 1991	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	–	–	–	–	–	–	–	–
Oxytricha setigera Stokes 1891	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	+	–	–	+	–	–	+
Oxytricha siseris Vuxanovici 1963	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–	–	–	–	–	–	–	–	–	–
Oxytricha sp.1[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
Oxytricha sp.2[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Parabryophrya penardi (Kahl 1931)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Paraenchelys terricola Foissner 1984	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	–	–	+	–	–	–
Parafurgasonia sorex (Penard 1922)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Pattersoniella vitiphila Foissner 1987	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Phacodinium metchnicoffi (Certes 1891)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Phialina sp.[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Phialinides australis Foissner 1988	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Plagiocampa rouxi Kahl 1926	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–
Platyophrya macrostoma Foissner 1980	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Platyophrya paoletti sp. nov.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Platyophrya similis (Foissner 1980)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–
Platyophrya spumacola Kahl 1927	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–	–	–
Platyophrya vorax Kahl 1926	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	+	–	+	+	+	–	–	–	–
Podophrya sp.[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Protospathidium bonneti (Buitkamp 1977)	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	+	–
Protospathidium sp.1[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	–	–	–	–	–	–	–	–
Protospathidium sp.2[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	–	–	–	–	–	–	–	–	–	–
Pseudochilodonopsis mutabilis Foissner 1981	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–	–	–	–	–	–	–	–	–	–
Pseudocyrtolophosis alpestris Foissner 1980	+	–	–	+	+	+	+	+	+	–	–	–	–	–	–	–	–	–	+	–	+	+	+	+	+	–	+	+	+	–	+	+	+

Table 2 (continued)

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Pseudoplatyophrya nana (Kahl 1926)	+	+	+	+	+	+	–	–	–	+	+	+	+	+	–	–	–	–	–	–	+	–	+	+	+	–	+	+	+	+	+	+	+
Pseudoplatyophrya saltans Foissner 1988	–	+	+	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–	+	–	+	–	–	+	+	–	–
Pseudouroleptus sp.[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Pseudovorticella sphagni Foissner & Schiffmann 1974	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	+	–	–	–	–	–	–	–
Rostrophryides australis Blatterer & Foissner 1987	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Sathrophilus muscorum (Kahl 1931)	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	+	–	–	–	+	–	–	–	–
Spathidium muscicola Kahl 1930	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	+	–	–	–	–	–
Spathidium procerum Kahl 1930	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	–	–	–	+	–	–	–	–	–	–
Spathidium spathula (Müller 1773)	+	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–
Spathidium sp.1[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	–	–	–	–	–	–	–	–	–
Spathidium sp.2[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Spathidium sp.3[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Sphaerophrya terricola Foissner 1986	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
Stammeridium kahli (Wenzel 1953)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–
Sterkiella cavicola (Kahl 1935)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	+	–	–	–
Sterkiella histriomuscorum (Berger et al. 1991)	–	+	–	+	–	–	–	–	–	+	–	–	–	–	–	–	+	–	–	–	–	+	+	–	–	–	–	–	–	+	–	–	–
Stylonychia bifaria (Stokes 1887)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–
Tachysoma humicola Gellért 1957	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Tachysoma humicola longisetum Foissner (in press)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Tokophrya muscicola (?) Penard 1914	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–
Trihymena terricola Foissner 1988	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–
Uroleptus lepisma (Wenzel 1953)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–
Uroleptus notabilis (Foissner 1982)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–
Urosoma macrostyla (Wrześniowski 1866)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Urosoma sp.[a]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Urosomoida agiliformis Foissner 1982	+	–	+	–	–	–	+	–	–	–	–	+	+	–	–	–	+	–	–	–	–	–	–	–	–	–	+	+	–	+	+	–	–
Urosomoida agilis (Engelmann 1862)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–
Vorticella astyliformis Foissner 1981	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	–	–	–	–	–	–	–	–
Vorticella microstoma Ehrenberg 1830	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Number of taxa determined	13	21	11	7	16	17	12	5	5	8	2	13	8	9	6	3	4	2	2	0	44	74	88	42	42	33	16	16	23	19	31	12	19
Number of undetermined taxa	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	5	3	2	0	0	0	0	2	0	0	1
Number of (supposedly) new species	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	9	10	13	6	5	1	0	0	0	0	0	1	0

[a] These are very likely new species, to be described in a later publication

nutrient status (Bick 1989), could be responsible for the paucity of the ciliate fauna. However, these and other possible explanations were not satisfying, considering that samples were taken from a great variety of habitats and included the litter layer and root-carpet, i.e. contained much and highly diverse organic matter, which usually favours the development of a rich and diverse ciliate fauna (Foissner 1987). To check whether special soil conditions possibly inhibit excystment and growth of ciliates, rain forest samples 18 and 20 were mixed with 5 g each of a neighbouring rich field (Mahada) soil. A diverse ciliate fauna (30 and 50 species, respectively) developed in the mixed samples, very similar to that found in the pure field soil.

Only then did I take into account that the non-flooded Petri dish method, with which I discovered hundreds of new species in a great variety of habitats and localities (for reviews, see Foissner 1987, 1997a,b), might be inappropriate for rain forest soils. I could not verify this idea for a long time, i.e. look at fresh samples, because the sites were in the tropics and usually too remote from a university or a similar institution having a good microscope. Only recently was I able to do such comparisons thanks to the kindness of Prof. Maximina Monasterio (Merida University) and Prof. Maurizio Paoletti (Padua University). A sample was taken from the cloud rain forest in the Sierra Nevada National Park (Venezuela) near the town of Tabay (La Mucuy village, near the entrance to the Humboldt trail). Part of the sample was analysed on the same day at Merida University, while the other part was treated as usual, i.e. air-dried and rewetted in the Salzburg laboratory. The fresh sample looked as if it had been taken from a polluted river, i.e. it contained about 1000 ciliates/g wet mass of litter, belonging to at least 40 different taxa. There was also a fascinating number and variety of other protozoans and micro-metazoans, especially testate amoebae and nematodes. In contrast, only two ciliate species (*Colpoda steinii* and *C. inflata*) developed in the air-dried and rewetted sample.

Apparently, the non-flooded Petri dish method is inappropriate for studying soil ciliate diversity in evergreen rain forests, although there are some exceptions (see below). Admittedly, this conclusion is based on a single case and thus cannot withstand statistical analysis. However, the differences between the fresh and the rewetted samples were so apparent and impressive that I have no doubt that further, more detailed analysis will confirm my conclusion. Furthermore, my assumption is strongly supported by another observation, viz. that prolonged cultivation of soil ciliates in liquid media often drastically reduces their ability to make resting cysts. I have observed this in many species but have not mentioned it in my previous publications because I did not recognize the significance. There is also support in the literature for this phenomenon. Pigon and Edström (1961) observed that laboratory-produced permanent cysts of *Colpoda cucullus* did not survive desiccation, although it is one of the most common ciliates in temperate and arid soils and ephemerial limnetic habitats (Foissner 1987, 1993). Fenchel (1969) showed that neither slowly nor quickly desiccated cysts of a marine sand *Aspidisca* were able to excyst when water was added. Sand samples from Nivå Bay, which were dried at various temperatures, and samples first drained for water and then dried did not contain living ciliates some time after water had been added again. Thus cysts of marine ciliates seem not to survive desiccation.

Very likely, the lack of a reservoir of resting cysts and/or the inability of the resting cysts to tolerate longer periods of desiccation, as they usually occurred with the investigation method used, is the essential point. Litter and soil of evergreen rain forests are at least slightly wet most of the time due to the frequent rainfalls and the high air humidity. Thus, most protozoa are probably permanently active and hardly forced to produce dry-resistant dormant stages. Hence, the non-flooded Petri dish method, which depends on the reactivation of dry-restistant resting cysts, necessarily provides incomplete results with such material. However, other, still unknown, factors are very likely involved, as I have observed a rich fauna in the Manaus samples (Table 2) and in coastal rain forests of Africa (Mombasa) and Venezuela (Henry Pittier National Park). At least the floodplain soils represent a more varying environment than the terra firma rain forests. In fact, it seems likely that floods perform a similar adaptive force as drought on soil ciliates because most species do not excyst and grow in soil infusions or rainpools, where a specific ephemeral ciliate fauna develops (Dingfelder 1962; Foissner 1980, 1981, 1987). In accordance with Hutchinson's (1961) theory on species diversity, a certain degree of disturbance seems necessary for soil ciliates (protozoa ?) to obtain and/or maintain the ability to produce dormant stages. Thus, soil protozoan communities could be a valuable model system for testing Hutchinson's (1961) idea that non-equilibrium mechanisms promote and maintain species diversity. Evidence for this widely accepted theory is still meagre and conflicting (McGrady-Steed and Morin 1996).

Community structure

The data obtained with the non-flooded Petri dish method are obviously strongly biased. Thus, they cannot provide definite insights in the community structure of rain forest soil ciliates. In spite of this, some of the more evident features will be briefly discussed.

The most frequent species (found in >50% of samples) were *Colpoda inflata*, *C. maupasi*, *C. steinii*, *Cyrtolophosis mucicola*, *Gonostomum affine*, *Pseudocyrtolophosis alpestris* and *Pseudoplatyophrya nana* (Table 2). All are common soil inhabitants and most belong to the Colpodea, which easily produce resting cysts and usually dominate terrestrial ciliate faunas (Foissner 1987). Furthermore, most feed on bacteria, except for *Pseudoplatyophrya nana*, an obligate fungal feeder.

With respect to species similarity, samples group primarily according to species richness; however, at least the Manaus samples form a dense cluster (Fig. 1). The two floodplain samples were the richest I have ever investi-

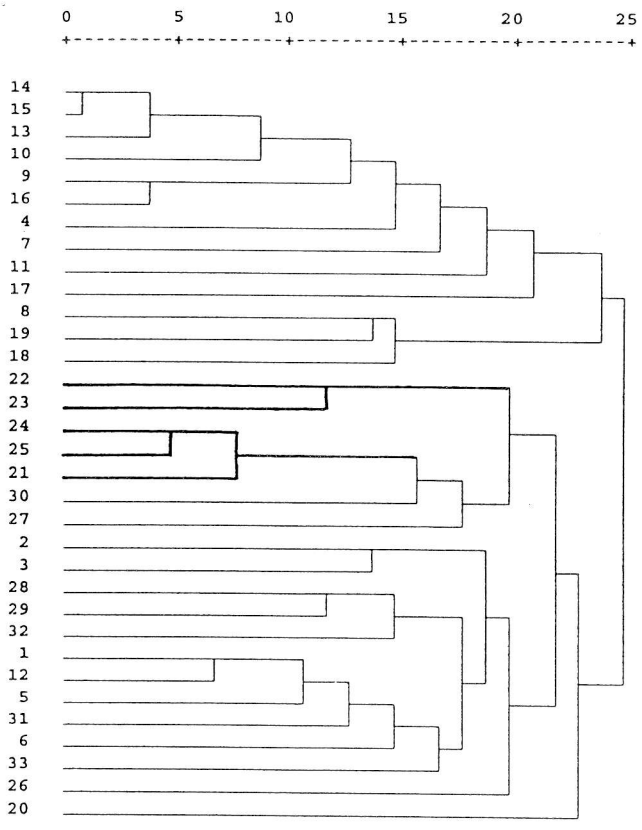


Fig. 1 Clusters of Jaccard similarity indices for the soil ciliates of 33 rain forest samples; those from Manaus are indicated by *bold lines* (see Materials and methods section for numbering and origin of samples)

gated and contained at least 21 new species. Vertical zonation is very likely similar to that in temperate soils, viz. most species are found in the upper 5 cm litter and root layer (see profiles, samples 1–4 and 5–9; Table 2). Compared to the global ciliate fauna, rain forests contain more colpodids, fewer large species, more species feeding on bacteria, more anaerobics, and more species occurring in both soil and freshwater (Table 3). Very likely, most of these differences are methodological artifacts. The increased percentage of anaerobics and freshwater species is apparently caused by the floodplain samples. Evidently soils became anaerobic during flood periods, which is also found in limnological studies (Junk and Weber 1996).

