

# A Compilation of Soil and Moss Ciliates (Protozoa, Ciliophora) from Germany, with New Records and Descriptions of New and Insufficiently Known Species

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## Summary

This review compiles and analyses the taxonomic and biogeographical information available on soil ciliates from Germany. At least 270 species have been reliably recorded from 20 sites and site groups; 52 are new records from 13 sites studied for the purpose of this paper. At least 14 new species were discovered, of which three are described: *Dileptus armatus* nov. spec., *Holostichides dumonti* nov. spec., and *Hemisincirra gellerti verrucosa* nov. spec.; four species are redescribed: *Pleuroplites australis*, *Enchelys geleii* nov. comb. (basonym: *Lagynophrya geleii* Foissner, 1981), *Plagiocampa ovata*, and *Haplocaulus terrenus*. Of the 643 soil ciliate species known worldwide, almost half occur in Germany because the area is comparatively well-investigated and most soil ciliates are still undescribed. Thus, local diversity can not be used for estimating global diversity.

**Key words:** Biodiversity; Germany; Biogeography; New species; Soil ciliates.

## Introduction

Studies on local and global biodiversity depend highly on reliable data collections, that is, carefully prepared species lists from certain geographic regions and/or habitats [61]. For ciliates, and heterotrophic protists in general, such data sets are extremely rare, with a few notable exceptions [1, 2, 6, 7, 8, 26, 31, 33]. Accordingly, even such basic knowledge as the total number of species described and the overall synonymy rate can be only roughly estimated [14]. Furthermore, most protozoan “faunal lists” are beset with misidentifications because they are frequently prepared by taxonomically inexperienced researchers; often they are a

disliked and superficially prepared by-product of ecological studies [20].

In the present paper, I compiled the soil ciliates known from Germany, amending the list with unpublished data of “occasional” samples collected over the years. This list, which is cleared of obvious misidentifications, supplements the “World Soil Ciliates” [29]. Furthermore, some of the new species discovered will be described.

## Materials and Methods

### Area

The compilation comprises Germany within the borders of 1999 (Fig. 1). Twenty sites and site groups were analysed and the species recorded compiled in Table 1. Sites 1–9, 12, 19, 20 are original data not previously published. Site groups 10, 11, 13–18 are from the literature. All records from green (living) *Sphagnum* were excluded because I do not consider it as a terrestrial habitat. Furthermore, I excluded the papers by Varga [57, 58] because half of the taxa listed are freshwater species, indicating a high proportion of misidentifications.

### Description of sites

Site 1: Reclaimed, opencast coal mining area near Görlitz (see [10] for detailed site description). The sample was taken on 24.3.1998 about 30 years after reclamation, and investigated on 16.4.1999. It consisted of the upper 0–2/3 cm fresh and fermented litter layer (mainly from poplar, beech, acacia), mosses from the soil surface, and the upper (up to 3/4 cm), black moder soil. pH 5.2.

Site 2: Mine site test plots near site 1, as described in [59]. The sample was taken on 24.3.1998 about two years after the experimental set up (reclamation), and investigated on 16.4.1999. It consisted of the upper 0–2/3 cm grey sand layer,

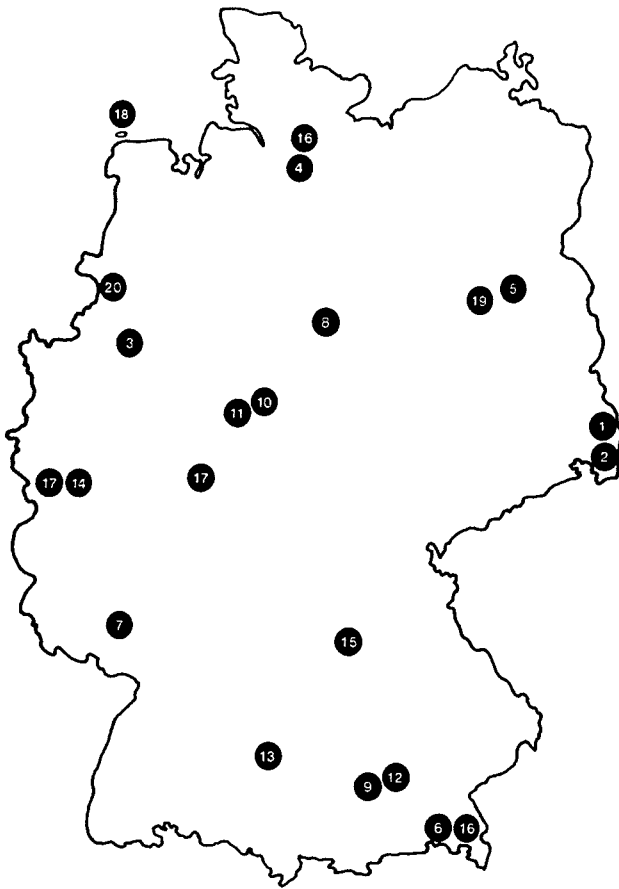


Fig. 1. Sampling sites for soil ciliates in Germany. The numbers correspond to those in the "description of sites" in the Materials and Methods section.

which was visibly colonised by cyanobacteria, algae, and fungal hyphae. pH 5.4.

Site 3: Litter and some soil from a mixed deciduous forest in the surroundings of Münster-Grievenbeck (about 20 m NW of "Haus Mariengrund"). The sample was collected by Dr. H. Zell (Aachen University) in autumn 1987 and investigated on 25.1. 1988.

Site 4: Leaf litter from the City Park of Hamburg, collected on 15.8. 1987 and investigated on 16.10.1987. pH 4.9.

Site 5: Mixed coniferous/deciduous forest in the surroundings of Berlin. The sample consisted of litter, grass roots, and darkbrown moder soil from the upper 0–4/5 cm. It was collected on 7.8.1986 and investigated in October 1986. pH 4.2.

Site 6: Three moss samples from Mittenwald in southern Germany, where Kahl collected, were investigated and lumped in Table 1. The samples consisted of moss with some adhering soil from tree-stumps, rocks, and the ground. Collected in autumn 1989 and investigated in January 1990.

Site 7: Mixed coniferous/deciduous "University Forest" in Kaiserslautern, Germany. The sample consisted of fresh and fermented litter and darkbrown moder soil from the upper 0–4 cm. It was collected in spring 1998 and investigated on 6.7.1998. pH 5.3.

Site 8: Two peat samples from 20 and 40 cm depth, respectively, of the "Grosses Moor" near Gifhorn, a small city near

Braunschweig. The samples, which were collected by Dr. E. Stackebrandt under sterile conditions, were pure, darkbrown peat.

Site 9: Blackish compost soil collected by Klaus Macknapp in a municipal compost plant of Munich. The sample was taken in August 1998 and investigated on 2.12.1998.

Site 10: Beech forest (*Fagus sylvatica*) about 7 km east of Göttingen (see [4, 52] for detailed site description). Two samples were investigated and lumped in Table 1, namely terra fusca-rendzina soil (pH 4.3–6.8) from within and around earthworm burrows. Most species were identified by Dr. M. Bonkowski (Göttingen University) and checked by myself.

Site 11: Beech forest on the "Kleinen Gudenberg" near Zierenberg, a small town about 30 km NW of Kassel (see [4] for detailed site description). Three samples were investigated and lumped in Table 1, namely, from a basaltic area, a limestone area, and the transition region in between. The samples, which consisted of litter and soil from the upper 0–5 cm layer, were investigated by Dr. M. Bonkowski and myself.

Site 12: Beech forest in the surroundings of Munich. The sample, which consisted mainly of fresh and fermented litter, was collected on 29.8.1987 and investigated on 16.10.1987.

Site 13: Comprises the species lists by Foissner ([20], habitat i), Lehle [45–48] and Lehle & Funke [49]. Dr. Eugen Lehle was a student of Prof. Dr. W. Funke (Ulm University) and myself, and I checked or performed most of the identifications from the Ulm area. The 14 sites investigated comprise the upper (0–5 cm) litter and soil layer of strongly acidified (pH 2.5–4) spruce forests in southern Germany (Ulm area and Schwarzwald area) and experimental plots treated with various substances, such as lime and ammonium-sulphate, increasing pH to up to 5.6. All sites were investigated with the non-flooded Petri dish method several times over a period of half a year to up to three years. See Lehle [45, 48] for details on sites and experimental design. All species contained in the papers cited above were included in Table 1.

Site 14: Contains the species list given by Buitkamp [5] from two brown earth soils in the surroundings of Bonn, viz., a pasture (dominant plants: *Poa annua*, *Poa pratensis*, *Lolium perenne*, *Taraxacum officinale*, *Trifolium repens*) and a mixed deciduous forest (*Quercus robur*, *Fagus sylvatica*, *Carpinus betulus*). Buitkamp's list, which appears rather incomplete, contains some typical freshwater ciliates (*Holophrya saginata*, *Oxytricha fallax*, *Tetrahymena pyriformis*), which I deliberately excluded from Table 1.

Site 15: Contains the species recorded in the milestone paper by Wenzel [60]. He investigated 298 moss and litter samples from coniferous and deciduous forests mainly in the surroundings of Erlangen, Bavaria. The list appears fairly complete, but contains several typical freshwater and marine species (e.g., *Blepharisma elongatum*, *Chaenea vorax*, *Enchelys gasterosteus*, *Euplotes affinis*, *Holophrya saginata*, *Phialina vermicularis*, *Trithigmostoma cucullus*, *Uronema marinum*), which I never found in terrestrial habitats and thus excluded from Table 1.

Site 16: Comprises the species found by Kahl [41–44] in mosses and litter of northern (Hamburg area) and southern (Berchtesgaden and Mittenwald areas) Germany. Kahl did not provide site details. All species were included in Table 1. Note, however, that those species which Kahl found only in mosses from other regions of the world, were excluded. Likewise, species originally found by Kahl in limnetic habitats and later reported by him also from terrestrial biotopes are not contained in Table 1.

Site 17: Contains the species reported by Greeff [36, 37] from the Marburg area, those found by Hemberger [38, 39] in the surroundings of Bonn, and some species described or re-described by Foissner [19, 22, 24] and others [3]. Unfortunately, Hemberger, who studied soil samples from Peru and Germany, did not mention the localities of some of the species he described; these were not included in Table 1. In Germany, Hemberger investigated a forest soil, a garden soil, and snail excrements.

Site 18: Contains the species found by Goralczyk and Verhoeven [35] in coastal sand dunes of Norderney, a small island at the north coast of Germany. Several samples from different sites (coastal sand, primary dunes, white dunes, grey dunes) were analysed with the non-flooded Petri dish method. Goralczyk and Verhoeven [35] could not identify all taxa, and two of them (*Enchelys gasterosteus*, *Phialina vertens*) are typical, probably misidentified, freshwater species. These species and those identified to genus or group level only were excluded from Table 1.

Site 19: Contains the species found by Schade [51] in five samples from sewage irrigation fields of Berlin-Buch (52°40'N/13°30'E) and in one sample from a sewage irrigation field at Ruhlsdorf, Brandenburg (52°21'N/13°13'E). Mag. S. Schade was a student of Prof. Dr. Klaus Hausmann (Berlin University) and myself, and I checked most of the identifications. The Berlin fields were used for about 80 years and abandoned about 10 years before our investigation. The artificial sand soil, which is strongly polluted by heavy metals and toxic organics, contains about 12% organic matter and has pH 4.8–6.5; it is colonised by various grasses, such as *Aspera spicaventi*, *Agropyron repens*, and *Dactylis glomerata*. Samples from the upper 5 cm were collected in June 1993 and analysed with the non-flooded Petri dish method in autumn 1993.

Site 20: Contains the species found by Niebuhr [50] in soils at Nordhorn, a small city about 110 km SW of Oldenburg. Dipl. Biol. J. Niebuhr was a guest in my laboratory, and I performed or checked most of the identifications. The material investigated is "Technosoil" from the area of an abandoned textile manufacturing plant. Actually, it is a rubbish-dump composed of some natural soil, sand, garbage, building debris, ashes, and slags to a depth of up to 4 m. The material has a pH between 5.7 and 8.5 and is slightly to moderately contaminated with heavy metals (copper and lead) and toxic organics. The dump surface is colonised by shrubs and grasses. Samples were taken from seven sites within an area of 1 m<sup>2</sup> each and up to 10 cm depth. Usually, 10 small subsamples were mixed to a composite and analysed with the non-flooded Petri dish method. Not all species seen were identified, and at least four were undescribed, but not studied in detail.

## Sampling and sample processing

For details on sampling, see description of sites. As concerns the old literature, where details are sometimes sparse, there is reason to assume that most samples were collected and processed in a similar way to that described below and in Foissner [20, 29]. Kahl [41] and Wenzel [60], for instance, used rain-wet or dried and rewetted mosses with adhering soil, which is similar to my non-flooded Petri dish method.

My samples and those of my students and guests were collected and processed as described in Foissner [20, 29]. Briefly, we take about 10 small subsamples from an area of about 100 m<sup>2</sup> and mix them to a composite, which is air-dried for at least one month and then sealed in plastic bags. The material

collected includes mineral top soil (up to 5–10 cm depth) with fine plant roots, the humus layer, small surface mosses, and the deciduous and/or grass litter from the soil surface. Upon investigation, the material is placed in a Petri dish (10–20 cm in diameter, 2–3 cm high) and saturated but not flooded with distilled water. Such cultures are analysed for ciliates by inspecting about 2 ml of the run-off on days 2, 7, 14, 21, and 28. The non-flooded Petri dish method is selective, that is, probably only a small proportion of the resting cysts present in a sample is reactivated, and undescribed species or species with specialised demands are very likely undersampled [28]. Thus, the real number of species, described and undescribed, in the samples investigated is probably much higher. Unfortunately, a better method for broad analysis of soil ciliates is not known.

## Identification of species, species concept, and species descriptions

As concerns my material, see Foissner [25, 29] for a description of the methods used. Buitkamp [5], Hemberger [39], Lehle [46] and Niebuhr [50] also used protargol impregnation, while the identifications by Kahl [41] and Wenzel [60] are based entirely on live observation. However, many of the new species they described have been redescribed with modern methods [29].

## Site descriptions for the species described

*Pleuroplites australis*: 0–5 cm litter and soil layer of a deciduous forest on Mount Ryu-ga-take in Japan, Amakusa, Kumamoto Prefecture (E130° N32°10'). Soil brown, with many root and leaf remnants, pH 4.8. Collected by Dr. Tadao Matsusaka (Kumamoto University) on April 6, 1985.

*Enchelys geleii*: 0–5 cm litter and soil layer from an island of the Galápagos archipelago (W92° S1°). Soil brownish, with much shrub litter. Collected by Dr. Annemarie Schmid (Salzburg University).

*Dileptus armatus*: 0–5 cm soil layer from a grassland in Helgoland (Oberland), Germany (E7° N54°). Soil red, with many grass roots, pH 7.5. Collected in March 1990. The second population was collected at Berlin, site 19, as described above.

*Plagiocampa ovata*: Madeira archipelago, Pico de Arieiro, about 1800 m above sea-level. Upper 0–5 cm of a grassland on reddish, very fine-grained, dusty soil, pH 3.8. Collected by Dr. Wolfgang Petz (Salzburg University) on June 22, 1985.

*Haplocaulus terrenus*: Found at site 12 as described above.

*Holostichides dumonti*: Litter and some dark moder soil (pH 4.3) from a coniferous forest (mixed with some birch and ash trees) near the town of Savonlinna, Finland (E29° N61°50'). Collected by Dr. Ilse Foissner on June 20, 1987.

*Hemisincirra gellerti verrucosa*: 0–5 cm litter and soil layer of a pine forest near the village of Arafo, Tenerife, Canary Islands, 1400 m above sea-level (W17° N28°). Soil reddish brown, with many grass roots and more or less completely decomposed pine-needles, pH 6.2. Collected by Dr. Brigitte Krassnigg (Salzburg University) in May 1988. The second population was collected at Berlin, site 19, as described above.

## Results and Discussion

Table 1 lists the 270 soil ciliate species which have been recorded from 20 sites and site groups in Ger-

**Table 1.** Species recorded from terrestrial habitats in Germany. Those in boldface are new records for Germany. + = present, – = absent.

Species <sup>1,2</sup>	Sites <sup>3</sup>																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Acineria uncinata</i>	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	+	–	–	–	–
<i>Acropisthium mutabile</i>	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–
<i>Amphileptus muscicola</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–
<i>Amphisiella binucleata</i>	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–
<b><i>Amphisiella magnigranulosa</i></b>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
<i>Amphisiella terricola</i>	–	–	–	–	–	+	–	–	–	–	–	–	+	–	–	–	+	–	–	–
<i>Archinassula muscicola</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
<i>Arcuospathidium atypicum</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–
<i>Arcuospathidium cultriforme</i>	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–
<i>Arcuospathidium lionotiforme</i>	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	+	–	–	+	–
<b><i>Arcuospathidium multinucleatum</i></b>	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–
<b><i>Arcuospathidium muscorum</i></b>	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
<i>Aspidisca turrita</i>	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–
<i>Australocirrus octonucleatus</i>	–	–	–	–	–	–	–	–	–	+	+	+	–	–	–	–	–	–	–	–
<i>Avestina acuta</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
<i>Balantidioides bivacuolata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–
<b><i>Balantidioides dragescoi</i></b>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
<i>Birojimia muscorum</i>	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	+	–	–	–	+
<i>Blepharisma bimicronucleatum</i>	–	–	–	–	–	–	–	–	–	–	+	–	+	–	–	–	–	–	–	–
<i>Blepharisma hyalinum</i>	+	–	+	–	–	+	+	–	–	+	+	+	+	+	+	–	–	+	–	–
<i>Blepharisma sphagni</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–
<i>Blepharisma steini</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–
<i>Blepharisma</i> sp. <sup>5</sup>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
<i>Brachyosoma brachypoda mucosa</i>	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	+	–
<b><i>Bresslaia insidiatrix</i></b>	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bresslaia vorax</i>	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
<i>Bresslauides discoideus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
<i>Bryometopus pseudochilodon</i>	–	–	–	+	–	–	+	–	–	+	–	–	+	–	+	+	–	–	–	–
<b><i>Bryometopus atypicus</i></b>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
<i>Bryometopus sphagni</i>	–	–	–	–	+	–	–	–	–	–	–	–	+	–	+	–	–	–	–	–
<b><i>Bryometopus triquetrus</i></b>	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	+	–
<i>Bryophrya bavariensis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–
<i>Bryophyllum loxophylliforme</i>	–	–	–	–	–	–	+	–	–	–	–	–	+	–	+	+	–	–	–	–
<i>Bryophyllum tegularum</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
<i>Bryophyllum vorax</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–
<i>Chilodonella aplanata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
<i>Chilodonella uncinata</i>	–	–	–	–	–	–	–	–	–	+	+	–	–	+	+	–	–	–	–	–
<i>Chilodontopsis depressa</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–
<i>Chilodontopsis muscorum</i>	–	–	–	–	–	–	–	–	–	–	+	–	+	–	+	+	–	–	–	–
<i>Chilophrya terricola</i>	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–
<i>Cinetochilum margaritaceum</i>	–	–	–	–	–	–	–	–	–	–	+	+	+	–	+	–	–	+	+	–
<i>Circinella filiformis</i>	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	+	–	+
<i>Colpoda aspera</i>	–	–	–	–	–	+	–	–	–	+	–	–	–	–	–	–	–	+	+	+
<i>Colpoda cavicola</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
<b><i>Colpoda augustini</i></b>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
<i>Colpoda colpodiopsis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	–	–	–	–
<i>Colpoda cucullus</i>	+	+	+	+	+	–	+	–	+	+	+	+	+	+	+	–	–	+	+	+
<i>Colpoda edaphoni</i>	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–
<i>Colpoda henneguyi</i>	+	+	–	–	+	–	+	–	–	–	+	+	+	–	–	–	–	–	+	–
<i>Colpoda inflata</i>	+	+	+	+	+	+	+	+	+	–	+	+	+	+	+	–	–	–	+	–
<i>Colpoda irregularis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–
<i>Colpoda lucida</i>	+	+	–	–	–	–	+	–	–	–	+	–	–	–	–	–	+	–	+	–
<i>Colpoda maupasi</i>	+	+	+	+	–	+	+	+	+	–	+	+	+	–	–	–	–	–	+	+
<i>Colpoda reniformis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–
<i>Colpoda simulans</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
<i>Colpoda steinii</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	–	–	+	+
<i>Colpoda tripartita</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–





Table 1. (Continued).