Conclusions

The 175 ciliate species found are very likely only a small proportion of the total because the non-flooded Petri dish method does not work very well with most rain forest soils. Thus, further progress on ciliate diversity and ecology in rain forest soils will depend on studying fresh material and on the development of appropriate isolation and culture methods. Provided that the single fresh sample studied was not an exception, it should be possible to collect sufficient numbers of ciliates with micropipettes and/or study drops of the soil solution with Foissner's protargol protocol.

Table 3 Comparison of functional groups of soil ciliates in evergreen rain forests (present study) and in the global soil ciliate fauna

Parameters	Rain forests	Global soil ciliate fauna[a]
Number of valid species	175	1092
Colpodids (%)	22.9	13.4
Cyrtophorids (%)	1.1	1.5
Gymnostomatids (%)	22.9	26.5
Heterotrichids (%)	9.1	3.2
Hymenostomes (%)	4.0	3.2
Hypotrichids (%)	29.7	39.2
Nassulids (%)	5.1	4.6
Oligotrichids (%)	0.6	0.3
Peritrichids (%)	2.3	3.7
Prostomatids (%)	0.6	2.0
Suctorians (%)	1.7	2.4
Small species (biomass ≤100 mg/10^6 cells) %	83.4	70.9
Large species (biomass ≥400 mg/10^6 cells) %	3.4	8.2
Omnivores (%)	13.7	20.2
Mainly bacterivorous (%)	50.9	38.5
Mainly predaceous (%)	32.0	34.1
Mainly (filamentous) cyanobacteria (%)	0	3.6
Mainly mycophagous (%)	3.4	1.6
Anaerobics (%)	6.3	1.6
Occurring only in terrestrial habitats (%)	26.3	36.4
Probably occurring only in terrestrial habitats (%)	52.0	47.6
Occurring in soil and freshwater (%)	21.7	16.0

[a] From Foissner (1997b)

Description of new and insufficiently known species

Morphometric data shown in Tables 4–7 are repeated in this section only as needed for clarity. For methods used and location of type slides, see section on materials and methods.

Platyophrya paoletti n. sp. (Figs. 2–19; Tables 4, 5)

Diagnosis. Size in vivo about 41×14 µm. Roughly reniform with oral apparatus subapical on ventral side. Macronucleus distinctly ellipsoidal, length:width ratio in vivo 2.5–3.5:1. Area between somatic kineties 1 and 2 slightly widened and with specialized silverline system. On average eight somatic kineties, five postoral pseudomembrane dikinetids, four adoral organelles, and 17 paroral dikinetids.

Type location. Soil of a gallery forest at Pozo Azul, about 10 km north of Puerto Ayacucho, Venezuela, South America (about 68°W 5°N).

Dedication. Named in honour of Prof. Dr. Maurizio Paoletti, soil zoologist at Padua University (Italy), who gave me the opportunity to participate in his research project in Venezuela.

Description. Size in vivo 32–50 × 12–20 µm ($\bar{x}$ 40.9 × 14.1, n = 7), laterally flattened up to 2:1 and sometimes distinctly curved (Fig. 8), very flexible. Slenderly to rather

Table 4 Morphometric data from *Platyophrya paoletti*, based on protargol-impregnated and mounted specimens from raw cultures. Measurements in μm. (*CV* coefficient of variation in %, *M* median, *Max* maximum, *Min* minimum, *n* number of individuals investigated, *SD* standard deviation, *SE* standard error of mean, $\bar{x}$ arithmetic mean)

Character	$\bar{x}$	M	SD	SE	CV	Min	Max	*n*
Body length	42.1	42.0	4.5	1.0	10.8	32.0	49.0	21
Body width	13.1	13.0	1.6	0.3	12.1	10.0	16.0	21
Anterior end to proximal end of paroral, distance	5.5	6.0	–	–	–	5.0	6.0	21
Anterior end to macronucleus, distance	19.7	20.0	3.2	0.7	16.1	14.0	27.0	21
Posterior end to excretory pore, distance	4.3	4.0	1.0	0.2	23.3	2.0	6.0	21
Macronucleus length[a]	8.3	8.0	0.8	0.2	9.5	7.0	10.0	21
Macronucleus width[a]	3.7	4.0	0.5	0.1	13.2	3.0	5.0	21
Macronuclei, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	30
Somatic kineties, number	8.1	8.0	–	–	–	8.0	9.0	41
Dikinetids in kinety 2, number	14.7	15.0	1.6	0.4	11.3	11.0	18.0	21
Dikinetids in kinety 7, number	10.5	10.0	2.5	0.6	23.8	5.0	16.0	21
Postoral pseudomembrane dikinetids, number	5.1	5.0	–	–	–	5.0	6.0	32
Paroral dikinetids, number	16.9	17.0	0.8	0.2	4.6	15.0	18.0	22
Adoral organelles, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	41

[a] Without peripheral membrane

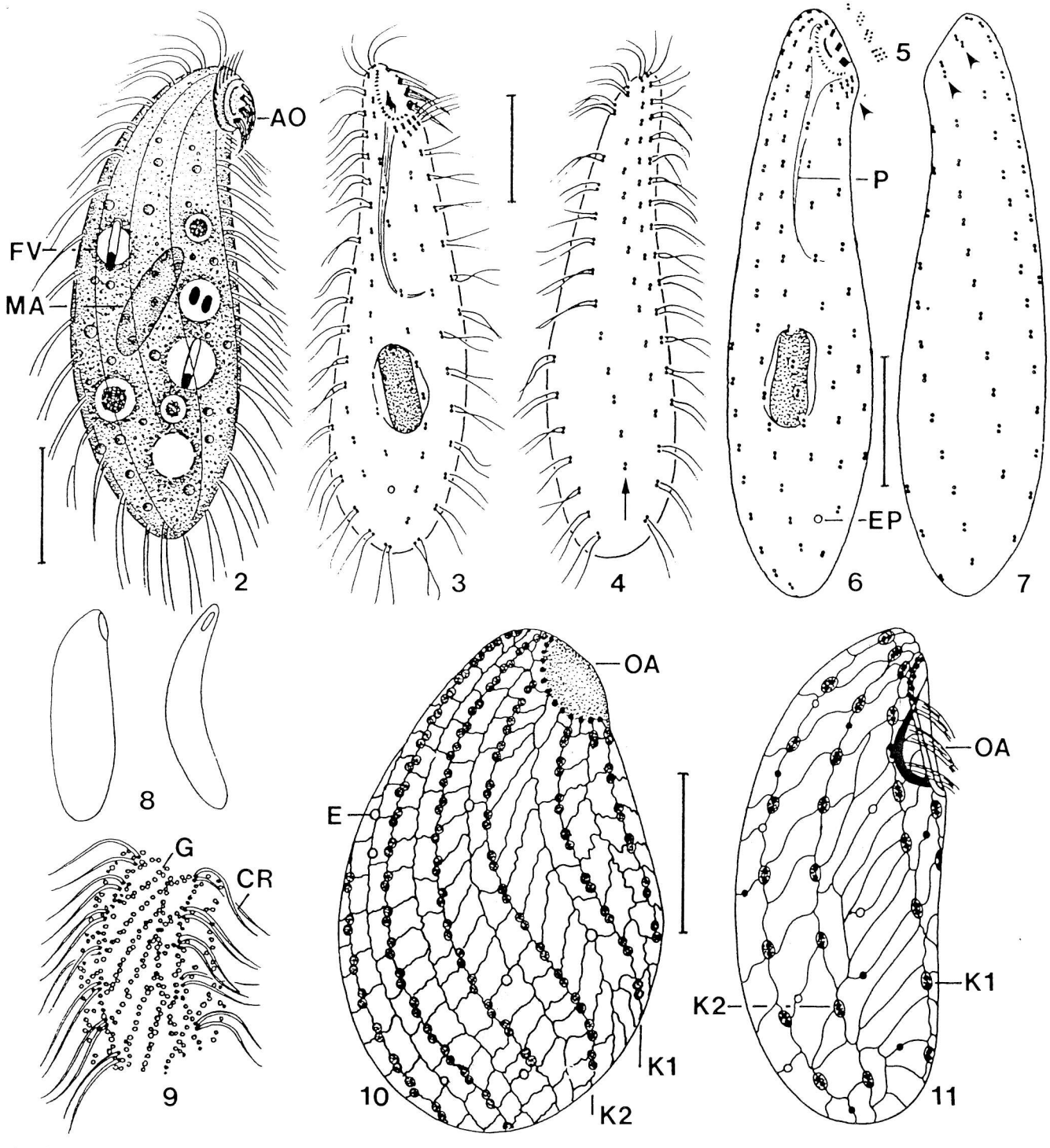
Table 5 Morphometric comparison of *Platyophrya paoletti*, *P. vorax*, *P. macrostoma*, and *P. hyalina*. Data from Foissner (1993), except those of *P. paoletti*. Mean values, if available, in brackets (? unknown)

Character	*P. paoletti*	*P. vorax*	*P. macrostoma*	*P. hyalina*
Length in vivo (μm)	32–50 (41)	30–80 (50)	25–35	36–45
Somatic kineties, number	8–9 (8)	9–13 (19)	9–10 (9)	~14
Paroral dikinetids, number	16–18 (17)	~15	9–13 (11)	?
Postoral pseudomembrane dikinetids, number	5 (5)	~10	5–7 (6)	~10
Adoral organelles, number	4 (4)	4 (4)	4 (4)	4–5

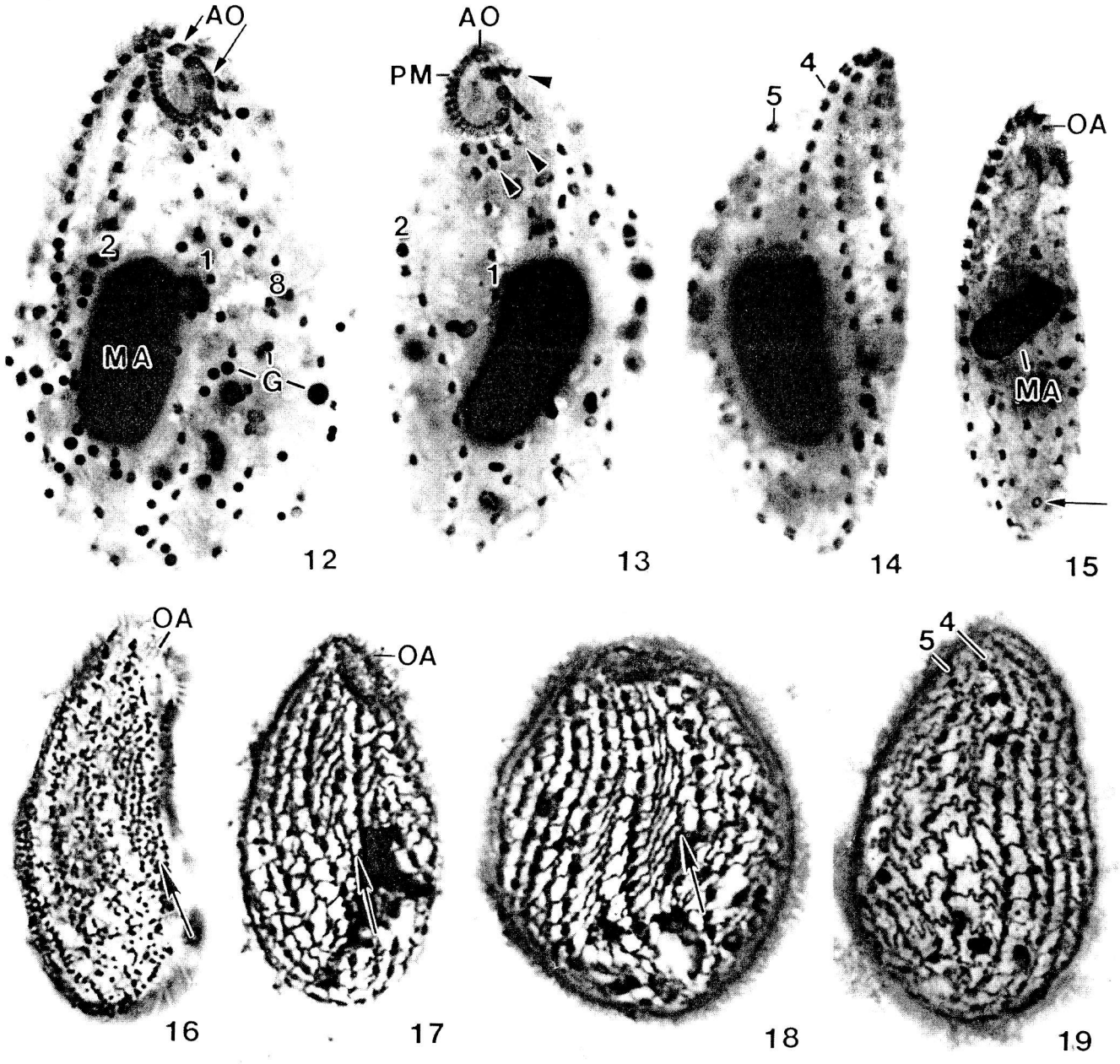
broadly reniform, dorsal margin slightly to distinctly convex, ventral somewhat sigmoidal, both ends narrowly rounded (Fig. 2). Macronucleus in body centre, in vivo distinctly ellipsoidal (Fig. 2), i.e. about 10 × 3 μm, usually more roundish (about 2:1) and covered by distinct, wrinkled membrane in protargol-impregnated cells (Table 4; Figs. 3, 6, 15), oriented parallel to broad body axis and thus roundish when cell is viewed ventrally; nucleoli inconspicuous because small (about 1 μm across) and transparent. Micronucleus neither recognizable in vivo nor after protargol impregnation or methyl green-pyronin staining. Contractile vacuole distinctly subterminal (Table 4) with one (two in 1 of 30 specimens investigated) excretory pore underneath end of kinety 3 (Figs. 2, 6, 15). Cortex colourless, rather distinctly furrowed by ciliary rows; cortical granules (mucocysts) colourless, in vivo about 0.3 μm across and arranged as silverlines (Fig. 9), stain red (Fig. 16) and are extruded after addition of methyl green-pyronin but do not form conspicuous envelope, frequently stained black by silver carbonate (Fig. 12). Cytoplasm colourless, rather hyaline, with some 1- to 2-μm fat globules mainly in posterior half and 2- to 5-μm food vacuoles containing bacilli. Swims and glides moderately fast on slide surface and soil particles.

Somatic cilia in vivo about 6 μm long, paired throughout except in middle kineties of left side, where anterior basal body frequently is barren. Ciliary rows slightly spirally arranged, composed of dikinetids, those on right and dorsal side more narrowly spaced and more densely ciliated than those on left and ventral side, kineties 3, 4 and 7 distinctly shortened posteriorly, distance between kineties 1 and 2 slightly enlarged (Figs. 2–7, 12–15; Table 4). Dikinetids of postoral pseudomembrane ciliated, three rightmost pairs on ventral side and narrowly spaced, those on left side widely spaced and separated by rather distinct break from somatic kineties (Figs. 3–7, 12, 13).

Oral apparatus subapical on ventral side, obliquely oriented to main body axis if cell is viewed laterally, minute, i.e. in vivo only 4–5 μm long. Paroral cilia in vivo about 4 μm long and not fused, form C-shaped membrane at left margin of rather distinct ridge, originate from narrowly and obliquely arranged dikinetids having very likely only one basal body ciliated. Adoral cilia in vivo about 4 μm long, curved backwards and almost immobile, grouped to four minute organelles having slightly different fine structures (Figs. 1, 3, 5, 6, 12, 13): anterior organelle composed of only two or four basal bodies and thus distinctly smaller than other adorals; middle organelles composed of two kineties with three basal bodies each; posterior organelle largest because consisting of three kineties with three basal bodies each, less obliquely oriented than other organelles. Oral opening slenderly reniform, right lip rather distinct, left merging into slightly deepened buccal cavity. Paroral and adoral kinetids associated with fine fibres forming long, narrow funnel recognizable only after protargol impregnation (Figs. 3, 6).



Figs. 2–11 *Platyophrya paoletti* (2–10) and *Pseudocyrtolophosis alpestris* (11) from life (2, 8, 9) and after protargol (3–7) and dry silver nitrate (10, 11) impregnation. **Fig. 2** Right lateral view of typical specimen containing food vacuoles with sporulating bacilli, spores of bacilli, and bacterial residues. Note distinctly ellipsoidal macronucleus (*MA*), the main species character. **Figs. 3, 4** Ciliary pattern of ventral and dorsal side of same specimen. *Arrow* marks shortened ciliary row 7. **Fig. 5** Likely fine structure of adoral organelles. **Figs. 6, 7** Ciliary pattern on right and left side of same specimen. *Arrowheads* mark dikinetids of postoral pseudomembrane. **Fig. 8** Shape variant in lateral and ventral view. **Fig. 9** Surface view showing arrangement of cortical granules (mucocysts) between ciliary rows 1 and 2 (cp. Fig. 16). **Figs. 10, 11** Silverline system of right side of *Platyophrya paoletti* and *Pseudocyrtolophosis alpestris* (from Foissner 1993). Note that distance between ciliary rows 1 and 2 (*K1*, *K2*) is slightly increased and silverlines extend more obliquely. Scale bars 10 µm [*AO* adoral organelles, *CR* ciliary row (kinety), *E* silverline surrounding extrusomes (cortical granules), *EP* excretory pore of contractile vacuole, *G* cortical granules, *K1*, *K2* kineties (ciliary rows) 1 and 2, *FV* food vacuole, *MA* macronucleus, *OA* oral apparatus, *P* pharynx]



Figs. 12–19 *Platyophrya paoletti* after silver carbonate impregnation (12–14), protargol impregnation (15), silver nitrate impregnation (17–19), and methyl green-pyronin staining (16). **Figs. 12–14** Heavily squashed specimens showing somatic and oral infraciliature (ciliary pattern) of ventral (12, 13) and dorsal (14) side. Note distinctly ellipsoidal macronucleus (*MA*), the main species character, and somatic cilia pairs (dikinetids), which are more closely spaced in the right (ciliary rows 1–4) than in the left (rows 5–8) lateral kineties. *Arrowheads* (13) denote dikinetids of postoral pseudomembrane. **Fig. 15** Right lateral view showing pore of contractile vacuole (*arrow*) and ellipsoidal macronucleus, the main species character. **Fig. 16** The cortical granules (very likely mucocysts) form strongly oblique rows between kineties 1 and 2 (*arrow*). **Figs. 17, 18** Silverline system of right and ventral side. *Arrows* mark elongated and strongly oblique silverlines between ciliary rows 1 and 2. **Fig. 19** Silverline system of dorsal side [*AO* adoral organelles, *G* cytoplasmic granules, *MA* macronucleus, *OA* oral apparatus, *PM* paroral (undulating) membrane, *1–8* ciliary rows (kineties)]

Silverline system similar to other members of genus (Foissner 1993). Silverlines between kineties 1 and 2, however, elongated and more obliquely arranged than those between other ciliary rows, producing highly characteristic, unique pattern (Figs. 10, 17–19).

Occurrence. As yet only found at type location.

Comparison with related species. Platyophyra paoletti differs from all congeners by its distinctly ellipsoidal macronucleus and the specialized silverline area between somatic kineties 1 and 2 (for detailed genus revision, see Foissner 1993). This area highly resembles that found in *Pseudocyrtolophosis* spp. (Fig. 11), suggesting a closer relationship between cyrtolophosidids and platyophryids

than supposed by Foissner (1993). The other features of *Platyophyra paoletti* are rather similar to those found in *P. vorax*, *P. macrostoma* and *P. hyalina*, though there are small differences in some morphometric characteristics (Table 5). Specifically, *P. paoletti* is slightly smaller than *P. vorax* and slightly larger than *P. macrostoma*. Indeed, it was this small difference which gave me the first indication that this population could be something special. A further difference concerns the number of dikinetids comprising the postoral pseudomembrane, which is distinctly lower in *P. paoletti* (5) than in *P. vorax* (10), but similar to that of *P. macrostoma* (6), whose oral apparatus, however, occupies the entire anterior end (Foissner 1993). Similar differences are found in the number of somatic kineties, while the number of adoral organelles is the same in all species (Table 5).