Species <sup>1,2</sup>	Sites <sup>3</sup>																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Halteria grandinella</i>	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	-	-	-	+	-
<i>Haplocaulus terrenus</i> <sup>6</sup>	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
<i>Hausmanniella discoidea</i>	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-
<i>Hausmanniella patella</i>	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	+	-	-	-	-
<i>Hemiamphisiella terricola</i>	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Hemisincirra gellerti</i>	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	+
<i>Hemisincirra gellerti verrucosa</i> <sup>6</sup>	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	+	-
<i>Hemisincirra gracilis</i>	+	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-	+
<i>Hemisincirra heterocirrata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Hemisincirra inquieta</i>	+	-	+	+	+	+	+	-	+	-	-	-	+	-	-	-	-	-	+	+
<i>Hemisincirra interrupta</i>	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
<i>Hemisincirra kahli</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
<i>Hemisincirra similis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
<i>Holosticha adami</i>	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-
<i>Holosticha bergeri</i>	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Holosticha monilata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
<i>Holosticha multistilata</i>	-	-	-	+	-	-	+	-	-	+	+	-	+	+	-	-	-	-	+	+
<i>Holosticha muscorum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	-	-	-	-
<i>Holosticha sigmoidea</i>	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
<i>Holosticha sylvatica</i>	-	-	-	+	-	-	+	-	-	-	-	-	+	-	-	-	-	-	-	-
<i>Holosticha tetracirrata</i>	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Holostichides chardezi</i>	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
<i>Holostichides dumonti</i> <sup>6</sup>	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Holostichides terricola</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
<i>Homalogastra setosa</i>	+	+	+	-	-	-	-	-	+	-	-	-	+	+	+	+	-	+	+	+
<i>Kahlilembus attenuatus</i>	-	-	-	+	+	-	+	-	-	-	-	+	+	+	-	+	-	-	+	-
<i>Keronella gracilis</i>	-	-	-	-	-	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-
<i>Keronopsis alpestris</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
<i>Keronopsis wetzeli</i>	-	-	-	-	+	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-
<i>Keronopsis</i> sp. (cf. <i>tasmaniensis</i> )	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Kreyella muscicola</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
<i>Kuehneltiella muscicola</i>	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lacrymaria pulchra</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
<i>Lamtostyla australis</i> (?)	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lamtostyla edaphoni</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
<i>Lamtostyla hyalina</i>	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
<i>Lamtostyla kirkeniensis</i>	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lamtostyla perisincirra</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Leptopharynx costatus</i>	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	-	-	+	+	+
<i>Leptopharynx eurystoma</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
<i>Litonotus muscorum</i>	-	-	-	-	-	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-
<i>Metopus basei</i>	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
<i>Microdiaphanosoma arcuatum</i>	-	-	-	-	-	-	+	-	-	-	-	-	+	-	+	-	-	-	+	-
<i>Microthorax scutiformis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+
<i>Microthorax simulans</i>	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	+	+	-
<i>Mykophagophrys terricola</i>	+	+	-	+	-	-	-	-	-	-	+	+	+	-	-	-	-	-	+	-
<i>Nassula exigua</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-
<i>Nassula parva</i>	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Nassula picta</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-
<i>Nassula pusilla</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
<i>Nivaliella plana</i>	+	+	-	+	+	+	+	-	-	-	+	-	+	-	-	-	-	+	-	+
<i>Nivaliella</i> sp. <sup>5</sup>	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Notoxoma parabryophryides</i>	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Odontochlamys alpestris</i>	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
<i>Odontochlamys convexa</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-
<i>Odontochlamys gouraudi</i>	-	-	-	-	-	-	-	-	-	+	+	+	+	-	+	-	-	-	-	-
<i>Odontochlamys wisconsinensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-

Table 1. (Continued).

Species <sup>1,2</sup>	Sites <sup>3</sup>																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Opercularia arenicola</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Opercularia curvicaule</i>	-	-	-	-	-	-	+	-	-	-	+	+	-	-	-	-	+	-	+	-
<i>Ophryoglena marginata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Orthoamphisiella franzi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
<i>Orthoamphisiella stramenticola</i>	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Oxytricha granulifera</i>	-	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	+	-
<i>Oxytricha lanceolata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
<i>Oxytricha longigranulosa</i>	+	-	-	-	+	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-
<i>Oxytricha setigera</i>	-	-	-	+	-	-	+	-	+	+	-	+	+	+	-	-	-	+	+	+
<i>Oxytricha siseris</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-
<i>Parabryophrya penardi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
<i>Paracineta lauterborni</i>	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
<i>Paraenchelys terricola</i>	-	+	-	-	-	-	+	-	+	+	+	-	+	-	-	-	-	-	-	+
<i>Paraenchelys wenzeli</i>	-	-	-	+	-	-	-	-	-	-	+	+	+	-	-	-	-	-	-	-
<i>Parafurgasonia sorex</i>	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
<i>Paragastrostyla lanceolata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Paragonostomum caudatum</i> <sup>4</sup>	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Paraholosticha muscicola</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-
<i>Parakabliella macrostoma</i>	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Parakabliella terricola</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
<i>Paraurostyla pulchra</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
<i>Periholosticha acuminata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Phacodinium metchnikoffi</i>	-	-	-	+	-	-	+	-	-	-	+	-	+	-	+	-	-	-	-	-
<i>Phialina binucleata</i>	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	+
<i>Phialina terricola</i>	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	+
<i>Plagiocampa difficilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
<i>Plagiocampa rouxi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
<i>Plagiocampa ovata</i> <sup>6</sup>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
<i>Platyophrya binucleata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
<i>Platyophrya macrostoma</i>	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	+
<i>Platyophrya similis</i>	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
<i>Platyophrya spumacola</i>	-	-	+	-	-	-	-	-	-	+	+	-	+	+	+	+	-	-	+	+
<i>Platyophrya vorax</i>	-	-	-	+	-	+	+	-	+	-	+	+	+	+	+	-	-	-	+	+
<i>Platyophryides dragescoi</i>	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
<i>Platyophryides latus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-
<i>Pleuropilites australis</i> <sup>6</sup>	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	+
<i>Podophrya halophila</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
<i>Protospathidium bonnetti</i>	-	-	+	+	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-
<i>Protospathidium serpens</i>	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-	+	-	-
<i>Protospathidium</i> sp. <sup>5</sup>	-	-	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-
<i>Pseudochilodonopsis mutabilis</i>	+	-	-	-	+	-	-	-	-	-	-	+	+	-	-	-	-	+	+	+
<i>Pseudocryptolophosis alpestris</i>	+	-	+	+	+	-	+	-	+	-	+	+	+	-	-	-	-	-	+	+
<i>Pseudoglaucoma muscorum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-
<i>Pseudoholophrya terricola</i>	+	-	-	-	-	-	+	-	-	-	-	+	+	-	-	-	-	-	-	+
<i>Pseudomicrothorax agilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
<i>Pseudoplatyophrya nana</i>	+	+	+	+	+	+	+	+	-	-	-	-	+	-	+	+	-	-	+	+
<i>Pseudoplatyophrya saltans</i>	-	+	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	+	-
<i>Pseudouroleptus terrestris</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Rhabdostyla</i> (?) <i>arborea</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Rhabdostyla muscorum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
<i>Rhabdotricha terricola</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Rostrophryides africana</i>	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sathrophilus muscorum</i>	+	-	+	+	+	+	+	-	-	-	-	-	-	+	+	+	-	+	+	-
<i>Siroloxophyllum utriculariae</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
<i>Spathidium anguilla</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+
<i>Spathidium bavariense</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-
<i>Spathidium chlorelligerum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-

**Table 1.** (Continued).

Species <sup>1,2</sup>	Sites <sup>3</sup>																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Spathidium claviforme</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-
<i>Spathidium holsatae</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-
<i>Spathidium lieberkühni</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
<i>Spathidium longicaudatum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
<i>Spathidium muscicola</i>	+	+	-	-	-	-	-	-	-	-	-	-	+	+	+	+	-	-	-	-
<i>Spathidium procerum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+
<i>Spathidium rusticanum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
<i>Spathidium scalpriforme</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-
<i>Spathidium spathula</i>	-	-	+	-	-	-	-	-	-	+	+	-	+	-	+	-	-	-	+	-
<i>Spathidium vermiculus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-
<i>Sphaerophrya parva</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Stammeridium kahli</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
<i>Sterkiella cavicola</i>	-	+	-	-	-	-	-	-	+	+	+	-	+	-	-	+	-	-	-	+
<i>Sterkiella histriomuscorum</i>	+	+	-	+	-	-	+	-	+	+	+	+	+	-	+	-	-	+	+	+
<i>Strongylidium californicum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
<i>Strongylidium muscorum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-
<i>Stylonychia stylomuscorum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
<i>Suctorina</i> div. spec.	-	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
<i>Tachysoma humicola humicola</i>	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	+	+
<i>Terricirra livida</i>	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Territricha stramenticola</i>	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
<i>Tetrahymena edaphoni</i>	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-
<i>Tetrahymena rostrata</i>	-	-	-	+	-	+	+	-	-	+	+	+	+	-	+	+	-	-	+	-
<i>Thecacinetia caepula</i>	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Trachelochaeta gonostomoida</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Trachelophyllum apiculatum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
<i>Trihymena terricola</i>	-	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	+
<i>Trithigmostoma bavariensis</i>	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	+	-	-	-	-
<i>Uroleptoides kihni</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
<i>Uroleptus lepisma</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
<i>Uroleptus matthesi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
<i>Urosomoida agilisformis</i>	-	-	-	+	-	+	+	-	+	-	+	-	+	-	-	-	-	-	-	+
<i>Urosomoida agilis</i>	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	-	+	+
<i>Urosomoida dorsiincisura</i>	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Urosomoida minima</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Urostyla muscorum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-
<i>Vaginicola terricola</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Vorticella astyliiformis</i>	-	+	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-	+	-
<i>Vorticella infusionum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
<i>Vorticella lichenicola</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Vorticella microstoma</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
<i>Vorticella similis</i>	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	+

<sup>1</sup> See [29] for authorship and date of species. Those not contained are as follows: *Amphileptus muscicola* (Kahl, 1931) nov. comb. (basonym: *Hemiophrys muscicola* Kahl, 1931); *Arcuospathidium multinucleatum* Foissner, 1999; *Aspidisca turrita* (Ehrenberg, 1831) Claparède & Lachmann, 1858; *Blepharisma sphagni* Lepsi, 1926; *Brachyosoma brachypoda mucosa* Foissner, 1999; *Bryophyllum vorax* (Stokes, 1884) Kahl, 1931; *Chilodontopsis depressa* (Perty, 1852) Blochmann, 1895; *Endosphaera terebrans* Matthes & Guhl, 1973; *Microthorax scutiformis* Penard, 1922; *Nassula exigua* Kahl, 1931; *Nassula parva* Kahl, 1928; *Nassula pusilla* Kahl, 1931; *Plagiocampa ovata* Gelei, 1954; *Siroloxophyllum utriculariae* (Penard, 1922) Foissner & Leipe, 1995; *Spathidium chlorelligerum* Kahl, 1930; *Spathidium lieberkuehni* Bütschli, 1889; *Spathidium vermiculus* Kahl, 1926.

<sup>2</sup> Nomenclature of literature data has been adapted to the recent review by Foissner [29]. Accordingly, very recent new generic combinations (e.g. [2]) were omitted.

<sup>3</sup> Site descriptions, see Materials and Methods.

<sup>4</sup> Description in preparation.

<sup>5</sup> Very likely a new species.

<sup>6</sup> For description, see systematic part of this paper.

many. Actually, the number is about 300, but taxa not identified to species level and obvious misidentifications were sorted out. About 120 of the 270 species were discovered in Germany, most by Kahl [41–44]. Later, Wenzel [60], Buitkamp [5], Hemberger [39], and Foissner [19, 21–23, 26] each added a few new species. A considerable portion, viz., 52 species are new records for Germany from the 13 sites investigated in the course of the present study; they appear in boldface in Table 1.

As concerns the 13 new sites investigated, at least 18 new species were discovered, which is well in the range observed in soils worldwide [28], indicating that the soil ciliate biota of Germany are still poorly explored, although they belong to the most extensively studied of the world. Thus, many new species can be expected in more detailed investigations. Four of the new species found have been described previously: *Paraenchelys wenzeli* Foissner, 1984 (Giessen area; not detailed here); *Platyophryides dragescoi* Foissner, 1987 (from site 13); *Australocirrus octonucleatus* Foissner, 1988 (from site 12); and *Kuehneliella muscicola* Foissner, 1993 (from site 6); three have been described very recently or will be described in the near future: *Arcuospathidium multinucleatum* Foissner, 1999 (site 12), *Brachyosoma brachypoda mucosa* Foissner, 1999 (site 12), and *Paragonostomum caudatum* (site 9); three are described in the present paper: *Dileptus armatus*, *Holostichides dumonti*, and *Hemisincirra gellerti verrucosa*; four will be described later: *Protospathidium* sp. (sites 7, 8, 9), *Nivaliella* sp. (sites 6, 8), *Blepharisma* sp. (site 19), and *Euplotes* sp. (site 19); and four, probably new, species were not investigated in detail.

At present, 643 soil ciliate species are known worldwide [29]. At least 270 of them have been reliably recorded from Germany, seemingly giving strong support to Fenchel's and Finlay's [13a] hypothesis that, in protists, "everything is (almost) everywhere". However, a closer examination reveals that calculations of global diversity from local diversities are extremely misleading if the full diversity of the group under investigation is unknown. In 1987, when only about 250 species of soil ciliates were known [20], 100% of the global diversity occurred in Germany. In 1998, when 643 soil ciliate species had been described [29], the percentage dropped to 42%, and when the 500–600 undescribed (new) species, which I have in my records [29], are added, the percentage drops to about 23%. Finally, when the estimated global soil ciliate diversity (up to 2000 species; [28]) is taken, the ratio approaches 14%. See [13a] and [30a] for a more detailed discussion of this and related problems.

## Description of new and insufficiently known ciliates

### *Pleuroplites australis* Foissner, 1988 (Fig. 2–12; Tab. 2)

**Material:** Two voucher slides with protargol-impregnated specimens from the Japanese population have been deposited in the Oberösterreichische Landesmuseum in Linz (LI). Relevant specimens are marked by a black ink circle on the cover glass.

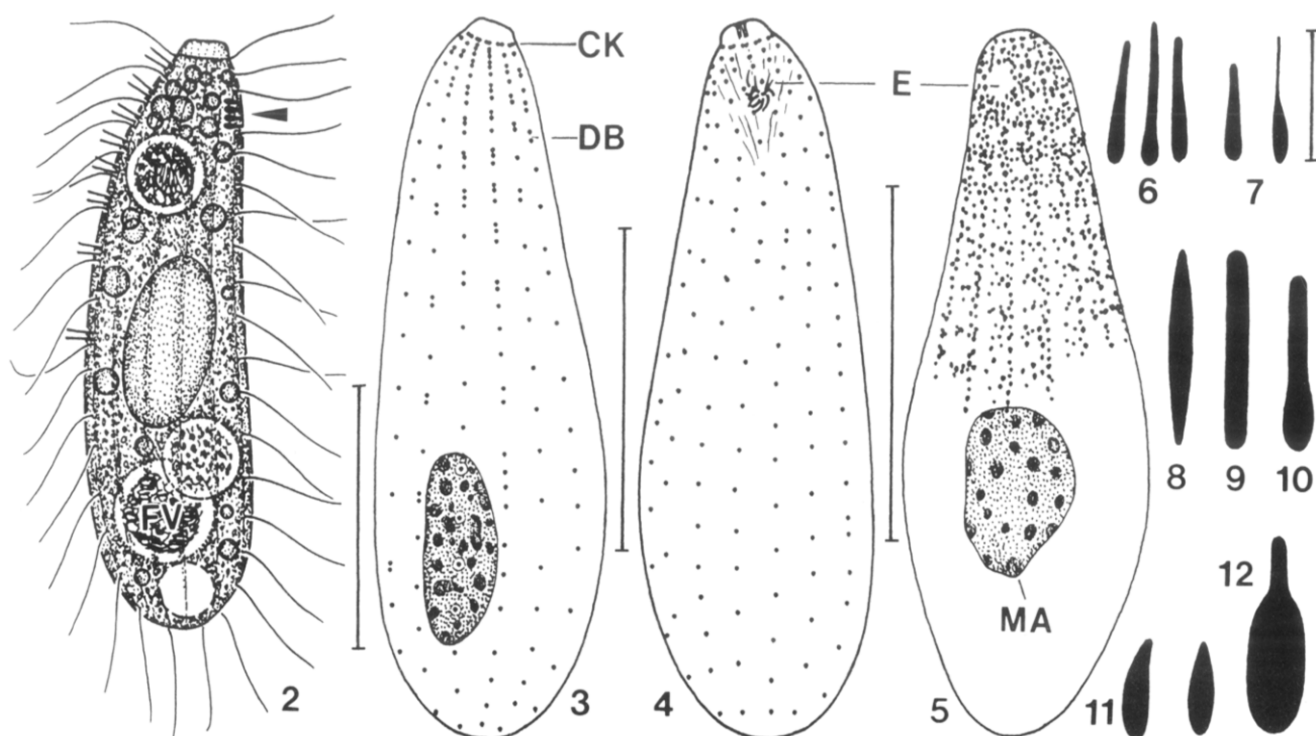
**Observations and discussion:** Over the years, I studied several populations of this species from soils worldwide. All agree well with the original description both in general morphology and main morphometrics. The species is inconspicuous, but easily identified by the small size (length about 40–60  $\mu\text{m}$ ); the ellipsoidal macronucleus; the subapical extrusome bundle, which, however, is difficult to recognise due to its small size and unusual location; and the characteristic dorsal brush, which consists of six to eight rows each composed of kinetid triads the anterior two kinetids of which bear 2–3  $\mu\text{m}$  long bristles, while the posterior kinetid has an ordinary cilium (Fig. 2, 3).

There is, however, a feature which is rather different in various populations, namely the shape and size (1.5–3  $\mu\text{m}$ ) of the extrusomes (for details, see explanation to figures 6–12). Unfortunately, the exact shape and size of the extrusomes are difficult to recognise, even with optimum equipment, because they are so minute. Thus, and because no geographic pattern is recognisable, I do not separate the populations at species/subspecies level. Usually, however, I consider extrusome shape as an important species character (see *Dileptus armatus*), and if the differences shown in figures 7–12 can be substantiated by transmission electron microscopy, at least the Japanese and Moyreuan populations should be considered as distinct species.

### *Enchelys geleii* (Foissner, 1981) nov. comb. (Fig. 13–28; Tab. 3)

**Material:** Two voucher slides with protargol-impregnated specimens from the Galápagos population have been deposited in the Oberösterreichische Landesmuseum in Linz (LI). Relevant specimens are marked by a black ink circle on the cover glass.

**Description** (of the Galápagos population): Size in vivo 100–200  $\times$  20–45  $\mu\text{m}$ , usually about 150  $\times$  30  $\mu\text{m}$ , that is, considerably larger than type specimens (110  $\times$  20  $\mu\text{m}$ ), possibly because it was a flourishing culture; length:width ratio 2.3:1–6.5:1, on average 5:1 in protargol preparations. Shape also highly variable, slenderly to broadly cylindroidal and often slightly reniform, rarely ovoidal or pyriform, oral area flattened and obliquely narrowed ventrally (Fig. 13–17, 26). Macronucleus in middle third of cell, highly tortuous



**Fig. 2–12.** *Pleuroplites australis* from life (2, 6–12) and after protargol impregnation (3–5). **2:** Right lateral view of a representative specimen from Japanese population. The arrowhead marks the minute, subapical extrusome bundle. **3, 4:** Ciliary pattern of dorsal and ventral side of a Japanese specimen. The dorsal brush (DB), which usually consists of six rows, has a highly characteristic structure, that is, consists of triads of which the anterior two kinetids have short bristles, while the posterior kinetid bears an ordinary cilium (cp. figure 2). **5:** Cortical granulation of a specimen from Antarctica. The granules leave the extrusome site blank. **6–12:** Extrusomes of various populations, drawn to scale. (6) Australia, bush in Brisbane Water National Park [from 23]. (7) Africa, Kenya, grassland soil from Nairobi Arboretum, left in vivo, right from cytoplasm of a protargol-impregnated specimen. (8) Australia, soil from rain forest near Cairns. (9) Africa, Kenya, Masei Mara savannah. (10) Antarctica, grass sward from Signy Island. (11) Japanese population described in this paper. Extrusomes of similar size and shape were found in specimens from Germany and Venezuela. (12) Moyreau Island in the Caribbean Sea, highly saline swamp soil. CK = circumoral kinety, DB = dorsal brush, E = extrusome bundle, FV = food vacuole, MA = macronucleus. Scale bars 20 µm (2–5) and 2 µm (6–12).

and occasionally slightly nodular (Fig. 16, 17, 24), highly variable in different populations (Fig. 19), with many minute nucleoli. Micronuclei globular, most rather distant from macronucleus (Fig. 16, 24), difficult to recognise in vivo and preparations because of similar size as cytoplasmic fat inclusions. Contractile vacuole in posterior end, with about 10 excretory pores in pole area (Fig. 13, 23, 24). Shape and size of extrusomes as in type specimens and very constant in populations worldwide (Fig. 13, 15, 19, 21, 28): 5–7 µm, usually 6 µm long, slenderly fusiform and slightly curved, in oral bulge and perpendicularly attached to pellicle forming meridional rows, which are easily overlooked because the extrusomes are fine and rather hyaline; those attached to pellicle never impregnated with protargol, while certain developmental stages (?) occasionally stain within the cytoplasm. Cortex about 1 µm thick, bright, indistinctly furrowed by ciliary rows; contains many colourless granules about 0.5 µm

across, which usually impregnate with protargol and silver carbonate covering the ciliary pattern (Fig. 14, 22, 28). Cytoplasm colourless and usually opaque due to many fat inclusions 1–7 µm across. Feeds on heterotrophic flagellates, naked amoebae and middle-sized ciliates, e.g., *Colpoda cucullus*. Divides in freely motile condition.

Cilia about 8 µm long, narrowly spaced, especially in oral area, arranged in equidistant, longitudinal to slightly spiral rows commencing underneath anterior body end at base of oral bulge. Three rows differentiated to dorsal brush anteriorly, middle brush row distinctly longer than right and left ones, rows gradually shortened from left to right and distinctly curved anteriorly, composed of narrowly spaced dikinetids having about 5 µm long bristles; pattern very constant and thus highly characteristic, but clearly recognisable only in properly orientated and well-impregnated specimens (Fig. 13, 18, 23–25, 27).

**Table 2.** Morphometric data on *Pleuroplites australis* from Japan (upper line) and Antarctica (lower line).

Character <sup>1)</sup>	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	40.0	41	4.4	1.2	10.9	34	48	13
	41.2	39	6.3	1.8	15.3	34	55	13
Body, width	16.2	17	1.4	0.4	8.7	14	18	13
	13.7	13	2.4	0.7	17.2	10	20	13
Oral bulge, diameter	2.9	3	–	–	–	2	3	13
	3.9	4	–	–	–	3	4	13
Oral bulge, height				about 1 $\mu\text{m}$ about 1 $\mu\text{m}$				
Macronucleus, length <sup>2)</sup>	9.0	9	1.9	0.5	20.8	7	13	13
	8.6	7	2.4	0.7	28.0	6	14	13
Macronucleus, width <sup>2)</sup>	6.3	7	1.8	0.5	28.5	4	10	13
	6.0	6	1.1	0.3	18.2	4	7	13
Ciliary rows, number	14.8	15	0.7	0.2	4.6	14	16	13
	15.3	15	1.0	0.5	6.3	14	16	4
Dorsal brush rows, number	6.1	6	–	–	–	6	7	13
				not determined				
Kinetids, number in an ordinary kinety	21.1	22	3.1	0.9	14.7	16	25	13
				not determined				
Anterior end to end of longest brush row, distance	12.3	12	1.7	0.5	13.4	9	15	13
				not determined				
Dikinetids in longest brush row, number	6.3	6	0.9	0.2	13.6	5	8	13
				not determined				

<sup>1)</sup> Data based on protargol-impregnated (Foissner's method), mounted specimens from non-flooded Petri dish cultures. Measurements in  $\mu\text{m}$ . CV = coefficient of variation in %, M = median, Max = maximum, Min = minimum, n = number of individuals investigated, SD = standard deviation, SE = standard error,  $\bar{x}$  = arithmetic mean.

<sup>2)</sup> About 70% of the Antarctic specimens have a dumb-bell shaped macronucleus or two macronuclear nodules connected by a more or less wide bridge.

Oral bulge only 1–2  $\mu\text{m}$  high and slightly depressed in centre, broadly elliptical and slightly obliquely truncated ventrally (Fig. 26), can open widely during ingestion of large food items. No dikinetidal circumoral kinety. Oral basket recognisable only in protargol preparations, composed of very fine rods originating from the anterior 10–20 basal bodies of the somatic ciliary rows; individual rods unite to rather conspicuous bundles, especially on ventral side (Fig. 16–18, 23).

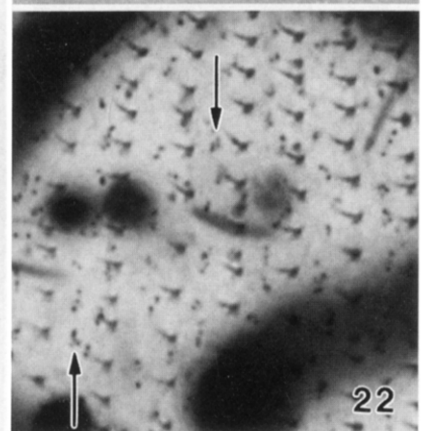
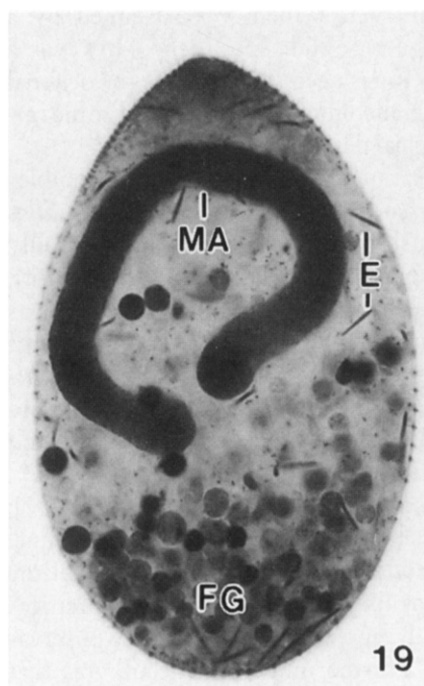
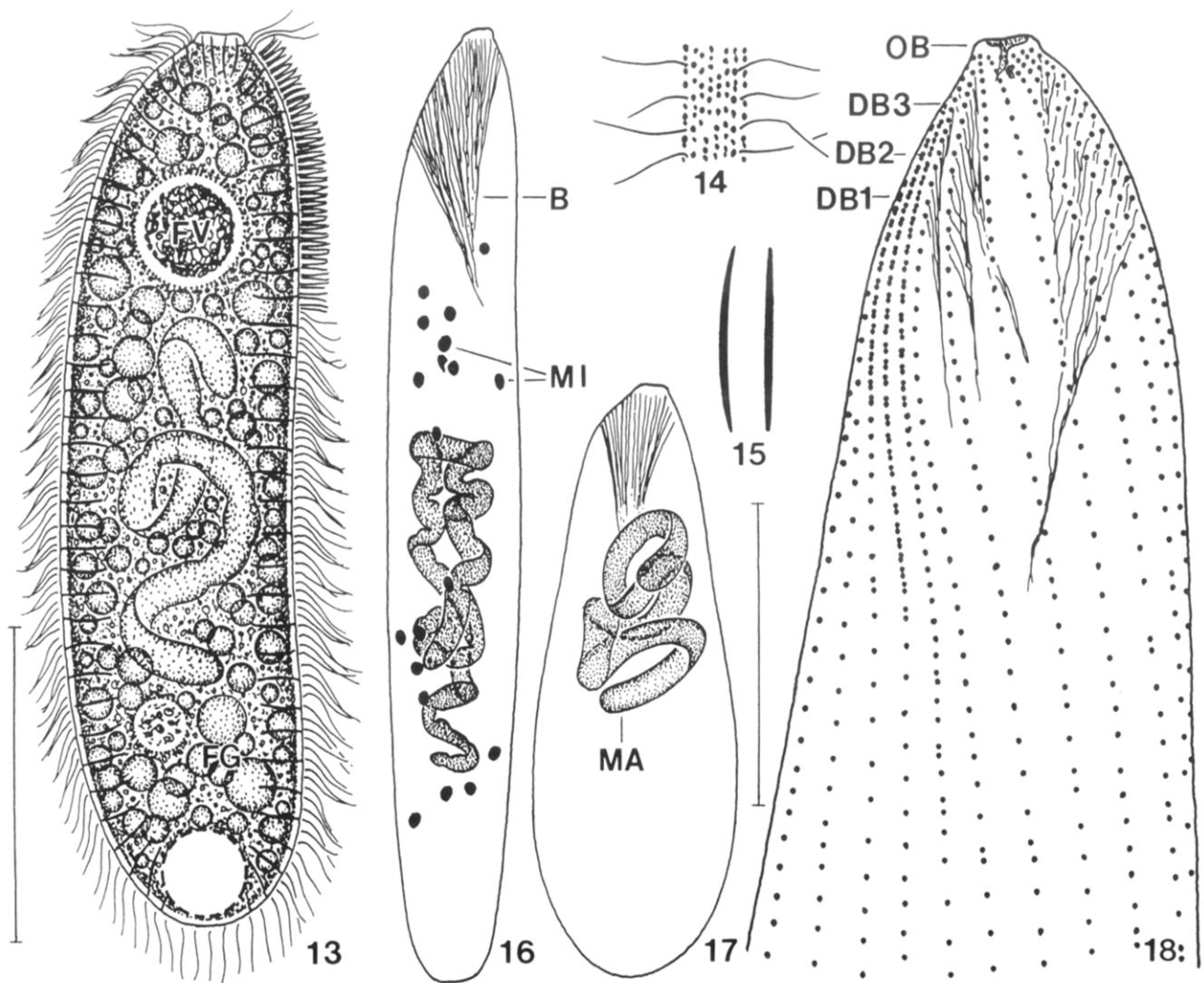
**Occurrence and ecology:** *Enchelys geleii* is, according to my experience, common in terrestrial biotopes worldwide, especially in leaf litter. However, it rarely gets high abundances with the method used; in the Galápagos sample, it was numerous.

**Comparison with original description and generic assignment:** *Enchelys geleii* is easily identified by the special arrangement of the extrusomes and the long, tortuous macronucleus. Note, however, that the extrusomes do not impregnate with protargol, at least with the method used; thus, live observation is indispensable. Furthermore, *E. geleii* is very difficult to impregnate with protargol; usually, mainly the cortical gran-

ules are revealed. The Galápagos specimens match the original description well, which was sustained by a comparison with the type slide specimens. However, a complete redescription is necessary because the original description lacks detailed morphometrics and some important morphological details.

The overall appearance of *E. geleii* highly resembles *Papillorhabdos* Foissner [19]. However, *Papillorhabdos* has four dorsal brush rows and as yet comprises only two freshwater species, namely *P. multinucleatus*, which has the same arrangement of the extrusomes as *E. geleii*, and *P. carchesii*, which has the same type of macronucleus. Also easily confused with *E. vermiciformis* Foissner [22], which is larger (180  $\times$  25  $\mu\text{m}$ ) and very slender (6:1–8:1), has rod-shaped extrusomes, and only 17 ciliary rows.

The original description of *E. geleii* mentions [17]: "Oral basket funnel-shaped, composed of very fine, about 15  $\mu\text{m}$  long rods originating from the base of the oral bulge and recognisable only in protargol preparations". This basically agrees with the present observations, which show a further important detail, viz., that





**Table 3.** Morphometric data on *Enchelys geleii*.

Character <sup>1)</sup>	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	133.4	136	27.8	7.2	20.8	91	185	15
Body, maximum width	29.9	28	5.4	1.4	17.9	21	43	15
Oral bulge, diameter	5.4	5	1.1	0.3	19.6	4	8	15
Oral bulge, height	1.8	2	–	–	–	1	2	15
Macronuclear figure, length	46.3	43	12.0	3.1	25.8	32	66	15
Macronucleus, width	4.6	5	0.7	0.2	16.0	3	6	15
Micronuclei, length	2.8	3	–	–	–	2	3	15
Micronuclei, width	2.4	3	–	–	–	2	3	15
Dorsal brush row 1, length	25.7	25	5.0	1.3	19.5	16	33	15
Dorsal brush row 2, length	36.9	37	8.4	2.2	22.8	23	53	15
Dorsal brush row 3, length	23.1	22	4.5	1.2	19.3	15	30	15
Ciliary rows, number	23.5	23	1.1	0.3	4.5	22	25	15
Dorsal brush rows, number	3.0	3	0.0	0.0	0.0	3	3	15
Kinetids in a ventral kinety, number	93.6	93	18.3	4.9	19.6	60	125	15
Dikinetids in brush row 1, number	23.1	22	4.5	1.2	19.3	15	30	15
Dikinetids in brush row 2, number	36.9	35	5.7	1.5	15.5	26	47	15
Dikinetids in brush row 3, number	25.3	25	3.5	0.9	13.9	19	34	15
Macronuclei, number	1.0	1	0.0	0.0	0.0	1	1	15
Micronuclei, number	15.9	16	2.8	0.7	17.5	10	20	15

<sup>1)</sup> Data based on protargol-impregnated (Foissner's method), mounted specimens from a non-flooded Petri dish culture. Measurements in  $\mu\text{m}$ . CV = coefficient of variation in %, M = median, Max = maximum, Min = minimum, n = number of individuals investigated, SD = standard deviation, SE = standard error,  $\bar{x}$  = arithmetic mean.

the basket rods originate from the anterior 10–20 basal bodies of the somatic kineties and a dikinetidal circumoral kinety is lacking (not expressly stated in the original description but recognisable in the figures and confirmed by the reinvestigation of the type material). Accordingly, the species, which Foissner [17] assigned to the genus *Lagynophrya*, belongs to the *Enchelyina* Foissner & Foissner [32]. *Lagynophrya* has a dikinetidal circumoral kinety and lacks oralised somatic kinetids [33]. Thus, the species must be transferred to *Enchelys*, as defined by Foissner [19]: *Enchelys geleii* (Foissner, 1981) nov. comb. (basonym: *Lagynophrya geleii* Foissner, 1981).

***Dileptus armatus* Foissner & Schade nov. spec.**  
(Fig. 29–50; Tab. 4)

**Diagnosis:** Size in vivo about  $200 \times 30 \mu\text{m}$ , proboscis 27% of body length on average, posterior body end

narrowly rounded. 2 macronuclear segments with micronucleus interposed. 2 contractile vacuoles in dorsal side of trunk. Two size and shape types of extrusomes: type 1 inconspicuous, rod-shaped, about  $3 \mu\text{m}$  long; type 2 conspicuous, clavate,  $4\text{--}6 \times 1 \mu\text{m}$ . 2 dorsal brush rows with up to  $3 \mu\text{m}$  long bristles.