Lamtostyla abdita n. sp. (Figs. 20–24; Table 6)

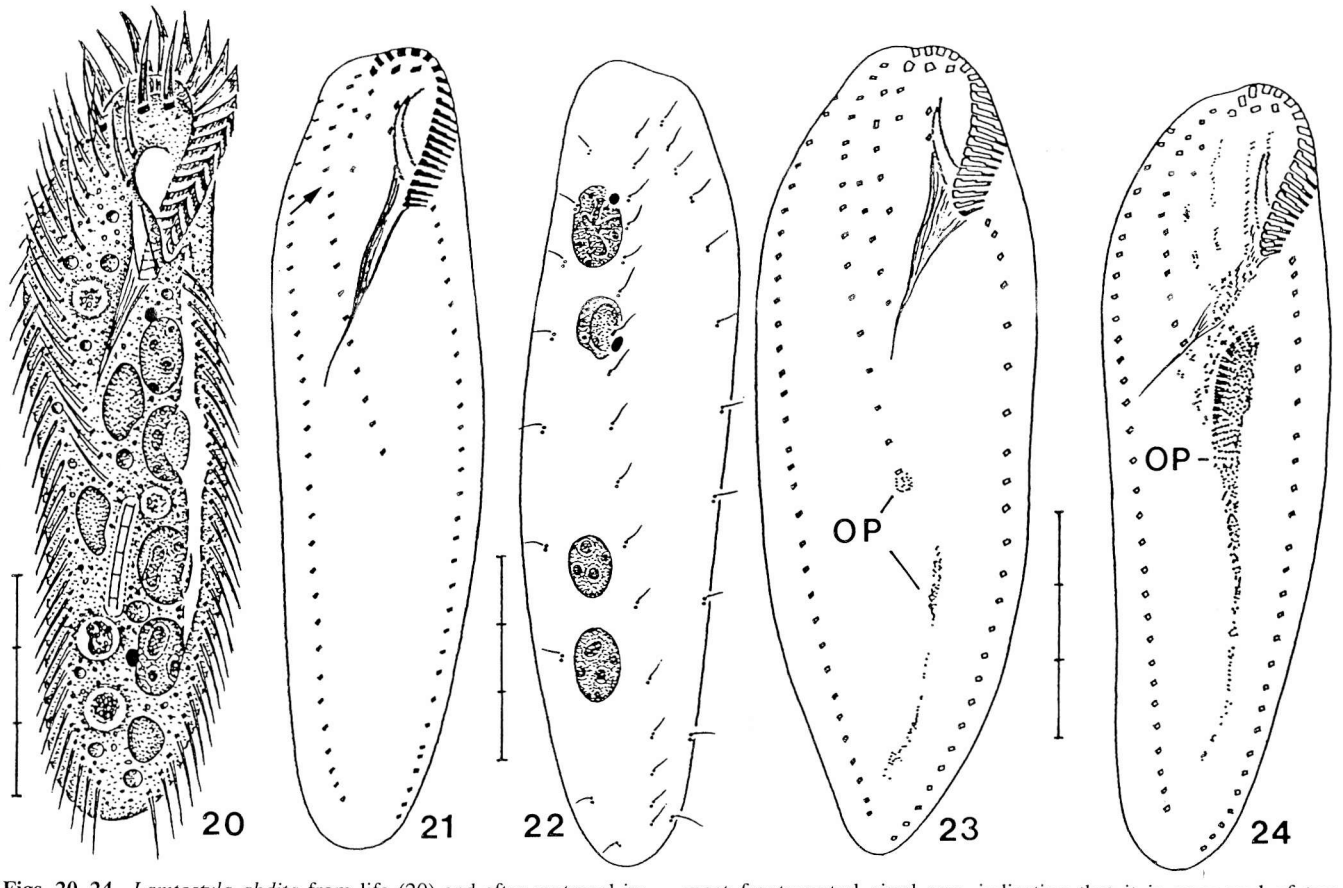
Diagnosis. Size in vivo about 100 × 25 µm. Slenderly elliptical and slightly sigmoidal. Usually four macronuclear nodules. Two short rows and one long row of frontoventral cirri extending far beyond adoral zone of membranelles. On average 19 adoral membranelles, 32 right and 28 left marginal cirri, 3 frontal cirri, 2 buccal cirri, 17 cirri in right frontoventral row, 3 cirri in middle frontoventral row, and 2 cirri in left frontoventral row. Three dorsal kineties.

Type location. Soil of rain forest near Cairns, Australia (about 145°E 17°S).

Table 6 Morphometric data from *Lamtostyla abdita* (*upper line*) and *L. granulifera* (*lower line*), based on protargol-impregnated and mounted specimens from raw cultures (for further explanations, see Table 4)

Character	$\bar{x}$	M	SD	SE	CV	Min	Max	*n*
Body length	97.9	97.0	10.1	2.5	10.3	80.0	117.0	17
	143.4	143.0	9.7	2.2	6.8	125.0	160.0	19
Body width	28.9	29.0	2.9	0.7	9.9	24.0	34.0	17
	64.5	65.0	9.0	2.1	14.0	49.0	80.0	19
Anterior somatic end to proximal end of adoral zone, distance	22.2	22.0	1.3	0.3	6.0	20.0	25.0	17
	41.0	40.0	2.2	0.5	5.3	38.0	46.0	19
Anterior somatic end to proximal end of rightmost ventral cirral row, distance	51.2	49.0	6.7	1.6	13.1	40.0	65.0	17
	38.5	38.0	3.4	0.8	8.7	33.0	48.0	19
Macronuclear nodules, length[a]	10.6	10.0	1.8	0.4	16.6	8.0	14.0	17
	24.5	25.0	2.2	0.5	9.1	21.0	28.0	19
Macronuclear nodules, width[a]	7.3	7.0	0.9	0.2	12.5	6.0	9.0	17
	9.1	9.0	0.9	0.2	10.1	7.0	10.0	19
Macronuclear nodules, number[b]	3.3	3.0	0.7	0.1	19.8	2.0	4.0	30
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
Micronuclei, largest diameter	2.2	2.0	–	–	–	2.0	3.0	17
	5.9	6.0	0.9	0.2	14.8	5.0	8.0	19
Micronuclei, number	2.2	2.0	–	–	–	2.0	3.0	17
	2.1	2.0	–	–	–	1.0	3.0	19
Adoral membranelles, number	19.6	19.0	1.1	0.3	5.4	18.0	22.0	17
	24.6	24.0	1.1	0.2	4.3	23.0	27.0	19
Right marginal cirri, number	32.4	32.0	2.1	0.5	6.5	30.0	37.0	17
	44.4	44.0	3.2	0.7	7.2	39.0	49.0	19
Left marginal cirri, number	27.8	28.0	3.7	0.9	13.3	22.0	34.0	17
	45.8	45.0	2.5	0.6	5.4	42.0	52.0	19
Anterior frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	17
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
Buccal cirri, number	1.5	2.0	–	–	–	1.0	2.0	17
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
Left ventral row, number of cirri	2.1	2.0	–	–	–	2.0	3.0	17
	–	–	–	–	–	–	–	–
Middle ventral row, number of cirri	3.4	3.0	0.8	0.2	23.3	2.0	5.0	17
	–	–	–	–	–	–	–	–
Right ventral row, number of cirri	17.5	17.0	1.7	0.4	9.9	14.0	21.0	17
	3.9	4.0	–	–	–	3.0	4.0	19
Cirri left of ventral row, number	–	–	–	–	–	–	–	–
	2.9	3.0	–	–	–	2.0	3.0	19
Pretransverse cirri, number	0.0	0.0	0.0	0.0	0.0	0.0	0.0	17
	1.9	2.0	–	–	–	1.0	2.0	19
Transverse cirri, number	0.0	0.0	0.0	0.0	0.0	0.0	0.0	30
	5.0	5.0	0.0	0.0	0.0	5.0	5.0	19
Dorsal kineties, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	17
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19

[a] Anterior macronuclear nodule of specimens with four nodules
[b] Dividing nuclei counted as one nodule



Figs. 20–24 *Lamtostyla abdita* from life (20) and after protargol impregnation (21–24). **Fig. 20** Ventral view of typical specimen. **Figs. 21, 22** Infraciliature (ciliary pattern) of ventral and dorsal side. Note lack of transverse and caudal cirri. *Arrow* marks small discontinuity in rightmost frontoventral cirral row, indicating that it is composed of two segments. **Figs. 23, 24** Ventral infraciliature of early dividers. The pattern is very similar to that found in congeners (Petz and Foissner 1996; Voß 1992). Scale bar division 10 μm [*OP* oral primordium]

Etymology. Abditus (lat.), concealed, distant from, referring to the interphase cirral pattern which would classify *L. abdita* in the genus *Orthoamphisiella*.

Description. Size in vivo 85–120 × 20–30 μm, dorsoventrally only slightly flattened, acontractile. Shape inconspicuous, slenderly elliptical and indistinctly sigmoidal, usually widest close underneath adoral zone and slightly narrowing posteriorly, both ends evenly rounded. Macronuclear nodules slightly ellipsoidal, with large nucleoli, arranged in two groups with two nodules each left of midline (Figs. 20, 22), second anterior nodule about same size (11 × 7 μm, n = 17) as anterior nodule (Table 6); number of nodules highly variable, very likely because many postdividers were contained in the slides, as indicated by the rather high proportion (~20%) of specimens having one or two dividing nuclei; thus, four nodules is very probably the usual number. Micronuclei globular, usually one in each macronuclear group. Contractile vacuole with two long collecting canals in mid-body near left margin of cell. Cortex flexible, colourless, without special granules. Cytoplasm without crystals, usually containing many small and large fat globules and food vacuoles with rod-shaped bacteria, small fungal hyphae, heterotrophic flagellates, and naked amoebae. Glides quickly on slide and soil particles.

Cirri about 12 μm long, very thin. Marginal rows open widely posteriorly, cirri rather evenly spaced. Long (rightmost) frontoventral row slightly curved, commences close to right of right frontal cirrus and extends obliquely to midline of cell, terminating near mid-body; frequently with small discontinuity in anterior third, indicating that it is composed of at least two fragments. Middle and left frontoventral rows very short, do not extend beyond adoral zone of membranelles. Transverse and caudal cirri lacking (Figs. 20, 21). Dorsal kineties almost as long as body, rather evenly spaced, middle row more densely ciliated than marginal rows (Fig. 22).

Adoral zone of membranelles conspicuously short, i.e. occupying only about 23% of body length, bases of largest membranelles in vivo about 7 μm wide. Buccal cavity rather conspicuous because deep and distinctly curved. Paroral and endoral membrane likewise curved and almost of same length, form wedge-shaped pattern because very near together anteriorly and widely separated posteriorly (Figs. 21, 23). Pharyngeal fibres conspicuous because long and numerous, extend obliquely backward.

Occurrence. As yet only found at two sites in the rain forest near Cairns, Australia (Table 2).

Comparison with related species and generic classification. Lamtostyla abdita differs from all congeners, which have two macronuclear nodules, by having four nodules and a long frontoventral cirral row extending far beyond the adoral zone of membranelles (Berger and Foissner 1988; Petz and Foissner 1996). Thus, it highly resembles some species formerly or presently assigned to the genera *Amphisiella* and *Orthoamphisiella*. *Lamtostyla abdita* differs from *Amphisiella* spp. by the lack of transverse cirri; and the possession of three dorsal kineties distinguishes it clearly from *Orthoamphisiella* spp., which have two (Eigner and Foissner 1993).

The new species belongs, according to its ventral interphase morphology, to the genus *Orthoamphisiella*, because it has two short rows of frontoventral cirri left of a long frontoventral row and lacks transverse and caudal cirri. However, two dividers (Figs. 23, 24) showed that the long frontoventral row does not originate by within-row proliferation, as in *Amphisiella* and *Orthoamphisiella* (Eigner and Foissner 1993), but forms an anlage at its posterior end, as is typical for *Lamtostyla* (Petz and Foissner 1996; Voß 1992). All *Lamtostyla* and *Amphisiella* species have transverse cirri, and thus *L. abdita*, which lacks such cirri, could even be considered as representative of a new genus. However, several *Lamtostyla* and *Amphisiella* species have a reduced number (2–4) of transverse cirri, indicating that this character should not be over-interpreted, i.e. used only in connection with other differential characters.