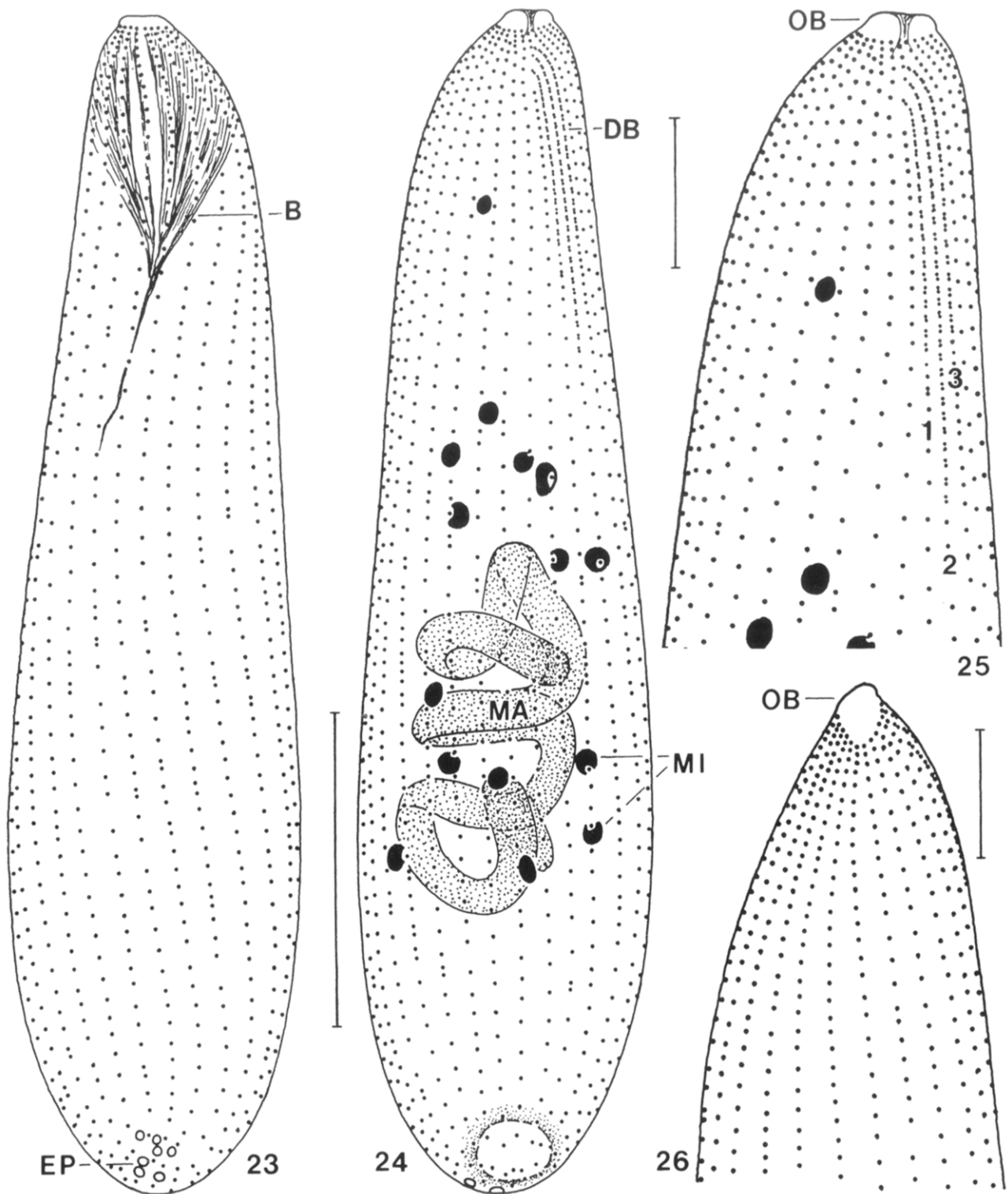
**Type location:** Soil from Helgoland (Oberland), Germany (E7° N54°).

**Type material:** One holotype slide and three paratype slides with protargol-impregnated (Foissner's method) specimens from the type population have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria. Relevant specimens are marked by a black ink circle on the cover glass.

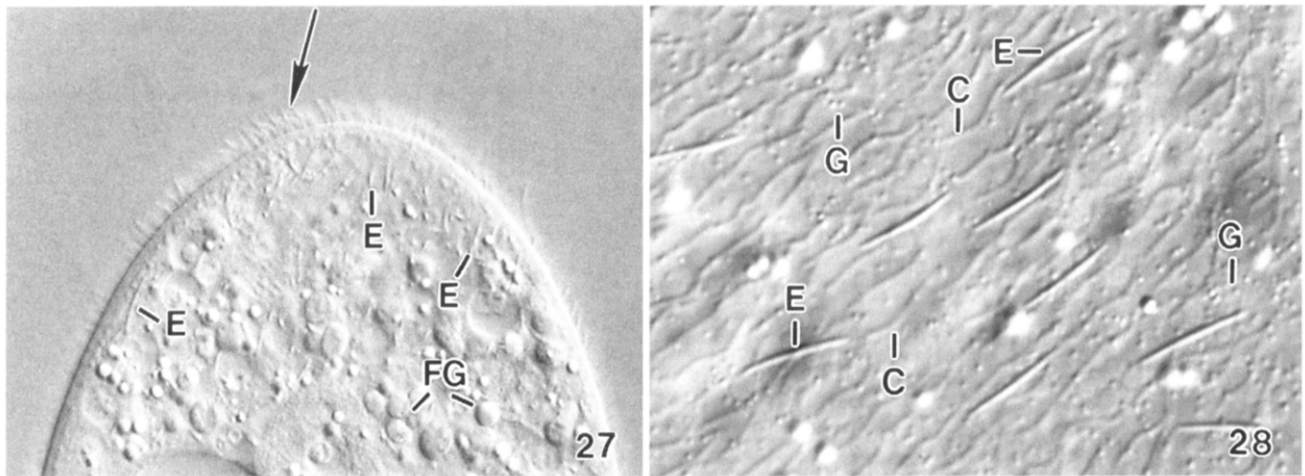
**Etymology:** “armatus” (Latin, armed) refers to the conspicuous extrusome apparatus.

**Description** (type population): Size in vivo  $140\text{--}250 \times 20\text{--}40 \mu\text{m}$ , on average about  $200 \times 30 \mu\text{m}$ ; acontractile.

**Fig. 13–22.** *Enchelys geleii* from life (13, 15, 21), after protargol impregnation (14, 16–18), and silver carbonate impregnation (19, 20, 22). **13:** Left lateral view of a representative specimen. Note the extrusomes which, although numerous and rather long, form an only indistinct fringe because they are rather fine. **14:** Surface view showing cortical granulation. **15:** Two views of the same extrusome, length  $7 \mu\text{m}$ . **16, 17:** The largest (length  $185 \mu\text{m}$ ) and one of the broadest specimen found in the slides, drawn to scale. **18:** Dorsolateral view of anterior body portion showing dorsal brush and oral basket rods originating from the anterior basal bodies of the ciliary rows. **19, 20, 22:** Optical section and surface view of a specimen from a slightly saline soil of Austria (Burgenland, Neusiedlersee region). The macronucleus of this population is only slightly tortuous and hardly nodulated. The extrusomes and some of the cortical granules (arrows) impregnate with silver carbonate. The kinetids are associated, at the right side, with a short, oblique fibre, very likely a kinetodesma (Fig. 22). **21:** Extrusomes of a specimen from Costa Rica. B = oral basket, DB1–3 = dorsal brush rows, E = extrusomes, FG = fat globules, FV = food vacuole, MA = macronucleus, MI = micronuclei, OB = oral bulge. Scale bars  $50 \mu\text{m}$  (13) and  $25 \mu\text{m}$  (18).



**Fig. 23–26.** *Enchelmys gelei*, oral and somatic infraciliature of specimens from the Galápagos archipelago after protargol impregnation. **23–25:** Ventrolateral and dorsolateral view of a representative specimen. Note the highly tortuous macronucleus and the three dorsal brush rows, which commence subapically with a distinct right turn. The oral basket is formed by oralised somatic monokinetids, that is, from nematodesmata originating from the anterior 10–20 basal bodies of the somatic ciliary rows. **26:** Ventral view of anterior body portion showing the broadly ellipsoidal oral bulge. Note absence of a dikinetidal circumoral kinety. B = oral basket, DB = dorsal brush, EP = excretory pores of contractile vacuole, MA = macronucleus, MI = micronuclei, OB = oral bulge, 1,2,3 = dorsal brush rows. Scale bars 30  $\mu\text{m}$  (23, 24) and 10  $\mu\text{m}$  (25, 26).



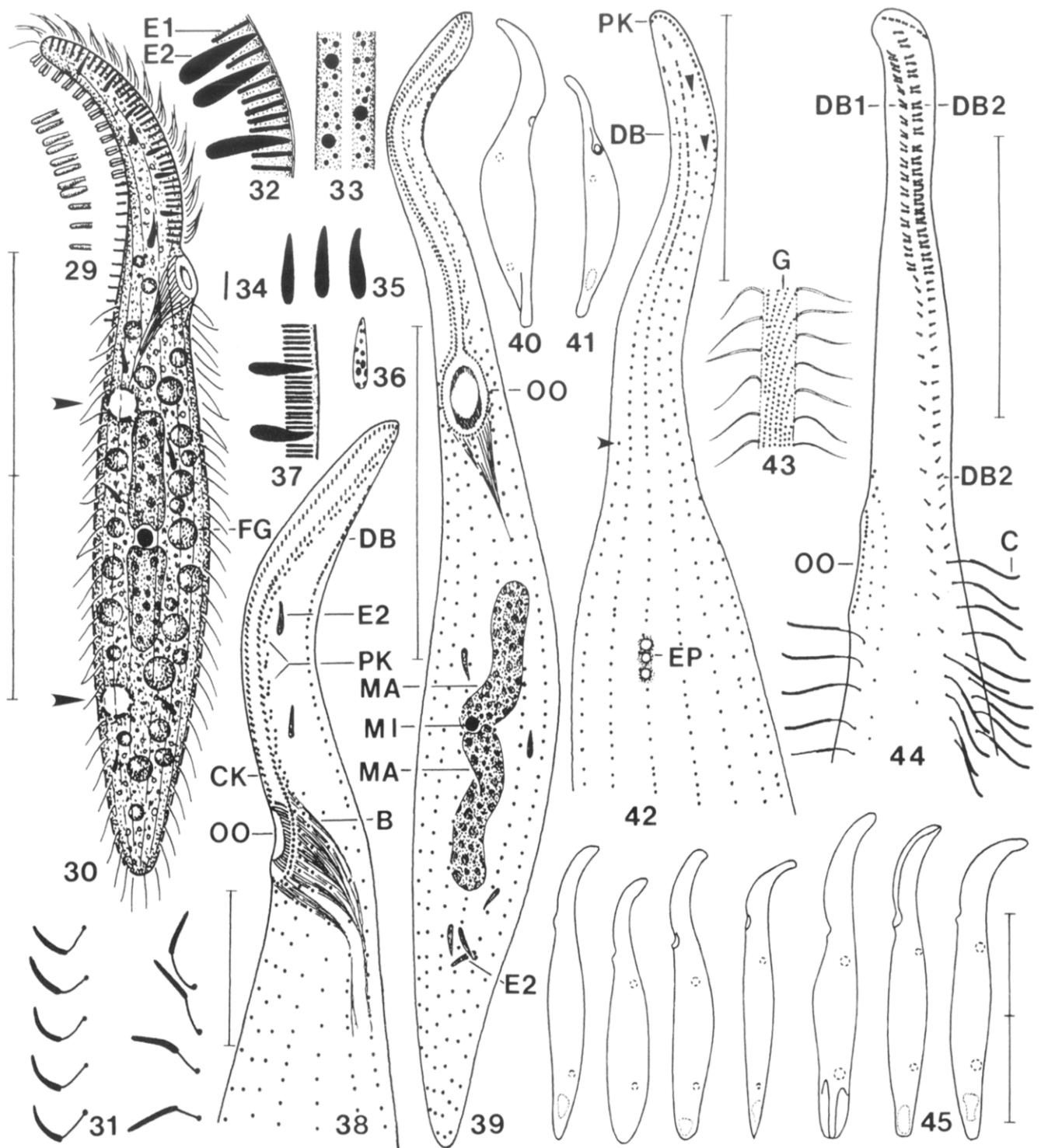
**Fig. 27, 28.** *Enchelys geleii* from life. **27:** Optical section of anterior body half of a squeezed specimen showing dorsal brush (arrow) and peripheral extrusome fringe. **28:** Surface view showing extrusomes and loosely arranged cortical granules. C = somatic cilia, E = extrusomes, FG = fat globules, G = cortical granules.

**Table 4.** Morphometric data on *Dileptus armatus* from Helgoland (upper line) and Berlin (lower line).

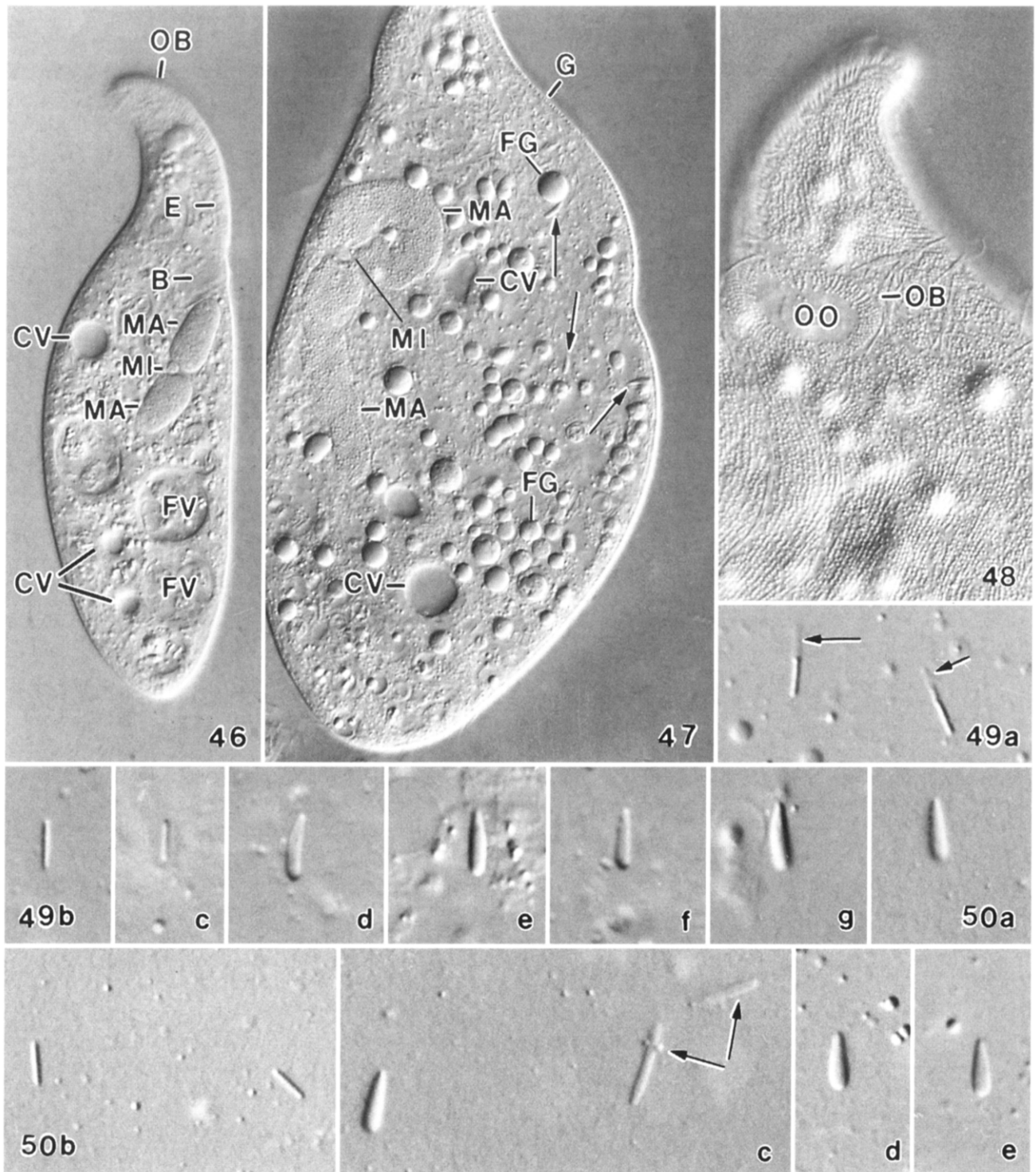
Character <sup>1)</sup>	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	179.3	166	30.1	6.9	16.8	132	238	19
	149.0	150	18.5	4.8	12.4	120	180	15
Body, maximum width	24.8	24	4.4	1.0	17.8	17	32	19
	18.7	18	2.4	0.6	12.8	15	23	15
Anterior body end to oral basket, distance	48.6	50	8.2	1.9	16.9	29	60	19
	45.2	46	8.2	2.1	18.1	35	65	15
Oral basket opening, length <sup>2)</sup>	12.2	12	1.7	0.4	13.8	9	15	19
Oral basket opening, width <sup>2)</sup>	7.5	7	1.1	not measured	not measured	6	10	13
				0.3	15.0			
Nuclear figure, length	43.4	44	7.3	1.7	16.7	28	54	19
	33.6	34	8.4	2.1	25.1	16	50	15
Macronuclear segment, length	21.5	22	3.3	0.7	15.1	15	26	19
	24.9	25	6.1	1.6	24.4	17	35	15
Macronuclear segment, width	7.6	8	1.4	0.3	18.2	5	10	19
	4.7	5	0.8	0.2	17.4	3	6	15
Micronucleus, maximum diameter	3.3	3	0.8	0.2	24.4	2	5	19
	1.6	2	0.5	0.1	29.3	1	3	12
Macronuclear segments, number	2.0	2	0.0	0.0	0.0	2	2	19
	2.0	2	0.0	0.0	0.0	2	2	15
Micronuclei, number	1.0	1	0.0	0.0	0.0	1	1	19
	1.0	1	0.0	0.0	0.0	1	1	12
Somatic ciliary rows, number	14.0	15	1.7	0.4	12.4	10	17	19
	11.3	11	1.5	0.4	13.1	10	15	14
Cilia in mid-body in 10 $\mu$ m, number	4.4	4	1.0	0.2	21.8	3	6	19
	6.2	6	1.0	0.3	16.9	5	8	14
Dorsal brush rows, number	2.0	2	0.0	0.0	0.0	2	2	19
	2.0	2	0.0	0.0	0.0	2	2	8

<sup>1)</sup> Data based on protargol-impregnated (Foissner's method), mounted specimens from non-flooded Petri dish cultures. Measurements in  $\mu$ m. CV = coefficient of variation in %, M = median, Max = maximum, Min = minimum, n = number of individuals investigated, SD = standard deviation, SE = standard error,  $\bar{x}$  = arithmetic mean.

<sup>2)</sup> Basket opening = circumoral kinety.



**Fig. 29–45.** *Dileptus armatus*, Helgoland (29–33, 38, 39, 42, 43) and Berlin (34–37, 40, 41, 44, 45) population from life (29, 30, 32–35, 37, 40, 41, 43, 45) and after protargol impregnation (31, 36, 38, 39, 42, 44). **29:** Small portion of dorsal brush, bristles 2–3 µm long. **30:** Right lateral view of a representative specimen. Arrowheads mark contractile vacuoles. **31:** Two ciliary rows with cilia inflated and heavily impregnated distally. **32, 33:** Lateral and frontal view of oral bulge of a Helgoland specimen showing the two types of extrusomes; type two 4–6 µm long. **34, 35, 37:** Type 1 and 2 extrusomes of Berlin specimens. **36:** Type 2 extrusome containing argyrophilic granules. **38:** Infraciliature of left side in anterior body portion. **39:** Infraciliature of ventral side. **40, 41, 45:** Shape and size variability of Berlin population, video records, drawn to scale. **42, 44:** Infraciliature of dorsal side in anterior body half. Arrowheads mark shortened ciliary rows. **43:** Surface view showing cortical granules. B = oral basket, C = somatic cilia, CK = circumoral kinety, DB1,2 = dorsal brush rows, EP = excretory pores, E1,2 = type 1 and 2 extrusomes, FG = fat globules, MA = macronuclear segments, MI = micronucleus, OO = oral opening, PK = preoral kineties. Scale bar division 50 µm (30, 39, 45), 30 µm (42), 20 µm (38, 44).