Lamtostyla granulifera n. sp. (Figs. 25–38; Table 6)

Diagnosis. Size in vivo about 150 × 35 μm. Slenderly elliptical and often slightly curved. Two macronuclear nodules. Cortical granules colourless, usually 1–2 μm across and arranged in conspicuous, narrowly spaced rows on ventral and dorsal side. Frontal cirral row about as long as adoral zone of membranelles, usually consisting of four cirri. Adoral zone continuous, proximal portion broadened spoon-like, consists of 24 membranelles on average. Buccal cavity deep and distinctly curved. On average 44 right and 45 left marginal cirri, 3 frontal cirri, 1 buccal cirrus, 2 pretransverse cirri, 5 transverse cirri, 3 cirri left of frontal row, and 3 dorsal kineties.

Type location. Field (Mahada) soil from the farm of Don Pedro Cortez, El Sapo village, about 50 km north of Puerto Ayacucho, Venezuela, South America (about 68°W 5°N).

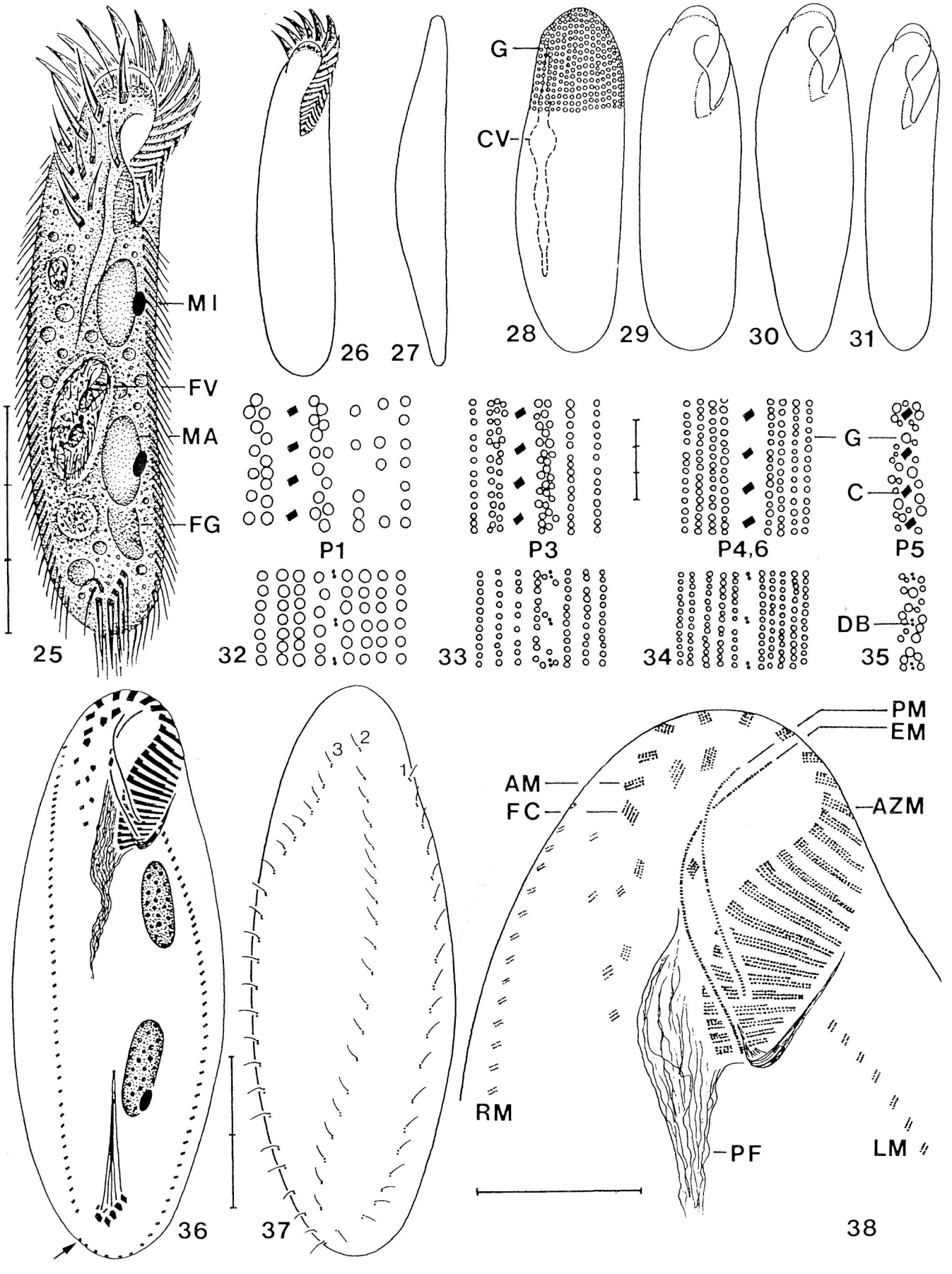
Etymology. Granulifera (bearing granules) refers to the conspicuous cortical granules.

Description. Seven populations were studied in vivo, usuable silver slides were obtained only from the Venezulean population, which is thus type. Specimens from all populations burst when conventional fixatives were applied; and even in fixatives containing osmium tetroxide few specimens maintained integrity. Only the rich population from a field near Puerto Ayacucho provided, after fixation in Stieve's solution mixed with 2% osmium tetroxide (3:1), sufficient specimens for a detailed analysis (Table 6). The reason for the extreme fragility of *L. granulifera* under various fixatives is not known and surprising because live specimens are rather robust and even withstand slight cover glass pressure.

The following description is based mainly on the type population from Venezuela. The in vivo observations largely agree for all populations and are thus combined where appropriate. However, the population from Cape Town (South Africa) might be a distinct (sub)species because it is markedly more slender (about 200 × 30 μm) and has the cortical granules (0.5–2 μm, colourless) arranged only around the cirral and bristle bases. The infraciliature matches, according to the live observations, that of the type population.

Size in vivo 120–170 × 20–55 μm, usually about 150 × 36 μm (n = 10), length: width ratio highly variable, viz. 3.5:1 to 6:1, dorsoventrally flattened up to 2:1, very flexible; prepared specimens usually broader (from 2:1 to 4:1) due to poor fixation (Table 6). Slenderly to rather broadly elliptical, often almost parallel-sided and slightly curved, widest usually in or near mid-body, both ends evenly rounded (Figs. 25–27); Thailand population and one Australian population slightly wedge-shaped because somewhat narrowed posteriorly (Fig. 30). Yellowish to brownish at low magnification (≤100), possibly due to dense cortical granulation and/or cytoplasmic inclusions. Macronuclear nodules in central body portion slightly left of midline, distinctly ellipsoidal (from 2:1 to 3:1), with many tiny nucleoli. Micronuclei in small indentation of macronuclear nodules, conspicuous because large, compact, and distinctly ellipsoidal (5–8 × 3–4 μm, $\bar{x}$ = 5.9 × 3.3, length: wide ratio from 1.5 to 3:1; Figs. 25, 36). Contractile vacuole with two lacunar collecting canals distinctly above mid-body near left margin of cell. Cortical granules (Figs. 28, 32–35) colourless, rather hyaline and bright, conspicuous because 1–4 μm (usually 1–2 μm) across and in narrowly spaced rows leaving blank only cirri and dorsal bristles (except for South African population,

Figs. 25–38 *Lamtostyla granulifera* from life (25–35) and after protargol impregnation (36–38). **Fig. 25** Ventral view of typical specimen with a large food vacuole (*FV*) containing a hypotrichous ciliate. **Figs. 26, 27** Ventral and lateral view of saccular shape variant. **Figs. 28–31** Shape variants from several populations. **Figs. 32–35** Arrangement and size of cortical granules in ventral (upper series) and dorsal (lower series) side of populations (*P*) 1, 3–6, drawn to scale. **Figs. 36, 37** Infraciliature (cirral pattern) of ventral and dorsal side of type population. Note that the left marginal row curves around the organism's posterior end (*arrow*). Numbers denote dorsal kineties. **Fig. 38** Infraciliature of anterior ventral portion at higher magnification. Scale bar division 20 μm (Figs. 25, 36–38) and 10 μm (Figs. 32–35) [*AM* distalmost adoral membranelle, *AZM* adoral zone of membranelles, *C* cirrus, *CV* contractile vacuole, *DB* dorsal bristle, *EM* endoral membrane, *FC* right frontal cirrus, *FG* fat globule, *FV* food vacuole, *G* cortical granules, *LM* left marginal row, *MA* macronuclear nodule, *MI* micronucleus, *PF* pharyngeal fibres, *PM* paroral membrane, *P 1–6* populations 1–6, *RM* right marginal row]


MI
FV
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1
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PM
EM
AM
FC
AZM
RM
PF
LM
38

see above and Fig. 35); found not only in somatic but also in buccal cortex and around cytopharynx; usually disappear (burst; become extruded?) when cells are slightly squeezed between slide and cover glass; do not stain with methyl green-pyronin, in protargol preparations occasionally appearing as dark, tiny (<0.3 μm) dots. Cytoplasm usually packed with 1- to 15-μm globular and irregularly shaped fat inclusions and food vacuoles containing naked amoebae, heterotrophic flagellates, and ciliates (*Cyclidium muscorum*, *Leptopharynx costatus*, *Drepanomonas* sp., *Oxytricha setigera*), which are ingested whole, and remain moving for some time in the food vacuoles (Fig. 25). Movement conspicuous because glide fast to and fro, frequently changing direction.

Marginal cirri in vivo about 12 μm long, composed of two kineties with from five to seven cilia each (Fig. 38). Left marginal row conspicuous because extending around posterior body margin, its rightmost cirri thus easily mistaken as caudal cirri; right marginal row commences at level of rightmost frontal cirrus and terminates near transverse cirri, thus being separated from left marginal row by small but distinct break (Figs. 25, 36). Anterior frontal cirri distinctly enlarged, composed of four or five kineties each, shape rather variable, rightmost cirrus occasionally difficult to identify because close to distalmost adoral membranelle (Figs. 25, 36). Buccal cirrus close to summit of curve formed by paroral membrane, composed of four kineties with about five cilia each (Fig. 38). Frontal cirral row short, extends slightly obliquely between rightmost frontal cirrus and proximal end of adoral zone of membranelles, usually composed of four cirri (Table 6), anterior pair consists, like marginal cirri, of two kineties with about five cilia each, posterior two cirri composed of three kineties with about five cilia each (Fig. 38). Usually three cirri left of frontal row in triangular pattern, each composed of three kineties with from four to six cilia each (Figs. 36, 38). Transverse cirri distinctly enlarged, in vivo about 20 μm long and projecting above posterior body margin, associated with long fibres extending to mid-body forming conspicuous, wedge-shaped bundle (Figs. 25, 36). Pretransverse ventral cirri easily identified because distinctly smaller than transverse cirri and invariably close to rightmost two transverse cirri (Fig. 36).

Dorsal cilia (bristles) in vivo 3–4 μm long, arranged in three rows almost as long as body. Rows 1 and 2 extend in slightly oblique bows from anterior right half to posterior left half of body; row 3 commences near midline of cell and extends by a short, sharp bow to left body margin, where it continues as straight line to posterior body end. Thus, a large, elliptical, barren area is formed between kineties 2 and 3. No caudal cirri (Fig. 37).

Adoral zone of membranelles provides cells with bushy appearance because occupying only about 28% of body length (Table 6) and spoon-like broadening of proximal half, with bases of largest membranelles about 12 μm wide and of conventional fine structure (Figs. 25, 26, 38); proximal quarter covered by buccal lip and undulating membranes (Figs. 25, 38). Buccal cavity deep but rather narrow, distinctly curved anteriorly, posterior half covered by bay-like projecting buccal lip (Fig. 25). Undulating membranes distinctly curved, both very likely composed of narrowly spaced dikinetids and optically intersecting in anterior third. Paroral distinctly shorter than endoral, which terminates near proximal end of adoral zone of membranelles. Paroral cilia in vivo about 15 μm long, endoral cilia about 40 μm (!) long, beating wave-like into conspicuously large, conical pharynx supported by fine fibres (Figs. 25, 36, 38).

Occurrence and ecology. Over the years, I have found seven populations of *L. granulifera* in terrestrial habitats from widely distant regions, indicating that is has a broad ecological and geographical range. However, I have never found it in Europe, and most populations were small, appearing about 1 week after rewetting of the sample and disappearing in the 2nd week, indicating that *L. granulifera* is more r- than K-selected. Population 1: Australia, vicinity of Cairns; thick bark from a tree at rain forest site 2; pH 4.6. Population 2: Australia, near Darwin, entrance to Foog Dam; litter and soil (0–5 cm) from a young *Eucalyptus* forest; pH 4.9. Population 3: Japan, near Tokyo, at base of "female" Tsukuba mountain; litter, roots and brown soil (0–5 cm) from mixed forest with bamboo and *Pinus* sp. Population 4: Thailand, Phuket peninsula, coastal rain forest near Kata Karon town; deciduous litter and redbrown soil; pH 6.4. Population 5: Republic of South Africa, Botanical Garden of Cape Town (Kirstenbosch); litter with much fungal hyphae and upper (0–5 cm) very sandy soil layer from secondary mixed (rain) forest (*Pinus* sp., deciduous trees) near bank of Skeleton River at base of Table Mountain; pH 6.7. Population 6: as described in type location; the Mahada (field) was 3 years old and planted with bananas and maniok; soil spongy, strongly enriched with organic material (mainly cow dung), light brown, many fine roots from grass cover; pH 6.5. Population 7: Brazil, Ilha de Marchantaria, an island in the Rio Solimões near Manaus, material from a termite (*Anoplotermes* sp.) hill.

Comparison with related species. The interphase morphology of *L. granulifera* perfectly matches the genus diagnosis given by Berger and Foissner (1988). It differs from the congeners by the large size, the distinct cortical granules, the spoon-shaped adoral zone of membranelles, and the conspicuous, *Cyrtohymena*-like buccal cavity. The fronto-ventral-transverse cirral pattern is identical to that of *L. longa*, a large-sized (85–130 × 35–50 μm) species too, which, however, has an inconspicuous buccal cavity and adoral zone of membranelles, and possibly lacks cortical granules.

Lamtostyla granulifera highly resembles *Tachysoma raptans* Hemberger 1985, especially in the cirral pattern, the nuclear apparatus, and the spoon-like broadening of the adoral zone of membranelles. Thus, I transfer Hemberger's species to *Lamtostyla*: *L. raptans* (Hemberger 1985) nov. comb. It differs from *L. granulifera* by its large size (prepared specimens 200 × 40 μm), the higher number of adoral membranelles (33), marginal cirri (about 60) and dorsal kineties (5)

and, possibly, by the lack of cortical granules. However, such granules might have been overlooked by Hemberger, who did not study live specimens in detail.

Apoamphisiella n. gen.

Diagnosis. Amphisiellidae (?) with two long ventral cirral rows, a short, oblique row of transverse cirri and at least one cirrus left of anterior end of ventral rows. Postperistomial and caudal cirri present. With dorsomarginal kineties producing irregular field of dorsal bristles near left anterior end. Both ventral rows participate in anlagen formation during ontogenesis, and the postperistomial cirrus obtains its characteristic position by distinct anlagen migration during cytokinesis.

Type species. Apoamphisiella tihanyiensis (Géllert and Tamás 1958) n. comb. (basionym: *Onychodromopsis tihanyiensis* Géllert and Tamás 1958).

Etymology. Composite of *apo* (derived from) and *Amphisiella*. Feminine gender.

Comparison with related genera. Very recently, I discovered *Apoamphisiella tihanyiensis* in Brazilian freshwaters and could study its ontogenesis in pure cultures. A preliminary analysis of the slides showed that both ventral rows develop cirral anlagen and the parental ventral infraciliature is completely resorbed. Thus, *Apoamphisiella* lacks a neokinetal wave as defined by Eigner (1995), i.e. does not belong to the Kahliellidae. This is essential with respect to the genus *Parentocirrus* Voß 1997, whose interphase cirral pattern highly resembles that of *A. tihanyiensis*. However, *Parentocirrus hortualis* has a neokinetal wave, i.e. the right ventral cirral row does not participate in anlagen formation but is generated by the left row.

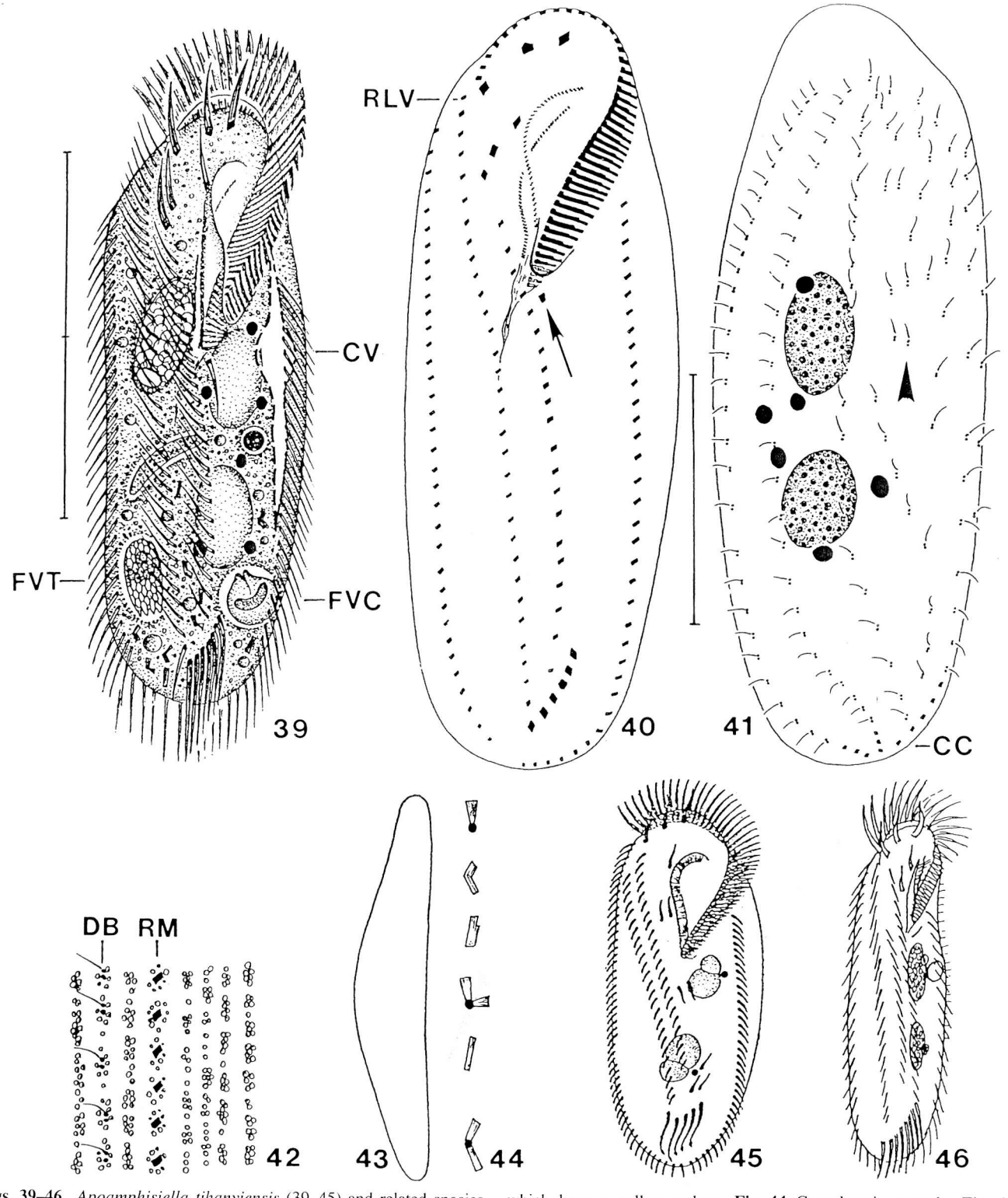
The final classification of *A. tihanyiensis* must await a more detailed analysis of the preparations. However, it is evident that it belongs neither to the Kahliellidae, as explained above, nor to *Onychodromopsis*, as suggested by Géllert and Tamás (1958), which has a typical oxytrichid ontogenesis and interphase morphology, i.e. six anlagen from which 18 fronto-ventral-transverse cirri originate (Petz and Foissner 1996). Very likely, *Apoamphisiella* belongs to or is near the Amphisiellidae, as indicated by the highly characteristic postperistomial cirrus. Within this family, *A. tihanyiensis* resembles the genus *Pseudoureoleptus* Hemberger 1985, which, however, has a long, vertical row of transverse cirri (Eigner and Foissner 1994), distinctly different from the short, oblique transverse cirral row found in *A. tihanyiensis*. Furthermore, *Pseudoureoleptus caudatus* Hemberger 1985 has a simple dorsal infraciliature (Hemberger 1982), i.e. lacks dorsomarginal kineties, which are present in *A. tihanyiensis* and responsible for the formation of a field of scattered dorsal bristles near the anterior left end of the organism (Fig. 41).

Apoamphisiella tihanyiensis (Géllert and Tamás 1958) n. comb. (Figs. 39–46, 47–50; Table 7).