**Fig. 46–50:** *Dileptus armatus*, Austrian (46), Helgoland (German) type (47–49), and Maldivian (50) specimens from life (interference contrast). **46:** Right lateral view of a slightly squeezed specimen showing main cell organelles. **47:** Dorsal view of a squashed specimen. Arrows mark type 2 extrusomes. **48:** Surface view of ventral anterior half showing the distinct rows of cortical granules, which extend into the oral bulge. **49a, b, c:** Partially or completely exploded (49a) and resting (49b, c) type 1 extrusomes, which are rod-shaped and about 3  $\mu\text{m}$  long. Extruded organelles have an about 3  $\mu\text{m}$  long, hyaline extension (49a, arrows). **49d–g:** Resting type 2 extrusomes are clavate and 4–6  $\mu\text{m}$  long. **50a–e:** Resting type 1 (50b) and type 2 (50a, c–e) extrusomes from the Maldivian specimens are very similar in size and shape to those of the German type population (49a–g). Figure 50c shows two partially or completely exploded type 2 extrusomes (arrows). B = oral basket, CV = contractile vacuoles, E = extrusomes, FG = fat globules, FV = food vacuoles, G = cortical granules, MA = macronuclear segments, MI = micronucleus, OB = oral bulge, OO = oral opening.

Shape blunt because proboscis rather broad and short and trunk not tailed; proboscis flattened leaf-like, proboscis:trunk ratio 3:1–4.4:1, on average 3.7:1; trunk cylindroidal, posterior end narrowly rounded, rarely bluntly pointed, never extended tail-like (Fig. 30, 40, 41, 45). Macronuclear segments in centre of trunk, sausage-shaped, sometimes slightly wrinkled, contain many small nucleoli. Micronucleus invariably between macronuclear nodules, about  $4 \times 3 \mu\text{m}$  in vivo (Fig. 30, 39, 46, 47). One contractile vacuole each in anterior and posterior third of trunk, each vacuole with one to six, usually three pores one after the other (Fig. 30, 42, 45–47). Two types of extrusomes in oral bulge and cytoplasm: type 1 numerous but inconspicuous because rod-shaped and only about  $3 \mu\text{m}$  long, does not impregnate with protargol, composed of a  $3 \mu\text{m}$  long hyaline and a  $3 \mu\text{m}$  long refractive portion when exploded (Fig. 30, 32–34, 49a–c, 50b); type 2 extrusomes sparse (only about 15 organelles in proboscis) but conspicuous because highly refractive, clavate and slightly curved, and  $4\text{--}6 \times 1\text{--}2 \mu\text{m}$  in size, impregnate lightly with protargol (Fig. 30, 32, 33, 35–39, 47, 49d–g, 50a, c–e). Cortex colourless, very flexible and robust, cells thus withstand even strong cover glass pressure; contains innumerable, highly refractive, about  $0.8 \times 0.3 \mu\text{m}$ -sized granules (mucocysts?) in oral bulge and body, where they form six to nine narrowly spaced rows between two kineties each, do not impregnate with protargol (Fig. 43, 47, 48). Cytoplasm colourless, contains few to many fat globules  $1\text{--}7 \mu\text{m}$  across and large food vacuoles with *Vorticella* sp. and *Thekamoeba* sp. (Fig. 30, 46, 47). Glides and winds moderately fast on slide surface and soil particles or swims slowly, moving the proboscis to and fro.

Somatic and oral infraciliature as in other small members of the genus [19, 24]. Thus, only some main features will be addressed (Fig. 38, 39, 42, 44; Tab. 4): (1) Somatic and oral cilia about  $8 \mu\text{m}$  long in vivo, invariably impregnated as shown in figures 31 and 44, that is, with a distinctly inflated and darkly impregnated distal half. This peculiarity is found in all species of the genus, although I did not mention it in previous descriptions. (2) Postoral somatic ciliary rows abut at right angles to circumoral kinety (Fig. 39). (3) There is a rather broad, blank area on the left side of the proboscis because some ciliary rows commence at level of oral opening (Fig. 38, 39, 42, 44). (4) Two dorsal brush rows with paired,  $2\text{--}3 \mu\text{m}$  long, distally slightly inflated bristles in anterior half and single, about  $1.5 \mu\text{m}$  long bristles in posterior half (Fig. 42, 44). (5) Preoral kineties composed of two to four, usually three cilia at left side of circumoral kinety (Fig. 38, 39). (6) Pharyngeal basket distinct and of usual structure (Fig. 38, 39).

The Berlin population, which was also studied in detail (Fig. 34–37, 40, 41, 44, 45), is very similar to the type population, except for some morphometrics (Tab. 4).

**Occurrence and ecology:** As yet found at three sites in Germany (see site description and Table 1), in Austria (riparian forest soil near the river Enns in Upper Austria; Fig. 46), and the Maldives (Little Bandos, North Male Atol. Highly saline litter under coastal shrubs, pH 7.7, collected by Dr. W. Petz on 15.12.1990; Fig. 50). Thus, *D. armatus* is a euryhaline and very likely cosmopolitan ciliate.

**Comparison with related species:** *Dileptus armatus* belongs to a group of untailed dileptids with a length of  $100\text{--}200 \mu\text{m}$  and two contractile vacuoles, two macronuclear segments, and two dorsal brush rows. These species, viz. *Dileptus gracilis*, *D. americanus*, and *D. bivacuolatus* have only inconspicuous, rod-shaped extrusomes [9, 42]. Of course, one can assume that the big, clavate extrusomes were overlooked and then identify the present population with one of these species. However, *D. gracilis* lacks clavate extrusomes, according to a recent redescription [24], and *D. bivacuolatus*, a poorly known species, has a micronucleus attached to each macronuclear segment. Thus, there remains *D. americanus* Kahl [42]. Fortunately, I have a species in my unpublished material, which matches Kahl's description, including the rod-shaped, inconspicuous extrusomes. Thus, the German population can be classified as a new taxon. However, one can doubt whether extrusomes are a sufficient species character. They are, in my opinion, because they are a conspicuous feature very likely related to a special kind of predation. Furthermore, extrusomes show a high diversity in gymnostomatid haptorids and are a fairly constant feature, as also evident in *D. armatus*, where three spatially widely distant populations are highly similar in this respect (Fig. 32, 37, 49, 50).

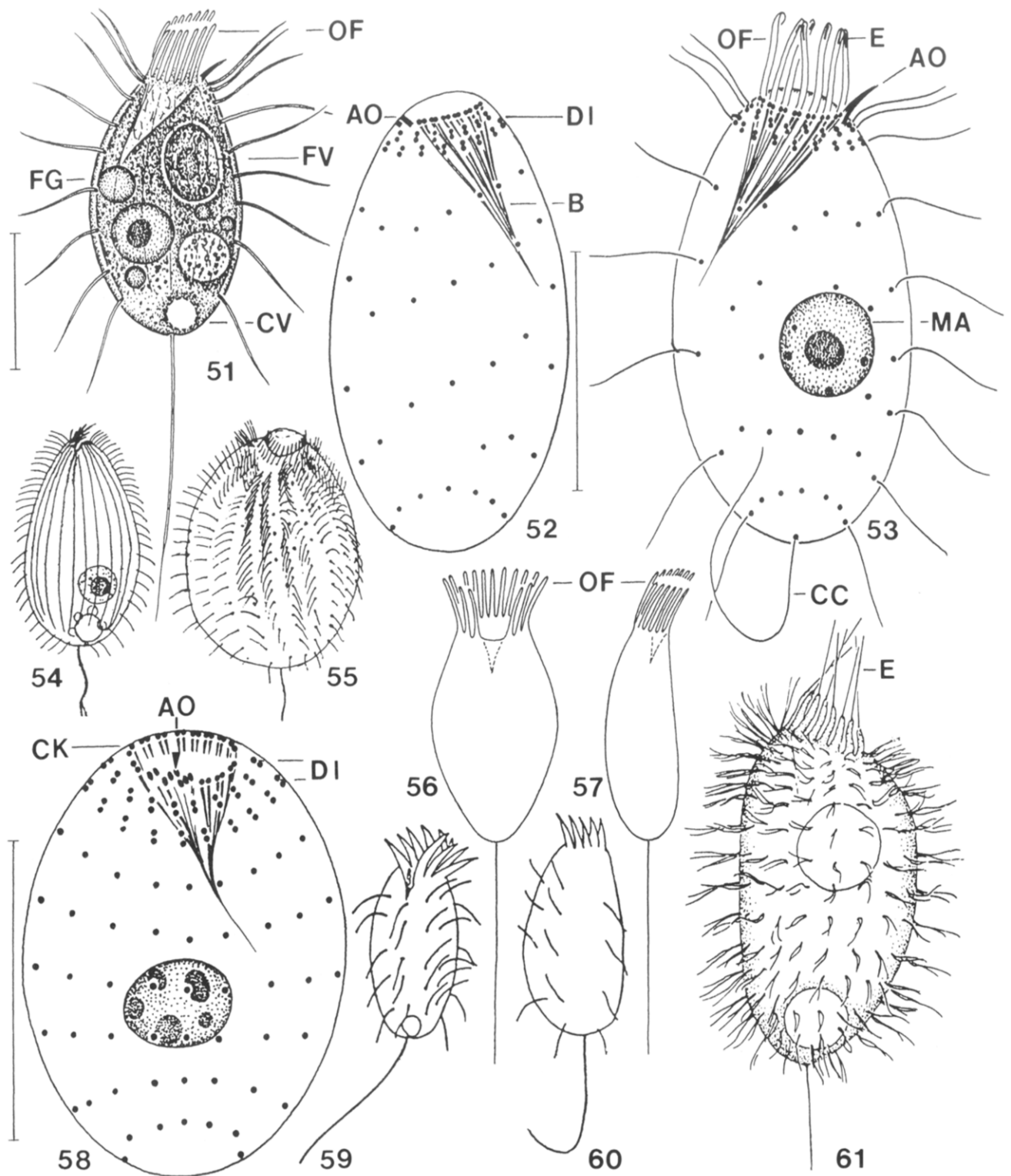
Conspicuous, thick extrusomes occur also in *D. costaricanus* Foissner, 1995 ([27] many small macronuclear nodules and contractile vacuoles, length  $230\text{--}330 \mu\text{m}$ ) and *D. orientalis* Song et al., 1988 ([56]  $5\text{--}8$  contractile vacuoles, 3 dorsal brush rows, extrusomes only  $1\text{--}2 \mu\text{m}$  long and lemon-shaped), which is similar to *D. armatus* in body size, nuclear apparatus, number of ciliary rows, and habitat (soil).

*Plagiocampa ovata* Gelei, 1954 (Fig. 51–58, 61, 71; Tab. 5)

**Material:** Two slides with protargol-impregnated specimens from Madeiran population have been deposited in the Oberösterreichische Landesmuseum in Linz (LI). Relevant specimens are marked by a black ink circle on the cover glass.

**Redescription:** Size in vivo  $25\text{--}35 \times 12\text{--}20 \mu\text{m}$ , usually about  $30 \times 17 \mu\text{m}$ , as calculated from some live measurements and values shown in Table 5, taking into account a shrinkage of  $10\text{--}15\%$  due to the preparation





**Fig. 51–61.** *Plagiocampa ovata* (51–58, 61) and *Halterioforma caudata* (59, 60) from life (51, 56, 57), after protargol impregnation (52, 53, 58), and other methods (54, 55, 59–61). Figures 51–53, 58, originals from Madeiran population; 56, 57, originals from Australian population; 54, 55, from [34]; 59, 60, from [40]; 61, from [12]. 51: Right lateral view. 52, 53, 58: Infraciliature of right and left side, and oblique ventral view. 54, 55: Hungarian specimens from life and after mercuric chloride fixation (54) and after opal blue and silver preparations (55). 56, 57: Ventral and lateral view of same, distinctly flattened specimen. 59, 60: This 15–20 µm long species is very likely a *Plagiocampa* (mercuric chloride fixed and opal blue stained). 61: Lateral view of French specimen, length 32–38 µm (phase contrast after osmium fixation). AO = adoral organelles, B = oral basket, CC = caudal cilium, CK = circumoral kinety, CV = contractile vacuole, DI = dikinetids at anterior end of kineties, E = extrusomes in oral flaps, FG = fat globule, FV = food vacuole, MA = macronucleus, OF = oral flaps. Scale bars 15 µm.

**Table 5.** Morphometric data on *Plagiocampa ovata*.

Character <sup>1)</sup>	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	24.3	25	2.7	0.8	11.1	20	28	11
Body, width	14.7	14	2.2	0.7	14.9	11	18	11
Oral opening, diameter	6.0	6	0.6	0.2	10.5	5	7	11
Macronucleus, length	5.9	6	–	–	–	6	7	11
Macronucleus, width	5.8	6	–	–	–	5	7	11
Ciliary rows, number	15.9	16	0.8	0.3	5.2	15	17	11
Kinetids in a dorsal kinety, number <sup>2)</sup>	8.1	8	1.1	0.3	14.0	7	10	11
Oral flaps, number <sup>3)</sup>	13.1	13	0.8	0.3	6.3	12	14	11
Macronuclei, number	1.0	1	0.0	0.0	0.0	1	1	11

<sup>1)</sup>Data based on protargol-impregnated (Foissner's method), mounted specimens from a non-flooded Petri dish culture. Measurements in  $\mu\text{m}$ . CV = coefficient of variation in %, M = median, Max = maximum, Min = minimum, n = number of individuals investigated, SD = standard deviation, SE = standard error,  $\bar{x}$  = arithmetic mean.

<sup>2)</sup>Dikinetids counted as 1 kinetid.

<sup>3)</sup>Oral flaps = paroral dikinetids.

procedures. Shape fairly constant, ellipsoidal to broadly fusiform, an Australian population dorsoventrally flattened up to 2:1 (Fig. 51, 56, 57). Macronucleus in middle third of cell, globular, with a large, central nucleolus in about 70% of specimens, others have some small, peripheral nucleoli. Micronucleus not seen, not stained by protargol. Contractile vacuole in posterior body end slightly ventral of pole centre; excretory pore and cytopyge not seen. Cortex rather thick and opaque, without extrusomes. Extrusomes in oral flaps (see below) and in and around pharyngeal basket, slightly fusiform, difficult to recognise because only 1  $\mu\text{m}$  long. Cytoplasm colourless and rather transparent, contains some fat globules and 3–10  $\mu\text{m}$ -sized food vacuoles with remnants of heterotrophic flagellates and small ciliates, e.g., *Cyclidium muscicola*; never packed with refractive granules in anterior body portion as many congeners. Movement conspicuous because fast and shaky due to the oral flaps, which beat up and down causing a distinct vibration of the whole cell, making it unsharp at any focal plane.

Ordinary somatic cilia about 10  $\mu\text{m}$  long, equidistantly and widely spaced, except for narrowly spaced perioral dikinetids. Ciliary rows extend longitudinally and equidistantly, commence underneath oral opening with two pairs each of ciliated (perioral) dikinetids, anterior cilium lacking in posterior dikinetid; slightly shortened posteriorly, leaving blank small pole area containing a single caudal cilium about as long as cell (Fig. 51–53, 58).

Oral opening occupies anterior body end, circular, in vivo about 7  $\mu\text{m}$  across, almost entirely surrounded by (paroral) dikinetids associated with conspicuous, about 6  $\mu\text{m}$  long, ventrally directed flaps incessantly beating up and down, giving the impression of a digitate membrane or small adoral membranelles; individual flaps composed of two cilia and a sharply impregnating ex-

trusome anteriorly (Fig. 51, 53). Adoral organelles (brosse) minute, side by side at end of three ventral somatic kineties, interrupt dikinetidal paroral membrane, very likely composed of dikinetids, right organelle composed of four basal bodies, left organelles consist of six basal bodies each. Pharyngeal basket oblique-conical, that is, ventrally longer than dorsally, open on ventral (brosse) side, basket rods distinct and originating from dikinetids comprising paroral membrane (Fig. 52, 53, 58).

**Occurrence and ecology:** Gelei [34] discovered *P. ovata* in an infusion of mud from a temporary pool in Hungary. It survived for several weeks. Fauré-Fremiet and André [12] redescribed *P. ovata* from moss of France. I know *P. ovata* from terrestrial habitats worldwide, for instance: Madeira, as described in Material section; Australia, Adelaide, pasture on very sandy soil, pH 8.1; Africa, Namib Desert (Sossosvlei), litter and sand from a dune. If all identifications are correct, then *P. ovata* is a euryoecious cosmopolitan living in both, freshwater and soil. Abundances are low with the method applied.

**Comparison with original description and related species:** *Plagiocampa* comprises inconspicuous ciliates difficult to study due to their small size and often dense cytoplasmic granulation. Only few of the numerous species described have been reinvestigated with modern methods [15, 19, 30]. Thus, the interpretation of the old descriptions is difficult and the taxonomic value of various characteristics is uncertain. As concerns the present population, it matches *P. ovata*, a freshwater species, in three main features: one caudal cilium, 16–18 (15–17 in Madeiran specimens) ciliary rows, and 10–15 (12–14 in Madeiran specimens) oral flaps. Size (50  $\times$  30  $\mu\text{m}$  vs. 30  $\times$  17  $\mu\text{m}$ ), special cytoplasmic granulation (present vs. absent), movement (without vs. with particularities), live appearance of oral apparatus (narrow



vs. conspicuously wide, cp. Fig. 51, 54), and number of cilia in a row (about 30 vs. 8) are rather different, indicating that the Madeiran population is a different species, possibly identical with *P. ovata* from moss investigated by Fauré-Fremiet and André [12], which has the same conspicuous oral apparatus as the Madeiran specimens (Fig. 51, 61). Furthermore, length (32–38 µm) and number of ciliary rows (22) are similar. Unfortunately, Fauré-Fremiet and André [12] do not mention the number of oral flaps and obviously misinterpret the somatic ciliature as being composed entirely of ciliated dikinetids (Fig. 61). Considering that three main characteristics agree, I prefer, at the present state of knowledge, identifying the Madeiran population as *P. ovata*. However, I do not neotypify the species with this material. But neotypification will be necessary because the original description is too incomplete for a reliable identification.

*Plagiocampa ovata* is easily confused with *P. bitricha* Foissner [30], which has two caudal cilia and only one dikinetid at the anterior end of the somatic kineties. Another similar species is *Halteriiforma caudata* Horváth [40], at least as concerns the prominent oral flaps and sparse ciliation (Fig. 59, 60). However, it has only eight ciliary rows and might thus be a different species.