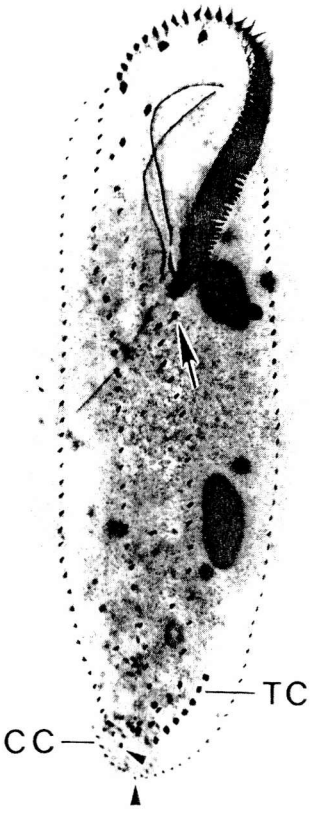
This species occurred in a soil sample from the Amazonian rain forest near the town of Iquitos, Peru, about 47°W, 4°S. It is very similar to the European type population and to two freshwater populations, which I found in

Table 7 Morphometric data from *Apoamphisiella tihanyiensis* (for further explanations, see Table 4)

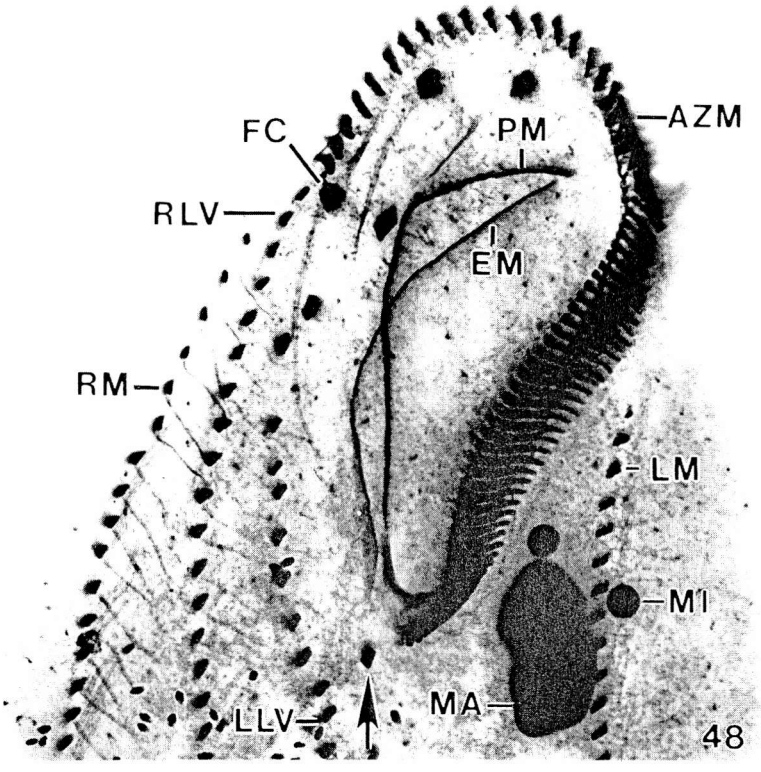
Character	$\bar{x}$	M	SD	SE	CV	Min	Max	*n*
Body length	163.1	160.0	13.8	4.2	8.5	147.0	190.0	11
Body width	62.6	65.0	8.8	2.6	14.0	47.0	76.0	11
Anterior somatic end to proximal end of adoral zone, distance	60.8	62.0	4.1	1.2	6.7	55.0	65.0	11
Anterior somatic end to right ventral row, distance	20.2	21.0	2.0	0.6	10.1	15.0	22.0	11
Anterior somatic end to left ventral row, distance	41.6	41.0	1.9	0.7	4.5	40.0	45.0	11
Macronuclear nodules, length	26.4	27.0	2.2	0.7	8.5	23.0	30.0	11
Macronuclear nodules, width	13.0	13.0	1.9	0.6	14.6	10.0	15.0	11
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
Micronuclei, length	4.0	4.0	0.0	0.0	0.0	4.0	4.0	11
Micronuclei, width	3.7	4.0	–	–	–	3.5	4.0	11
Micronuclei, number	6.1	6.0	1.3	0.4	21.4	4.0	8.0	11
Adoral membranelles, number	56.5	58.0	3.3	1.0	5.8	52.0	62.0	11
Right marginal cirri, number	35.4	35.0	4.2	1.3	11.9	28.0	43.0	11
Left marginal cirri, number	38.4	38.0	2.8	0.8	7.2	33.0	43.0	11
Right ventral row, number of cirri	33.4	34.0	2.9	0.9	8.6	27.0	37.0	11
Left ventral row, number of cirri	24.2	24.0	1.9	0.6	8.0	21.0	27.0	11
Anterior frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
Cirri left of ventral rows, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
Postperistomial cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
Transverse cirri, number	6.6	7.0	0.8	0.3	12.5	5.0	8.0	11
Caudal cirri, number	10.0	11.0	3.3	1.0	32.9	3.0	14.0	11
Unfragmented dorsal kineties, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11



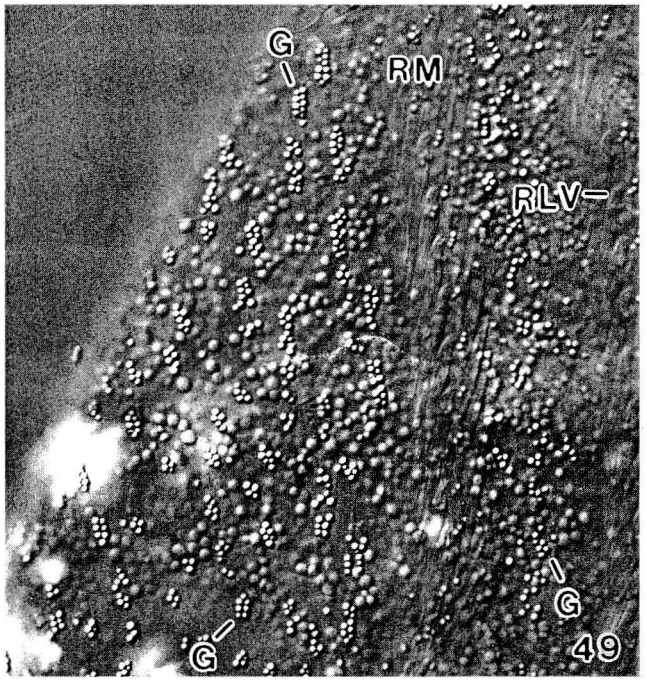
Figs. 39–46 *Apoamphisiella tihanyiensis* (39–45) and related species (46) from life (39, 42–44, 46) and after protargol impregnation (40, 41). **Figs. 39, 43** Ventral and lateral view of typical specimen with many food vacuoles containing testate amoebae, ciliates, and fungal spores. **Figs. 40, 41** Infraciliature (cirral pattern) of ventral and dorsal side. *Arrow* marks postperistomial cirrus, which indicates that *A. tihanyiensis* belongs to the Amphisiellidae; *arrowhead* marks field of disorganized dorsal bristles. **Fig. 42** Arrangement of cortical granules, which have a yellow colour. **Fig. 44** Cytoplasmic crystals. **Fig. 45** Original figure of *A. tihanyiensis*, opal blue preparation, length 220 µm (from Géllert and Tamás 1958). **Fig. 46** *Trichototaxis fossicola*, a species possibly related to *A. tihanyiensis*, length 200 µm (from Kahl 1932). Scale bar division 50 µm [*CC* caudal cirri, *DB* dorsal bristles, *CV* contractile vacuole, *FVC* food vacuole with a ciliate, *FVT* food vacuole with a testate amoeba, *RLV* right long ventral row, *RM* right marginal row]



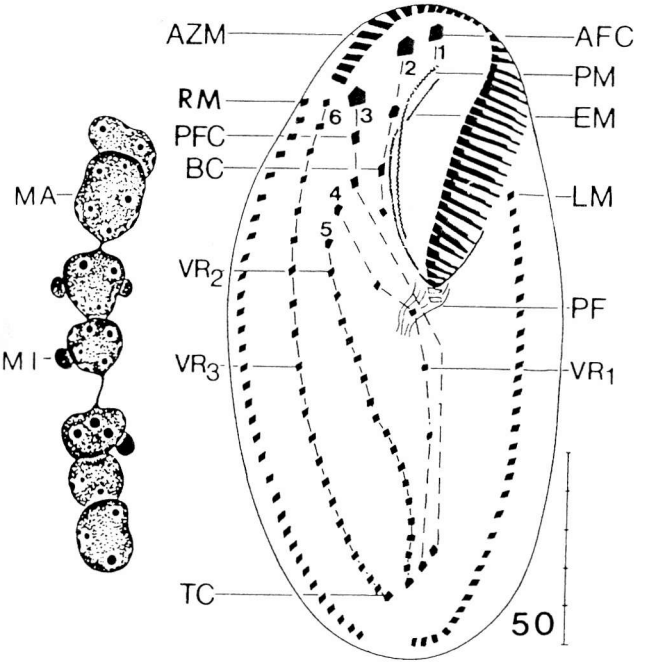
47



48



49



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Figs. 47–50 *Apoamphisiella tihanyiensis* and *Parentocirrus hortualis* (50; from Voß 1997) from life (49) and after protargol impregnation (47, 48, 50). **Figs. 47, 48, 50** Infraciliature (cirral pattern) of ventral side. *Arrows* mark postperistomial cirrus; *arrowheads* denote end of marginal rows. **Fig. 49** Surface view showing cortical granules, which are yellow and compact and thus bright in interference contrast. Scale bar division 10 µm [*AFC* anterior frontal cirri, *AZM* adoral zone of membranelles, *BC* buccal cirrus(i), *CC* caudal cirri, *EM* endoral membrane, *FC* rightmost frontal cirrus, *G* cortical granules, *LLV* left long ventral row, *LM* left marginal row, *MA* macronucleus, *MI* micronucleus, *PF* pharyngeal fibres, *PFC* posterior frontal cirri, *PM* paroral membrane, *RLV* right long ventral row, *RM* right marginal row, *TC* transverse cirri, VR_{1-3} ventral cirral rows, *1–6* anlagen during ontogenesis]

Rio de Janeiro and Praia do Forte, Brazil. No type material from *Onychodromopsis tihanyiensis* has been mentioned in the literature. Thus, I declare the population from Peru as a neotype and have deposited two slides with protargol-impregnated specimens in the Oberösterreichische Landesmuseum in Linz, Austria.

Redescription. Size in vivo 150–210 × 50–80 µm, dorsoventrally flattened up to 2:1, very flexible but acontractile. Elliptical, both ends broadly rounded, right margin almost straight, left slightly convex (Fig. 39). Distinctly yellowish at low magnification (≤ × 100) due to cortical granules. Macronuclear nodules rather close together in central third of body slightly left of midline, ellipsoidal (about 2:1), with many 0.5- to 2-µm nucleoli. On average six spherical to slightly ellipsoidal micronuclei close to macronuclear nodules, compact and thus easy to recognize in vivo (Figs. 39, 41). Contractile vacuole distinctly above midbody, with two lacunar collecting canals. Cortical granules 0.5–1 µm across, conspicuous because brightly citrine, as, for example, in *Holosticha multistilata*, arranged in rather widely spaced, longitudinal stripes, including cirral and bristle rows (Figs. 42, 49); do not stain with protargol. Cytoplasm colourless, with many 2- to 4-µm, yellowish crystals (Fig. 44) and food vacuoles containing coccal cyanobacteria, fungal spores and hyphae, heterotrophic flagellates, naked amoebae, testate amoebae (*Tracheleuglypha* sp., *Trinema lineare*, *Euglypha rotunda*, *E. compressa*), ciliates (*Blepharisma hyalinum*, *Vorticella* swarmers), and even cysts or eggs of gastrotrichs. Glides quickly on slide and on soil particles.

Marginal cirri in vivo about 25 µm long, become gradually thinner posteriorly. Left marginal row conspicuous because extending around posterior body margin, the rightmost cirri thus being easily confused with caudal cirri; right marginal row commences subapically at level of buccal cirrus and terminates near rightmost transverse cirrus, thus being separated from left marginal row by small but distinct break (Figs. 40, 47). Anterior frontal cirri distinctly enlarged, in vivo about 20 µm long, rightmost cirrus close to distal end of adoral zone of membranelles. Cirri left of anterior end of right ventral row and postperistomial cirrus slightly enlarged. Cirri of ventral rows in vivo about 15 µm long, right row almost as long as body, extends slightly obliquely between right anterior end and transverse cirral row, posteriormost cirrus slightly enlarged and thus possibly belonging to transverse cirri; left ventral row in parallel with right but distinctly separate, conspicuously shortened anteriorly, extends, like right row, to transverse cirri. Transverse cirri distinctly enlarged, in vivo about 30 µm long and with frayed distal end, project above posterior body margin, form slightly curved, oblique row left of midline (Figs. 39, 40, 47, 48).