#### *Haplocaulus terrenus* Foissner, 1981 (Fig. 62–70)

**Material:** Four slides with protargol-impregnated specimens from the Munich population have been deposited in the Oberösterreichische Landesmuseum in Linz (LI). Relevant specimens are marked by a black ink circle on the cover glass.

**Comparison with related taxa:** I got excellent protargol preparations from this rare species and can thus add important details to the original description, which is almost entirely based on observations of living material. In protargol slides, *H. terrenus* is distinguished from other terrestrial peritrichs by several features. *Vorticella astyliiformis*, a very common species similar to *H. terrenus* in many respects, has a much simpler and finer myoneme system, except for the myoneme bundle in the peristomial collar, which is more distinct in *V. astyliiformis* [15]. *Pseudovorticella sphagni* has a distinct gap between the adoral peniculi 1 and 2 [27], which are close together in *H. terrenus* (Fig. 65, 67). *Pseudocarchesium claudicans*, whose oral infraciliature is very similar to that of *H. terrenus*, lacks an epistome membrane and has a different myoneme system, i.e., possesses a myoneme tube, which is linked to the peristomial disk, in the peristomial collar [24]; furthermore, the myonemes bifurcate mainly between scopula and anlage of the aboral ciliary wreath.

**Additional observations:** (1) The species is apparently solitary because, although abundant, no colonies

have ever been seen. However, the stalk was spirally contracted in all protargol-impregnated specimens, although in vivo contraction was slow and S-like or in a wide, indistinct spiral. Thus, the generic assignment may be questioned (see [53] for a detailed discussion of genera). (2) There are about 33 transverse striae (silver-lines) between oral opening and aboral ciliary wreath and about 7 silverlines from there to the scopula. (3) In protargol preparations, the cortex occasionally appears as in *Pseudovorticella* spp., that is, composed of transversely arranged, square, granular alveoli (Fig. 64). (4) The scopula consists of a ring of minute rods surrounding an area with scattered granules (Fig. 65, 68). (5) The ciliary pattern of *H. terrenus* basically agrees with that of vorticellid peritrichs. Thus, mainly some special features will be described. The adoral ciliary spiral performs about one turn (360°) on the peristomial disk before it plunges into the buccal cavity, where it performs about half a turn (180°); the paroral spiral commences slightly later than the adoral. As usual, the adoral spiral separates into three peniculi, which consist of 3 ciliary rows each, in the vestibulum; all peniculi remain close together, and peniculus 2 ends slightly above peniculi 1 and 3, which abut proximally (Fig. 65, 67, 70). (6) The myoneme system is well developed, except in the peristomial collar, where only a few, weakly impregnated strands extend. Likewise, myonemes are lacking at the vestibular entrance. The myonemes, which appear thicker and more densely bundled in swimmers than adults, are strongly ramified above the aboral ciliary wreath, and some of the longest and thickest bundles extend into the peristomial disk, where they are anchored to the adoral ciliary spiral (Fig. 65–67). (7) Swimmers are cylindroidal with a slight, but distinct inflation above the aboral ciliary wreath, which consists of numerous oblique ciliary rows each composed of about seven cilia (Fig. 65, 66). Contracted swimmers are broadly pyriform and have two deep folds posteriorly (Fig. 64). At the vestibular entrance, there is a conspicuous epistome membrane, whose anlage is recognisable in adult specimens (Fig. 67), which consists of about seven long cilia widely projecting from the oral opening (Fig. 64, 65). The outer portion of the adoral spiral is heavily folded, as shown in Figures 65 and 69.

**Occurrence and ecology:** *Haplocaulus terrenus* is very likely a cosmopolitan [29]. However, it is a rare species occurring mainly in leaf litter. Abundances are usually very low with the non-flooded Petri dish method, except at the site with the population used for the present description.

#### *Holostichides dumonti* nov. spec. (Fig. 72–78; Tab. 6, 7)

**Diagnosis:** Size in vivo about 240 × 50 µm; elongate ellipsoidal. Cortical granules in rows, colourless, about

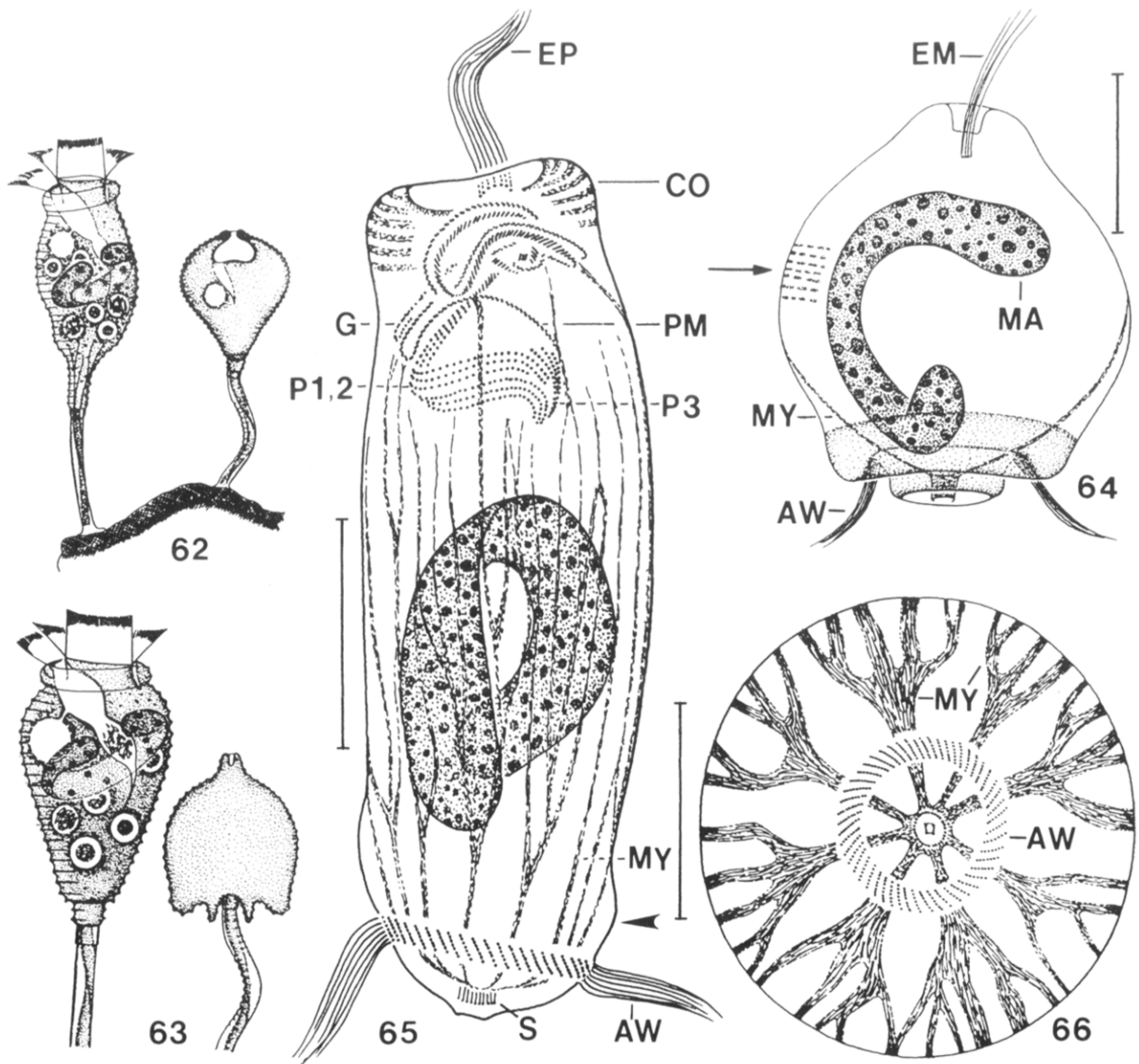


Fig. 62–66. *Haplocaulus terrenus* from life (62, 63; from [15]) and after protargol impregnation (64–66). 62, 63: Extended and contracted specimens, length of zooids 40–60  $\mu\text{m}$ . 64, 65: Extended and contracted swimmers. Arrow marks cortical granulation. Arrowhead denotes slight inflation above aboral ciliary wreath. 66: Posterior polar view of a contracted swimmer showing the extensive myoneme system. AW = aboral ciliary wreath, CO = peristomial collar, EP = epistome membrane, G = germinal kinety, MA = macronucleus, MY = myonemes, PM = paroral membrane, P1,2,3 = peniculi (adoral organelles), S = scopula. Scale bars 10  $\mu\text{m}$ .

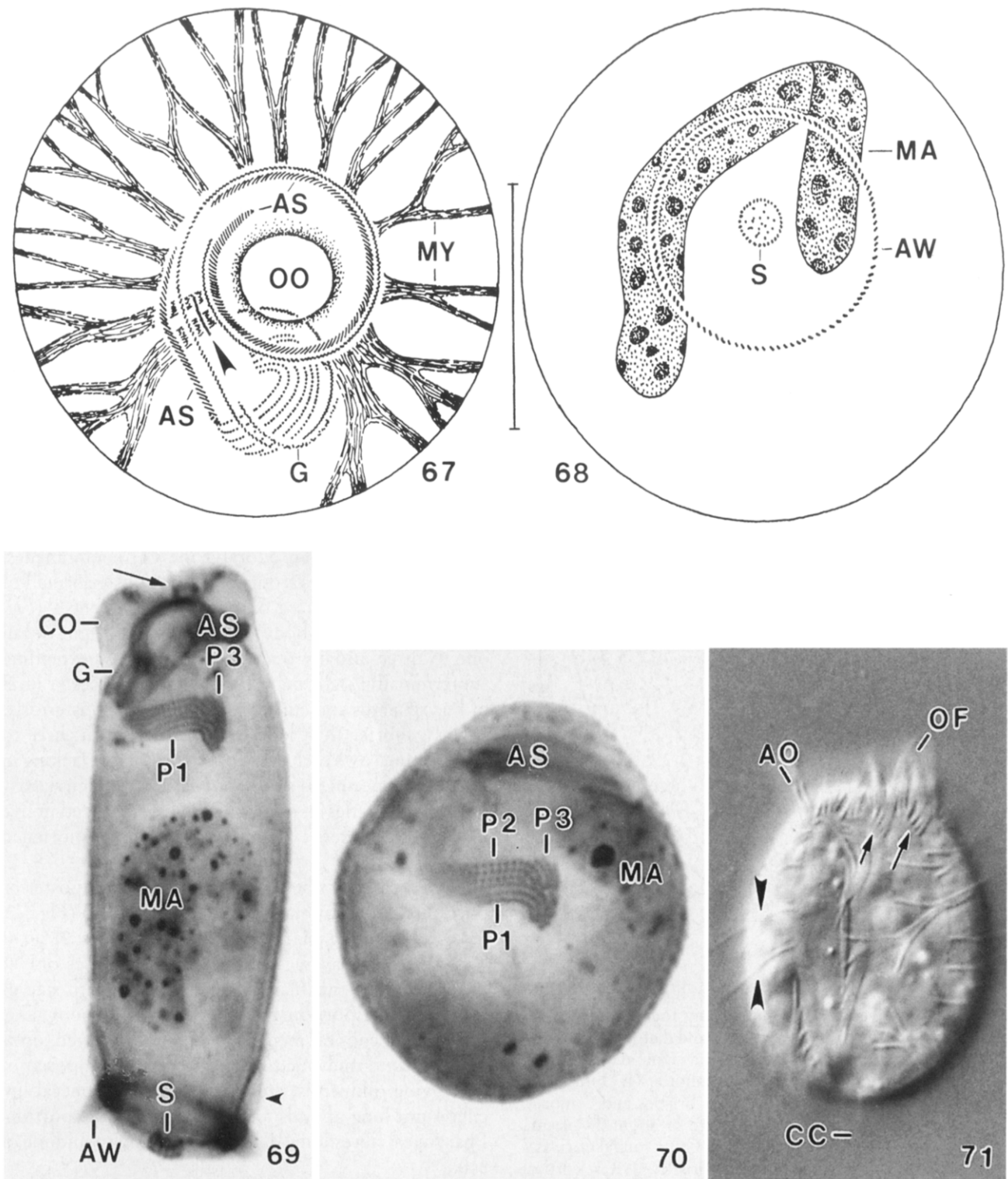
2  $\times$  1  $\mu\text{m}$ . On average, 120 macronuclear nodules, 42 adoral membranelles, 1 buccal cirrus, 4 frontoterminal cirri, 10 midventral pairs, 1 cirral row right of midventral tail, 7 caudal cirri, and 5 dorsal bristle rows.

**Type location:** Soil from a coniferous forest near the town of Savonlinna, Finland (E29° N61°50').

**Type material:** One holotype slide and three paratype slides with protargol-impregnated (Foissner's method) specimens have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria. Relevant specimens are marked by a black ink circle on the cover glass.

**Dedication:** I dedicate this new species to Prof. Dr. Henry J. Dumont, Ghent University, for supporting publication of the "Monograph of the Oxytrichidae (Ciliophora, Hypotrichia)" by Dr. Helmut Berger [2], my former student and later co-worker.

**Description:** Size in vivo 190–280  $\times$  40–60  $\mu\text{m}$ , length:width ratio 3.8–5.1:1, on average 4.6:1 (Tab. 6), flattened about 1.5:1 dorsoventrally. Shape very similar to *H. chardezi*, that is, usually elongate ellipsoidal and slightly twisted about main body axis, rarely more or less distinctly sigmoidal (Fig. 72, 73). Macronuclear nodules in central portion of cell, globular to elongate



**Fig. 67–70.** *Haplocaulus terrenus*, infraciliature after protargol impregnation. **67, 68:** Oral and aboral view of same, adult specimen. Arrowhead marks anlage of epistome membrane. Note lack of myonemes at buccal entrance. **69, 70:** Extended swarmer and contracted adult. Arrow marks epistome membrane. Arrowhead denotes slight inflation above aboral ciliary wreath. AS = adoral ciliary spiral, AW = aboral ciliary wreath, CO = peristomial collar, G = germinal kinety, MA = macronucleus, MY = myonemes, OO = oral opening, P1,2,3 = peniculi (adoral organelles), S = scopula. Scale bar 10  $\mu$ m.

**Fig. 71.** *Plagiocampa ovata* from life; slightly squeezed specimen showing long somatic cilia (arrowheads) and four cilia (two dikinetids) at anterior end of ciliary rows (arrows). AO = adoral organelles, CC = caudal cilium, OF = oral flaps.

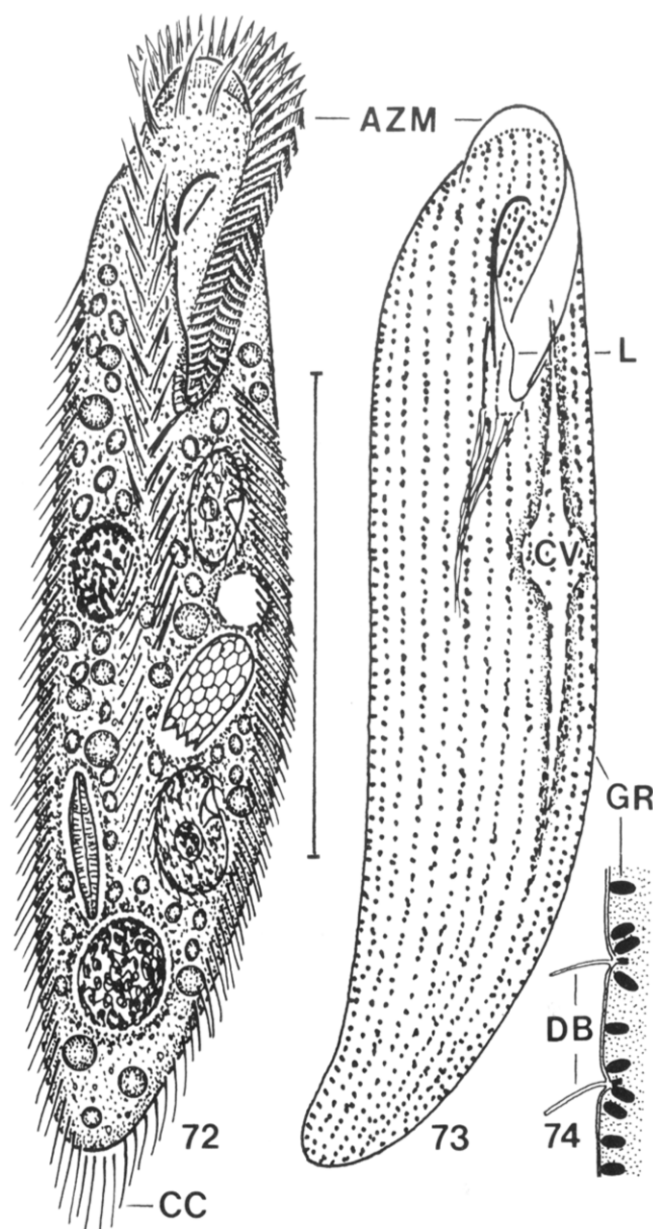


Fig. 72–74. *Holostichides dumonti* from life. 72: Ventral view of a representative specimen with many food vacuoles containing small ciliates, testate amoebae, and diatoms. Note lack of transverse cirri. 73: Ventral view of a sigmoidal specimen. The cortex contains rows of distinct granules. 74: Optical section of dorsal surface showing dorsal bristles and compact, colourless cortical granules with a size of about  $2 \times 1 \mu\text{m}$ . AZM = adoral zone of membranelles, CC = caudal cirri, CV = contractile vacuole, DB = dorsal bristles, GR = cortical granules, L = buccal lip. Scale bar  $100 \mu\text{m}$ .

ellipsoidal (3:1), on average  $6 \times 3 \mu\text{m}$  (Tab. 6), contain minute nucleoli. Micronuclei globular to broadly ellipsoidal, all left of cell's midline (Fig. 72, 77). Exact number of both macronuclear nodules and micronuclei difficult to count because of high number of nodules and many similar-sized and stained cytoplasmic inclusions.

Contractile vacuole in or slightly above mid-body, with two long collecting canals (Fig. 72, 73). Cortex thin, fragile, and very flexible. Cortical granules in rather widely spaced, meridional rows, colourless, compact and thus bright and easy to recognise, about  $2 \times 1 \mu\text{m}$ , stain red and become extruded when methyl green-pyronin is added (Fig. 73, 74). Cytoplasm colourless, often packed with fat globules  $1\text{--}2 \mu\text{m}$  across and food vacuoles containing fungal spores, diatoms, heterotrophic flagellates, testate amoebae (*Euglypha*) and small ciliates (*Drepanomonas pauciciliata*). Glides slowly on slide surface and on and between soil particles showing great flexibility.