Dorsal cilia (bristles) in vivo about 3 µm long, arranged in five or six rows, of which the left two or three are rather distinctly disordered anteriorly, forming conspicuous field of scattered bristles; right three rows almost as long as body and sharply curved posteriorly, extending to and above cell midline (Fig. 41). Ten caudal cirri on average associated with the two rightmost kineties and one of the fragmented left rows (Table 7; Figs. 41, 47).

Oral apparatus conspicuous, with strong resemblance to that of cyrtohymenid oxytrichids because of its large size, deep buccal cavity, and curved undulating membrane (Figs. 39, 40, 47, 48). Adoral zone of membranelles occupies about 37% of body length, proximal half slightly spoon-like broadened with bases of largest membranelles about 12 µm wide and of conventional fine structure; proximal end covered by buccal lip. Buccal cavity moderately wide but deep and semicircularly curved anteriorly, posterior half covered by bay-like projecting buccal lip (Figs. 39, 40, 47, 48). Undulating membranes distinctly curved, especially paroral, both very likely composed of narrowly spaced dikinetids; endoral optically intersects paroral in mid-portion and traverses buccal cavity, forming bow-string to strongly curved anterior portion of paroral (Figs. 40, 47, 48). Pharyngeal fibres short, inconspicuous.

Comparison with original description and related species. Most main characteristics of my population match Figure 45 and description of *Onychodromopsis tihanyiensis* Géllert and Tamás (1958): "Size 220 µm. Shape regular-ellipsoidal. The adoral zone consists of 50 membranelles. Peristomial lip strongly curved anteriorly. 3 single, enlarged cirri on frontal field and 1 cirrus near oral lip. Ventral cirri in 4 groups (2-2-1-2) and, additionally, two uninterrupted ventral cirral rows. Marginal rows confluent posteriorly. 5 transverse cirri which extend above body margin and have frayed ends. 2 macronuclear nodules with distinct reorganization bands. 2 micronuclei. Feeds on diatoms and small ciliates. Found in drift material on shore of Balaton Lake." There are, however, also differences which could justify considering my population as a new species, the most conspicuous being the yellowish colour due to the cortical granules. However, Géllert and Tamás (1958) very likely did not make careful live observations, but studied mainly specimens prepared with opal blue. Thus, they might simply have overlooked the cortical granules. There are also several differences in the cirral pattern, the most important being the two (one in my population) postoral ventral cirri and the left ventral row, which is distinctly shortened in my specimens (Figs. 39, 40, 45). As with the cortical granules, I tend to interpret these differences as being a result of the different methodology used by Géllert and Tamás (1958). This is supported by the notion of Géllert and Tamás that the marginal cirral rows are confluent posteriorly, a misobservation obviously caused by the caudal cirri, which Géllert and Tamás (1958) did not recognize. My identification is also supported by observations on the freshwater populations from Brazil mentioned above. These specimens are slightly larger (up to 250 µm), their cortical granules are less distinctly yellowish, and some have two postperistomial cirri.

Parentocirrus hortualis Voß 1997 strongly resembles *Apoamphisiella tihanyiensis* but has 6–12 macronuclear nodules and only three or four caudal cirri. Furthermore, it lacks cortical granules and has more cirri left of the left ventral row. Another species rather similar to my popula-

tions is *Trichototaxis fossicola* (Kahl 1932) which, however, has an inconspicuous buccal field and three ventral cirral rows (Fig. 46).

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References

Bamforth SS, Lousier JD (1995) Protozoa in tropical litter decomposition. In: Reddy MV (ed) Soil organisms and litter decomposition in the tropics. Oxford & IBH, New Delhi, pp 59–73

Beck L, Höfer H, Martius C, Römbke J, Verhaagh M (1997) Bodenbiologie tropischer Regenwälder. Geogr Rundsch 49:24–31

Berger H, Foissner W (1988) Revision of *Lamtostyla* Buitkamp, 1977 and description of *Territricha* nov. gen. (Ciliophora: Hypotrichida). Zool Anz 220:113–134

Bick H (1989) Ökologie. Fischer, Stuttgart

Bovee EC (1957) Protozoa of Amazonian and Andean waters of Colombia, South America. J Protozool 4:63–66

Bridgewater PB (1987) The present Australian environment – terrestrial and freshwater. In: Dyne GR (ed) Fauna of Australia, vol 1A. Australian Government Publishing Service, Canberra, pp 69–100

Dingfelder JH (1962) Die Ciliaten vorübergehender Gewässer. Arch Protistenk 105:509–658

Eigner P (1995) Divisional morphogenesis in *Deviata abbrevescens* nov. gen., nov. spec., *Neogeneia hortualis* nov. gen., nov. spec., and *Kahliella simplex* (Horváth) Corliss and redefinition of the Kahliellidae (Ciliophora, Hypotrichida). Europ J Protistol 31:341–366

Eigner P, Foissner W (1993) Divisional morphogenesis in *Orthoamphisiella stramenticola* Eigner & Foissner, 1991 and *O. grelli* nov. spec. (Ciliophora, Hypotrichida). Arch Protistenk 143:337–345

Eigner P, Foissner W (1994) Divisional morphogenesis in *Amphisiellides illuvialis* n. sp., *Paramphisiella caudata* (Hemberger) and *Hemiamphisiella terricola* Foissner, and redefinition of the Amphisiellidae (Ciliophora, Hypotrichida). J Euk Microbiol 41:243–261

Emmerich K-H (1997) Decksedimente in den Tropen. Geogr Rundsch 49:18–23

Fenchel T (1969) The ecology of marine microbenthos IV. Structure and function of the benthic ecosystem, its chemical and physical factors and the microfauna communities with special reference to the ciliated protozoa. Ophelia 6:1–182

Foissner W (1980) Artenbestand und Struktur der Ciliatenzönose in alpinen Kleingewässern (Hohe Tauern, Österreich). Arch Protistenk 123:99–126

Foissner W (1981) Die Gemeinschaftsstruktur der Ciliatenzönose in alpinen Böden (Hohe Tauern, Österreich) und Grundlagen für eine Synökologie der terricolen Ciliaten (Protozoa, Ciliophora). Veröff Österr MaB-Programms 4:7–52

Foissner W (1987) Soil protozoa: fundamental problems, ecological significance, adaptations in ciliates and testaceans, bioindicators, and guide to the literature. Progr Protistol 2:69–212

Foissner W (1991) Basic light and scanning electron microscopic methods for taxonomic studies of ciliated protozoa. Europ J Protistol 27:313–330

Foissner W (1992) Estimating the species richness of soil protozoa using the "non-flooded Petri dish method". In: Lee JJ, Soldo AT (eds) Protocols in protozoology. Society of Protozoologists. Allen Press, Lawrence, Kansas, pp B101–B102

Foissner W (1993) Colpodea (Ciliophora). Fischer, Stuttgart

Foissner W (1995) 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. Arch Protistenk 145:37–79

Foissner W (1997a) Global soil ciliate (Protozoa, Ciliophora) diversity: a probability-based approach using large sample collections from Africa, Australia and Antarctica. Biodiv Conserv (in press)

Foissner W (1997b) An updated compilation of world soil ciliates (Protozoa, Ciliophora), with ecological notes, new records, and descriptions of new species. Europ J Protistol (in press)

Frahm J-P, Kürschner H (1992) Moose tropischer Regenwälder. Spektrum Wiss, Oktober: 58–67

Gellért J, Tamás G (1958) Ökologische Untersuchungen an Diatomeen und Ciliaten der Detritus-Drifte am Ostufer der Halbinsel Tihany (in Hungarian with German summary). Annls Inst biol Tihany 25:217–240

Greenslade P, Rusek J (1996) *Tasphorura*, a new genus of Tullbergiinae (Collembola: Onychiuridae) abundant in Tasmanian *Nothofagus* forest. Syst Entomol 21:27–38

Hawksworth DL, Colwell RR (1992) Microbial diversity 21: biodiversity amongst microorganisms and its relevance. Biodiv Conserv 1:221–226

Hemberger H (1982) Revision der Ordnung Hypotrichida Stein (Ciliophora, Protozoa) an Hand von Protargolpräparaten und Morphogenesedarstellungen. Diss Univ Bonn

Hemberger H (1985) Neue Gattungen und Arten hypotricher Ciliaten. Arch Protistenk 130:397–417

Hutchinson GE (1961) The paradox of the plankton. Am Nat 95:137–145

Jaccard P (1902) Lois de distribution florale dans la zone alpine. Bull Soc Vaud Sci Nat 38:69–130

Junk WJ, Weber GE (1996) Amazonian floodplains: a limnological perspective. Verh Int Verein Limnol 26:149–157

Kahl A (1932) Urtiere oder Protozoa I: Wimpertiere oder Ciliata (Infusoria) 3. Spirotricha. Tierwelt Dtl 25:399–650

Lavelle P, Lattaud C, Trigo D, Barois I (1995) Mutualism and biodiversity in soils. In: Collins HP, Robertson GP, Klug MJ (eds) The significance and regulation of soil biodiversity. Kluwer, Dordrecht, pp 23–33

Lincoln RJ, Boxshall GA, Clark PF (1985) A dictionary of ecology, evolution and systematics. Cambridge University Press, Cambridge

May RM (1992) How many species inhabit the earth? Sci Am, October: 42–48

McGrady-Steed J, Morin PJ (1996) Disturbance and the species composition of rain pool microbial communities. Oikos 76:93–102

National Parks and Wildlife Services (1976) Mount Field National Park. Map and notes. Tasmanian Government

Odum EP (1980) Grundlagen der Ökologie, Band 2: Standorte und Anwendung. Thieme, Stuttgart

Petz W, Foissner W (1996) Morphology and morphogenesis of *Lamtostyla edaphoni* Berger and Foissner and *Onychodromopsis flexilis* Stokes, two hypotrichs (Protozoa: Ciliophora) from Antarctic soils. Acta Protozool 35:257–280

Pigon A, Edström JE (1961) Excystment ability, respiratory metabolism, and ribonucleic acid content in two types of resting cysts of *Colpoda cucullus* O.F. Müller. J Protozool 8:257–260

Sedlag U, Weinert E (1987) Wörterbücher der Biologie. Biogeographie, Artbildung, Evolution. Fischer, Stuttgart

Voß H-J (1992) Morphogenesis in *Amphisiella australis* Blatterer & Foissner, 1988 (Ciliophora, Hypotrichida). Europ J Protistol 28:405–414

Voß H-J (1997) Morphology and morphogenesis of *Parentocirrus hortualis* nov. gen., nov. spec.: a new genus within the redefined family Kahliellidae sensu Eigner 1995 (Ciliophora, Hypotrichida). Europ J Protistol 33:30–47

Walter H, Lieth H (1967) Klimadiagramm-Weltatlas. Fischer, Jena

World Conservation Monitoring Centre (1992) Global biodiversity: status of the earth's living resources. Chapman and Hall, London

Zech W (1997) Tropen – Lebensraum der Zukunft? Eine Analyse zur Rolle des Bodens aus der Sicht der Geoökologie. Geogr Rundsch 49:11–17