Cirri about  $14 \mu\text{m}$  long in vivo, rather thin and short as compared with size of cell, arrangement and variability as in other members of genus [21], thus only some details will be described (Fig. 72, 75, 76, 78; Tab. 6). Frontal cirri only slightly enlarged; frontoterminal cirri easily overlooked because minute and at right anterior margin of cell; buccal cirrus close to paroral membrane near mid-buccal cavity; midventral row conspicuous, distinctly longer than adoral zone of membranelles, size of cirri decreases from anterior to posterior; tail of midventral row, where ontogenesis commences (Fig. 78), extends to mid-body in cell's midline, right of tail one to three, usually one ventral cirral row extending subterminally; right marginal row commences at level of buccal cirrus and curves to cell's midline posteriorly, slightly shorter than left row; caudal cirri in three to four minute rows each composed of 1–4 cirri, lacking in 1 out of 18 specimens investigated; transverse cirri lacking; dorsal bristles  $3\text{--}4 \mu\text{m}$  long in vivo, arranged in five bipolar rows, except for anteriorly slightly shortened row 4.

Buccal cavity rather large and deep, right posterior portion covered by narrow, membranous lip (Fig. 72, 73). Adoral zone of membranelles occupies 28% of body length on average (Tab. 6), longest bases only  $7 \mu\text{m}$  wide, zone thus narrow as compared with size of cell, proximal portion broadened slightly spoon-like. Paroral and endoral membrane distinctly curved, optically cross in mid-buccal cavity; paroral composed of zigzagging dikinetids, emerges from slit in buccal lip, cilia  $4 \mu\text{m}$  long at ends and  $10 \mu\text{m}$  in middle portion. Pharyngeal fibres long, extend posteriorly in midline of cell.

**Occurrence and ecology:** As yet found at type location, at two sites in Africa, and in a soil sample from the Canary Islands. Thus, *H. dumonti* is very likely cosmopolitan. However, the African populations still have to be checked in detail.

**Comparison with related species:** I agree with Eigner [11] that *Parabakuella typica* [55] and *Periholosticha wilberti* [54] belong to *Holostichides* [21]. Thus, the genus presently comprises five species (Fig.

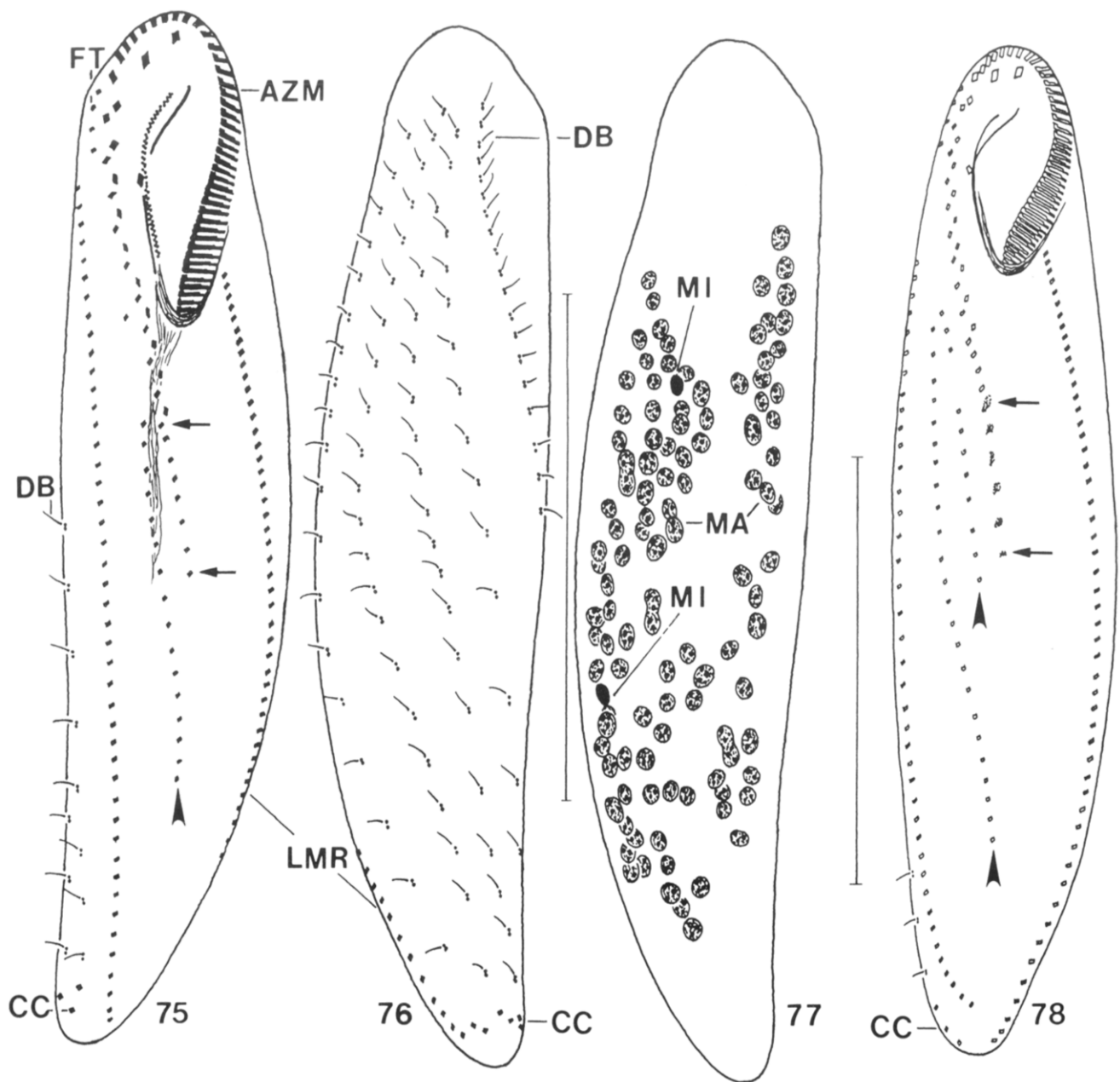


Fig. 75–78. *Holostichides dumonti* after protargol impregnation. 75–77: Infraciliature of ventral and dorsal side and nuclear apparatus of same, representative specimen. Arrows border tail of midventral row. Arrowhead marks cirral row right of tail of midventral row. 78: Very early divider showing ontogenesis commencing in tail of midventral row (arrows). Arrowheads mark two cirral rows right of tail of midventral row. AZM = adoral zone of membranelles, CC = caudal cirri, DB = rows of dorsal bristles, FT = frontoterminal cirri, LMR = left marginal row, MA = macronuclear nodules, MI = micronuclei. Scale bars 100  $\mu$ m.

79–83; Tab. 7): *Holostichides chardezi* (type) Foissner, 1987; *H. typicus* (Song & Wilbert, 1988) Eigner, 1994; *H. terricola* Foissner, 1988; *H. wilberti* (Song, 1990) Eigner, 1994; and *H. dumonti* nov. spec. *Holostichides terricola* and *H. wilberti*, which are probably synonymous, lack buccal cirri and are much smaller, thus forming a distinct subgroup within the genus. *Holostichides chardezi* and *H. typicus* are considerably smaller than *H. dumonti* and possess much fewer

macronuclear nodules and adoral membranelles (Tab. 7). Furthermore, *H. typicus* lacks cortical granules, while those of *H. chardezi* are minute (< 1  $\mu$ m) and yellowish.

In vivo, *H. dumonti*, *H. typicus*, and *H. chardezi* are rather easily confused with *Eschaneustyla* spp., which possess several cirral rows in the frontal area and lack distinct midventral cirri (see [11, 18] for detailed descriptions).

**Table 6.** Morphometric data on *Holostichides dumonti*.

Character <sup>1)</sup>	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	199.0	200	20.0	5.5	10.0	168	243	13
Body, width	43.5	44	3.9	1.1	8.9	35	50	13
Anterior body end to end of adoral zone, distance	56.5	58	3.2	0.9	5.6	52	63	13
Anterior body end to end of midventral pairs, distance	74.9	75	7.9	2.2	10.5	60	93	13
Anterior body end to end of midventral tail, distance	99.8	100	19.5	5.4	19.5	73	147	13
Macronuclear nodules, length	5.9	6	2.1	0.6	36.1	3	9	13
Macronuclear nodules, width	2.9	3	0.5	0.1	16.9	2	4	13
Micronuclei, length	4.1	4	–	–	–	4	5	13
Micronuclei, width	3.0	3	–	–	–	3	3	13
Adoral membranelles, number	42.4	42	1.8	0.5	4.1	40	46	13
Ventral cirral rows right of midventral row tail, number	1.3	1	–	–	–	1	3	35
Macronuclear nodules, number <sup>2)</sup>	122.3	120	–	–	–	100	150	13
Micronuclei, number <sup>3)</sup>	3.1	3	–	–	–	2	5	13
Dorsal ciliary rows, number	5.1	5	–	–	–	5	6	20
Midventral pairs, number	10.2	10	1.3	0.4	12.7	8	12	13
Right marginal row, number of cirri	51.6	51	4.7	1.3	9.0	45	59	13
Left marginal row, number of cirri	53.5	53	3.6	1.0	6.8	48	60	13
Frontoterminal cirri, number	3.8	4	0.7	0.2	17.9	3	5	13
Enlarged frontal cirri, number	3.0	3	0.0	0.0	0.0	3	3	13
Buccal cirri, number	1.0	1	0.0	0.0	0.0	1	1	13
Caudal cirri, number	6.5	7	1.9	0.4	29.5	0	9	19

<sup>1)</sup>Data based on protargol-impregnated (Foissner's method), mounted specimens from a non-flooded Petri dish culture. Measurements in  $\mu\text{m}$ . CV = coefficient of variation in %, M = median, Max = maximum, Min = minimum, n = number of individuals investigated, SD = standard deviation, SE = standard error,  $\bar{x}$  = arithmetic mean.

<sup>2)</sup>Rough values because difficult to count.

<sup>3)</sup>Rough values because sometimes difficult to distinguish from cytoplasmic inclusions and/or macronuclear nodules.

**Table 7.** Comparison of main morphometrics (arithmetic means) of protargol-impregnated *Holostichides* spp. (present investigation and from [21, 23, 54, 55]).

Character	<i>H. chardezi</i> (n=11)	<i>H. dumonti</i> (n=13)	<i>H. typicus</i> (n=11)	<i>H. terricola</i> (n=16)	<i>H. wilberti</i> (n=12)
Body, length ( $\mu\text{m}$ )	112	199	133	91	99
Adoral membranelles, number	31	42	34	19	17
Macronuclear nodules, number	36	122	30	16	15
Dorsal kineties, number	4	5	4	2	2
Buccal cirri, number	1	1	1	0	0
Frontoterminal cirri, number	5	4	8	3	4
Cortical granules	present	present	absent	present	absent

***Hemisincirra gellerti verrucosa* Foissner & Schade  
nov. subspec. (Fig. 84–91; Tab. 8)**

**Diagnosis:** Cortical granules only around bases of cirri and dorsal bristles.

**Type location:** Soil from a coniferous forest at Tenerife, Canary Islands (W17° N28°).

**Type material:** One holotype slide and two paratype slides with protargol-impregnated (Foissner's method) specimens have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria. Relevant specimens are marked by a black ink circle on the cover glass.

**Etymology:** “verrucosa” (Latin, warty) refers to the wart-like accumulations of cortical granules.

**Description and comparison with related species:** This new subspecies differs from *Hemisincirra gellerti gellerti* (Foissner, 1982) Foissner, 1984 only by the arrangement of the cortical granules (in small clusters around bases of cirri and dorsal bristles vs. narrowly spaced, longitudinal rows). All other features, even the morphometrics, are very similar within and among populations (cp. Table 8 and [18]). In spite of this, I provide a detailed description because the original description of *H. gellerti gellerti* is in German.

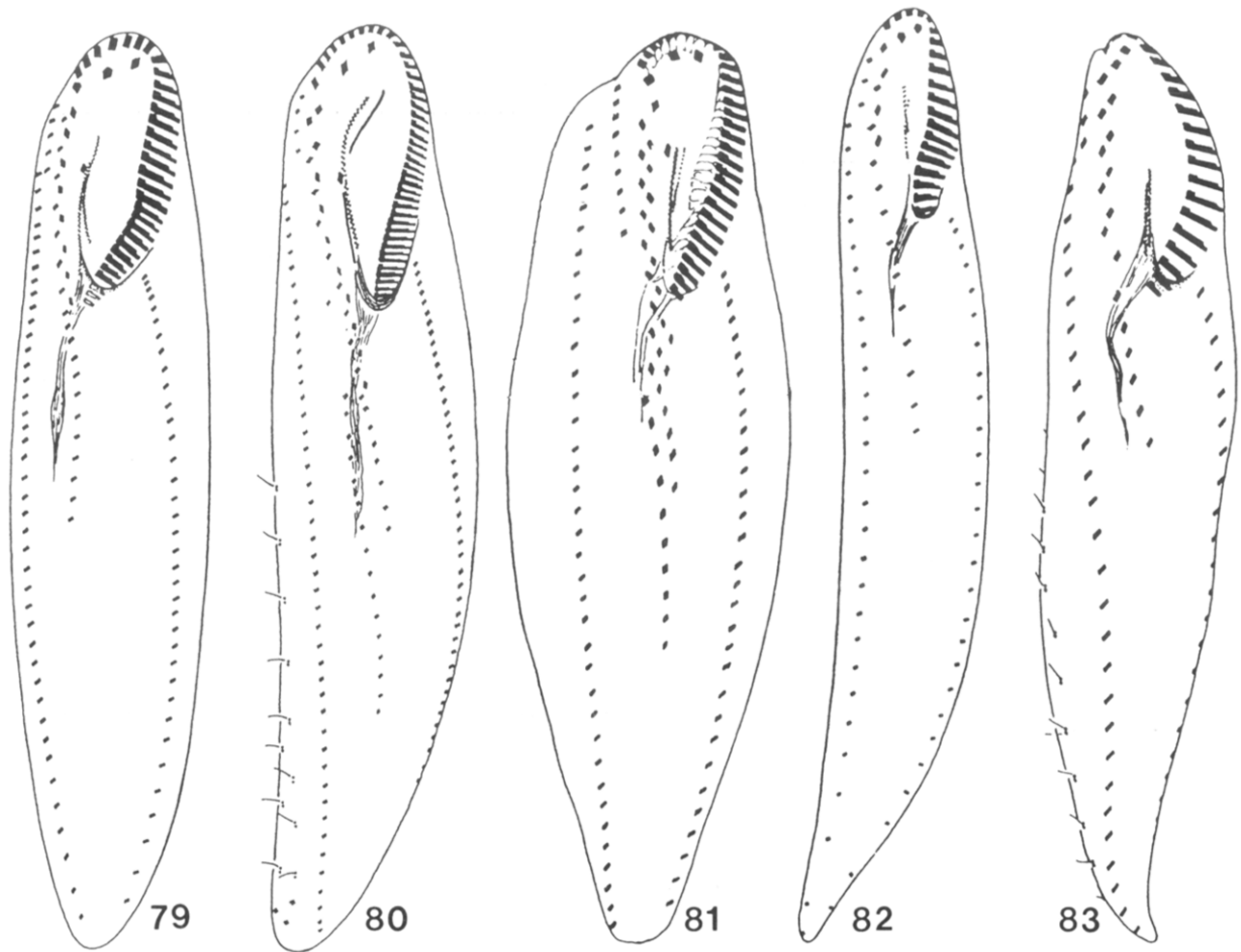


Fig. 79–83. Comparison of ventral infraciliature of *Holostichides chardezi* (length 113  $\mu\text{m}$ ; from [21]), *H. dumonti* nov. spec. (length 200  $\mu\text{m}$ ), *H. typicus* (length 133  $\mu\text{m}$ ; from [55]), *H. terricola* (length 95  $\mu\text{m}$ ; from [23]), and *H. wilberti* (length 87  $\mu\text{m}$ ; from [54]) after protargol impregnation. See text for detailed explanation.

Do not confuse *H. gellerti verrucosa* with *H. wenzeli* Foissner [21], whose cortical granules show the same pattern. However, *H. wenzeli* has caudal cirri, only three dorsal kineties, and a shorter ventral cirral row. Furthermore, identification of all taxa requires life observation because the granules do not stain with protargol.

**Type population:** Size in vivo 50–100  $\times$  15–22  $\mu\text{m}$ , usually about 70  $\times$  17  $\mu\text{m}$ , length:width ratio 3.6–7:1, on average about 4.3–5:1 in protargol preparations (Tab. 8); flattened up to 2:1 dorsoventrally. Outline elongate rectangular because both ends broadly rounded and margins straight or only slightly convex (Fig. 84, 85, 91). Macronuclear nodules invariably one after the other between adoral zone of membranelles and posterior body end left of cell's midline; individual nodules globular to elongate ellipsoidal (3:1), on average broadly ellipsoidal (1.6:1), contain many minute nucleoli. Usually one broadly ellipsoidal, compact micronucleus each near ends of macronuclear strand (Fig. 84, 86, 88).

Contractile vacuole in mid-body near left margin of cell, with two lacunar collecting canals. Cortex thin, fragile, and very flexible. Cortical granules conspicuous, although minute and only around bases of cirri and dorsal bristles, because compact and thus highly refractive, dorsal clusters appear as minute, bright warts at a magnification of  $\geq 200\times$ , specific arrangement preserved even in strongly squeezed specimens; individual granules, depending on population, colourless to yellowish, 0.3–0.7  $\mu\text{m}$  across, do not stain with methyl green-pyronin or protargol (Fig. 84, 85, 90). Cortical granules around and between cirri and usually semicircularly arranged around dorsal bristles in Berlin specimens. Cytoplasm colourless, contains some fat globules 1–3  $\mu\text{m}$  across and food vacuoles with bacterial remnants. Glides moderately fast on slide surface and between and on soil particles showing great flexibility.

All cirri about 10  $\mu\text{m}$  long, pattern of usual variability (Tab. 8) and similar to that of other members of

**Table 8.** Morphometric data on *Hemisincirra gellerti verrucosa* specimens from Tenerife (upper line) and Berlin (lower line).

Character <sup>1)</sup>	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	64.4	65.0	11.5	3.5	17.9	46.0	90.0	11
	60.5	60.0	5.7	1.5	9.3	53.0	70.0	14
Body, width	14.4	14.0	1.9	0.6	12.9	12.0	18.0	11
	12.4	12.0	2.1	0.6	17.9	10.0	18.0	14
Anterior body end to end of adoral zone of membranelles, distance	17.1	17.0	1.7	0.5	9.9	15.0	20.0	11
	18.6	19.0	1.4	0.4	7.5	16.0	21.0	14
Anterior body end to end of ventral cirral row, distance	27.0	25.0	6.1	1.8	22.6	20.0	41.0	11
	28.3	28.0	2.0	0.5	7.0	25.0	31.0	13
Macronuclear nodules, length	7.2	6.0	3.0	0.9	41.5	4.0	14.0	11
	6.6	7.0	1.3	0.3	19.4	5.0	10.0	14
Macronuclear nodules, width	3.9	4.0	0.7	0.2	17.9	3.0	5.0	11
	4.0	4.0	0.8	0.2	20.0	3.0	5.0	14
Micronuclei, length	2.5	2.5	0.5	0.1	19.6	2.0	3.5	11
	2.3	2.5	0.5	0.1	20.0	1.5	3.0	14
Micronuclei, width	1.6	1.6	0.2	0.1	15.0	1.2	2.0	11
	1.9	2.0	0.5	0.1	25.8	1.5	3.0	14
Adoral membranelles, number	15.2	15.0	0.8	0.2	4.9	14.0	16.0	11
	15.6	16.0	0.7	0.2	4.7	14.0	17.0	14
Macronuclear nodules, number	8.7	9.0	2.8	0.8	32.2	5.0	16.0	11
	8.1	8.0	1.9	0.5	23.7	5.0	13.0	14
Micronuclei, number	1.9	2.0	0.3	0.1	15.8	1.0	2.0	11
	1.9	2.0	0.3	0.1	14.2	1.0	2.0	14
Dorsal ciliary rows, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	11
	4.0	4.0	0.0	0.0	0.0	4.0	4.0	8
Right marginal row, number of cirri	15.3	15.0	1.4	0.4	9.3	13.0	18.0	11
	16.1	15.0	2.8	0.7	17.4	13.0	21.0	14
Left marginal row, number of cirri	15.3	15.0	1.0	0.3	6.6	14.0	17.0	11
	15.7	16.0	1.6	0.5	9.9	12.0	18.0	11
Ventral row, number of cirri	10.5	11.0	2.0	0.6	19.2	7.0	13.0	11
	11.9	12.0	1.8	0.5	15.4	9.0	15.0	12
Enlarged frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
	2.9	3.0	—	—	—	2.0	3.0	14
Frontoterminal cirri, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	11
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	14
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	14
Transverse cirri, number	3.7	4.0	0.5	0.1	12.7	3.0	4.0	11
	3.7	4.0	0.7	0.2	17.6	2.0	4.0	11

<sup>1)</sup> Data based on protargol-impregnated (Foissner's method), mounted specimens from non-flooded Petri dish cultures. Measurements in  $\mu\text{m}$ . CV = coefficient of variation in %, M = median, Max = maximum, Min = minimum, n = number of individuals investigated, SD = standard deviation, SE = standard error,  $\bar{x}$  = arithmetic mean.

genus (Fig. 86, 88). Frontal cirri slightly enlarged, form transverse line subapically; frontoterminal cirri between frontal cirri and ventral row at right margin of cell; buccal cirrus at summit of paroral membrane at level of mid-buccal cavity; ventral cirral row distinctly longer than adoral zone of membranelles, ends pre-equatorially in or near midline of cell, cirri slightly zigzagging especially in anterior half; transverse cirri near posterior margin of cell and thus distinctly pro-

jecting from body proper, rather irregularly arranged, finer than other cirri; both marginal rows end subterminally, left slightly longer than right, which commences at level of buccal cirrus, that is, rather distant from anterior end of cell. Dorsal bristles about 3  $\mu\text{m}$  long in vivo, very widely spaced, arranged in four rows as shown in Figures 87 and 89; rarely, a fifth row composed of two bristles only at right anterior end occurs (Fig. 87). No caudal cirri.



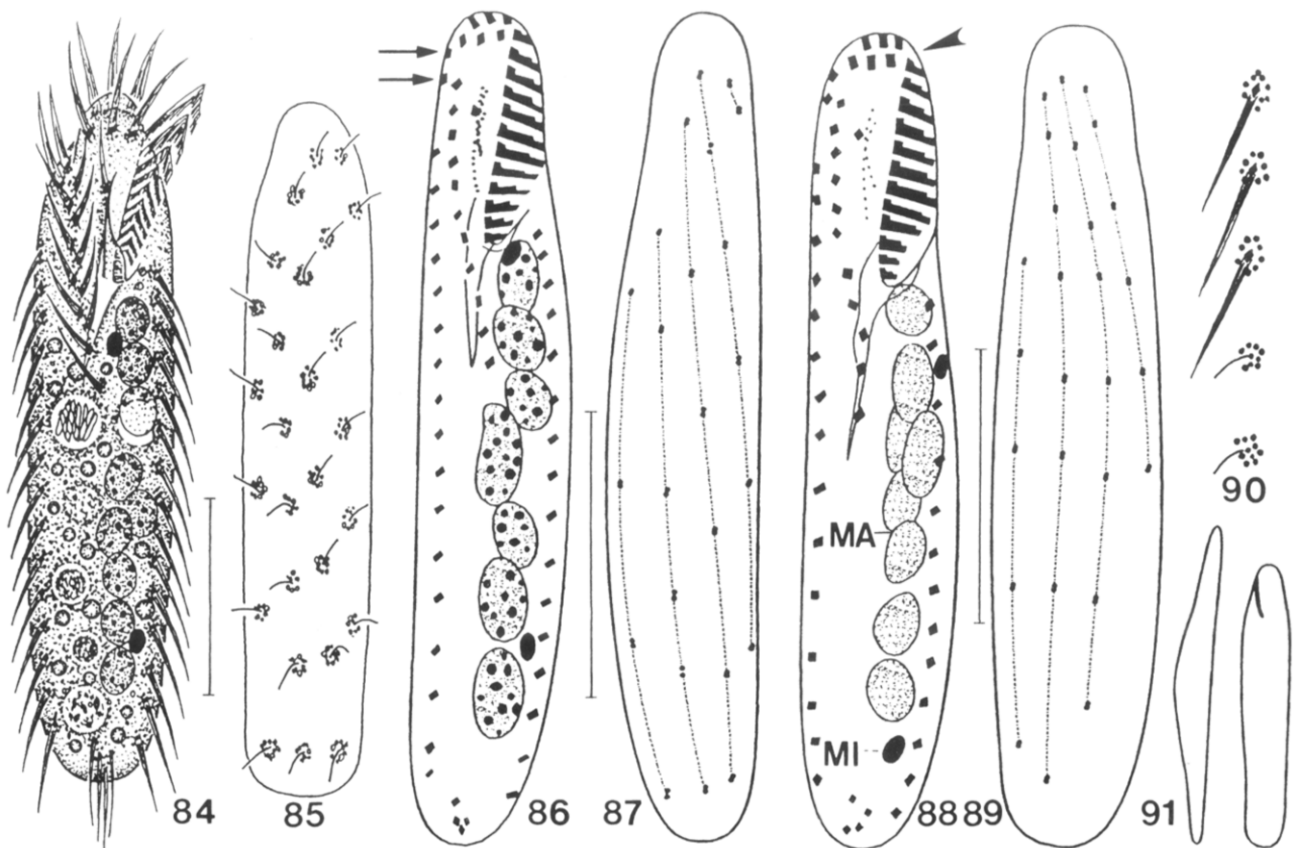


Fig. 84–91. *Hemisincirra gellerti verrucosa*, Tenerife type population (84–87, 90) and Berlin population (88, 89, 91) from life (84, 85, 90, 91) and after protargol impregnation (86–89). 84: Ventral view of a representative specimen. 85: Dorsal view showing cortical granules around dorsal bristles. 86–89: Infraciliature of ventral and dorsal side and nuclear apparatus of Tenerife (86, 87) and Berlin (88, 89) specimens. Arrows mark frontoterminal cirri. Arrowhead denotes gap in adoral zone of membranelles. Dorsal bristles connected by dotted lines. 90: Cortical granules occur only around cirral and dorsal bristle bases. 91: Lateral and dorsal view of shape variant. MA = macronuclear nodules, MI = micronuclei. Scale bars 20  $\mu$ m.

Buccal cavity narrow but rather deep, right posterior portion covered by narrow, inconspicuous lip. Adoral zone of membranelles occupying about 30% of body length, longest bases about 4  $\mu$ m wide in vivo; frontal (distal three) membranelles separated from ventral membranelles by an about one membranelle wide gap at left anterior body end. Paroral and endoral membrane inconspicuous, both possibly composed of monokinetids, curved, and optically intersecting in mid-buccal cavity. Pharyngeal fibres rather distinct.

**Berlin population:** The second population studied in detail is highly similar to the type population in morphology and all main morphometrics (Fig. 88, 89; Tab. 8).

**Occurrence and ecology:** Common in soils worldwide (Foissner, unpubl.), thus cosmopolitan and euryoecious. However, some populations might be distinct subspecies, for instance, those from Australia and Madagascar, which have only three or two dorsal kineties, respectively.

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## References

- 1 Aesch E. and Foissner W. (1989): Stamm: Rhizopoda (U.-Kl. Testacealobosia, Testaceafilosia). Catalogus Faurae Austriae Ia, 1–79.
- 2 Berger H. (1999): Monograph of the Oxytrichidae (Ciliophora, Hypotrichia). Kluwer, Dordrecht, Boston, London.
- 3 Biegel M. (1954): Beitrag zur Peritrichenfauna der Umgebung Erlangens. Arch. Protistenkd. 100, 153–182.
- 4 Bonkowski M. (1966): Protozoen und Lumbriciden in einem Kalkbuchenwald: Untersuchungen zur Interaktion von Populationen der Bodenfauna und ihrer Wirkung auf Stoffdynamik und Pflanzenwachstum. Berichte des Forschungszentrums Waldökosysteme der Universität Göttingen, Reihe A, 134, 1–133.

- 5 Buitkamp U. (1977): Über die Ciliatenfauna zweier mitteleuropäischer Bodenstandorte (Protozoa; Ciliata). *Decheniana* (Bonn) 130, 114–126.
- 6 Corliss J. O. (1979): The ciliated protozoa. Characterization, classification and guide to the literature. 2<sup>nd</sup> ed. Pergamon Press, Oxford, New York.
- 7 Detcheva R. B. (1992): Protozoa, Ciliophora. *Catalogi Faunae Bulgaricae* 1, 1–130.
- 8 Dini F., Lucchesi P. and Macchioni G. (1995): 'Protozoa': In: Minelli A., Ruffo S. and La Posta S. (eds.): *Checklist delle specie della fauna Italiana* 1, 92 pp. Calderini, Bologna.
- 9 Dragesco J. (1963): Révision du genre *Dileptus* Dujardin 1841 (Ciliata Holotricha) (systématique, cytologie, biologie). *Bull. biol. Fr. Belg.* 97, 103–145.
- 10 Dunger W. (1991): Zur Primärsukzession humiphager Tiergruppen auf Bergbauflächen. *Zool. Jb. Syst.* 118, 423–447.
- 11 Eigner P. (1994): Divisional morphogenesis and reorganization in *Eschaneustyla brachytoma* Stokes, 1886 and revision of the Bakuellinae (Ciliophora, Hypotrichida). *Europ. J. Protistol.* 30, 462–475.
- 12 Fauré-Fremiet E. and André J. (1965): L'organisation du cilié gymnostome *Plagiocampa ovata*, Gelei. *Archs Zool. exp. gén.* 105, 361–367.
- 13 Fenchel T., Esteban G. F. and Finlay B. J. (1997): Local versus global diversity of microorganisms: cryptic diversity of ciliated protozoa. *Oikos* 80, 220–225.
- 13a Finlay B. J. and Fenchel T. (1999): Divergent perspectives on protist species richness. *Protist* 150, 229–233.
- 14 Finlay B. J., Corliss J. O., Esteban G. and Fenchel T. (1996): Biodiversity at the microbial level: the number of free-living ciliates in the biosphere. *Q. Rev. Biol.* 71, 221–237.
- 15 Foissner W. (1978): Morphologie, Infraciliatur und Silberliniensystem von *Plagiocampa rouxi* Kahl, 1926 (Prostomatida, Plagiocampidae) und *Balanonema sapropelica* nov. spec. (Philasterina, Loxocephalidae). *Protistologica* 14, 381–389.
- 16 Foissner W. (1981a): Morphologie und Taxonomie einiger heterotricher und peritricher Ciliaten (Protozoa: Ciliophora) aus alpinen Böden. *Protistologica* 17, 29–43.
- 17 Foissner W. (1981b): Morphologie und Taxonomie einiger neuer und wenig bekannter kinetofragminophorer Ciliaten (Protozoa: Ciliophora) aus alpinen Böden. *Zool. Jb. Syst.* 108, 264–297.
- 18 Foissner W. (1982): Ökologie und Taxonomie der Hypotrichida (Protozoa: Ciliophora) einiger österreichischer Böden. *Arch. Protistenkd.* 126, 19–143.
- 19 Foissner W. (1984): Infraciliatur, Silberliniensystem und Biometrie einiger neuer und wenig bekannter terrestrischer, limnischer und mariner Ciliaten (Protozoa: Ciliophora) aus den Klassen Kinetofragminophora, Colpodea und Polyhymenophora. *Stapfia* (Linz) 12, 1–165.
- 20 Foissner W. (1987a): Soil protozoa: fundamental problems, ecological significance, adaptations in ciliates and testaceans, bioindicators, and guide to the literature. *Progr. Protistol.* 2, 69–212.
- 21 Foissner W. (1987b): Neue und wenig bekannte hypotriche und colpodeide Ciliaten (Protozoa: Ciliophora) aus Böden und Moosen. *Zool. Beitr. (N. F.)* 31, 187–282.
- 22 Foissner W. (1987c): Neue terrestrische und limnische Ciliaten (Protozoa, Ciliophora) aus Österreich und Deutschland. *Sber. Akad. Wiss. Wien* 195, 217–268.
- 23 Foissner W. (1988): Gemeinsame Arten in der terricolen Ciliatenfauna (Protozoa: Ciliophora) von Australien und Afrika. *Stapfia* (Linz) 17, 85–133.
- 24 Foissner W. (1989): Morphologie und Infraciliatur einiger neuer und wenig bekannter terrestrischer und limnischer Ciliaten (Protozoa, Ciliophora). *Sber. Akad. Wiss. Wien* 196, 173–247.
- 25 Foissner W. (1991): Basic light and scanning electron microscopic methods for taxonomic studies of ciliated protozoa. *Europ. J. Protistol.* 27, 313–330.
- 26 Foissner W. (1993): Colpodea (Ciliophora). *Protozoenfauna* 4/1, I–X + 1–798.
- 27 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. Protistenkd.* 145, 37–79.
- 28 Foissner W. (1997): Global soil ciliate (Protozoa, Ciliophora) diversity: a probability-based approach using large sample collections from Africa, Australia and Antarctica. *Biodiv. Conserv.* 6, 1627–1638.
- 29 Foissner W. (1998): An updated compilation of world soil ciliates (Protozoa, Ciliophora), with ecological notes, new records, and descriptions of new species. *Europ. J. Protistol.* 34, 195–235.
- 30 Foissner W. (1999): Notes on the soil ciliate biota (Protozoa, Ciliophora) from the Shimba Hills in Kenya (Africa): diversity and description of three new genera and ten new species. *Biodiv. Conserv.* 8, 319–389.
- 30a Foissner W. (2000): Protist diversity: estimates of the near-imponderable. *Protist* 150 (year 1999), 363–368.
- 31 Foissner W. and Foissner I. (1988a): Stamm: Ciliophora. *Catalogus Faunae Austriae* 1c, 1–147.
- 32 Foissner W. and Foissner I. (1988b): The fine structure of *Fuscheria terricola* Berger et al., 1983 and a proposed new classification of the subclass Haptoria Corliss, 1974 (Ciliophora, Litostomatea). *Arch. Protistenkd.* 135, 213–235.
- 33 Foissner W., Berger H. and Schaumburg J. (1999): Identification and ecology of limnetic plankton ciliates. *Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft* 3/99, 1–793.
- 34 Gelei J. (1954): Über die Lebensgemeinschaft einiger temporärer Tümpel auf einer Bergwiese im Börzsönygebirge (Oberungarn) III. Ciliaten. *Acta biol. hung.* 5, 259–343.
- 35 Goralczyk K. and Verhoeven R. (1999): Bodengenese als Standortfaktor für Mikrofauna – Ciliaten und Nematoden in Dünenböden. In: H. Koehler, K. Mathes and B. Breckling (eds.): *Bodenökologie interdisziplinär*, pp. 105–118. Springer, Berlin, Heidelberg.
- 36 Greeff R. (1873): Vorkommen von Vorticellen in der Erde. *Sber. ges. Beförd. ges. Naturw. Marburg* 3, 23–24.
- 37 Greeff R. (1888): Land-Protozoen. *Sber. Ges. Beförd. ges. Naturw. Marburg* 3, 90–158.
- 38 Hemberger H. (1982): Revision der Ordnung Hypotrichida Stein (Ciliophora, Protozoa) an Hand von Protagolpräparaten und Morphogenesedarstellungen. *Dissertation Universität Bonn*.
- 39 Hemberger H. (1985): Neue Gattungen und Arten hypotricher Ciliaten. *Arch. Protistenkd.* 130, 397–417.
- 40 Horváth J. (1956): Beiträge zur Kenntnis einiger neuer Bodenciliaten. *Arch. Protistenkd.* 101, 269–276.
- 41 Kahl A. (1930): Urtiere oder Protozoa I: Wimpertiere oder Ciliata (Infusoria) 1. Allgemeiner Teil und Prostomata. *Tierwelt Dtl.* 18, 1–180.

- 42 Kahl A. (1931): Urtiere oder Protozoa I: Wimpertiere oder Ciliata (Infusoria) 2. Holotricha außer den im 1. Teil behandelten Prostomata. Tierwelt Dtl. 21, 181–398.
- 43 Kahl A. (1932): Urtiere oder Protozoa I: Wimpertiere oder Ciliata (Infusoria) 3. Spirotricha. Tierwelt Dtl. 25, 399–650.
- 44 Kahl A. (1935): Urtiere oder Protozoa I: Wimpertiere oder Ciliata (Infusoria) 4. Peritricha und Chonotricha. Tierwelt Dtl. 30, 651–886.
- 45 Lehle E. (1989): Beiträge zur Fauna der Ulmer Region II. Ciliaten (Protozoa: Ciliophora) Bioindikatoren in Waldböden. Mitt. Ver. Naturwiss. Math. Ulm (Donau) 35, 131–156.
- 46 Lehle E. (1992): Formenreichtum im Protargolpräparat. Wimpertiere und andere Einzeller des Bodens. Mikrokosmos 81, 18–23.
- 47 Lehle E. (1994): Die Auswirkungen von Düngung und Kalkung auf die Bodenciliaten (Protozoa: Ciliophora) eines Fichtenbestandes im Schwarzwald (Süddeutschland). Arch. Protistenkd. 144, 113–125.
- 48 Lehle E. (1995): Soil ciliates in limed and fertilized areas of Schwarzwald spruce stands (Southern Germany). Acta zool. fenn. 196, 246–247.
- 49 Lehle E. and Funke W. (1989): Zur Mikrofauna von Waldböden. II. Ciliata (Protozoa: Ciliophora) Auswirkungen anthropogener Einflüsse. Verh. Ges. Ökol. (Göttingen) 17, 385–390.
- 50 Niebuhr J. (1989): Ökologische Studien an Bodenprotozoenpopulationen (Protozoa: Ciliophora) auf dem Gelände eines ehemaligen Textilindustriebetriebes in Nordhorn in Bezug auf ihre Verwendung als Bio-Indikatororganismen für anthropogen belastete Böden – unter Berücksichtigung einiger Verfahren aus der Spurenanalytik. Diplomarbeit Universität Oldenburg.
- 51 Schade S. (1994): Bodenciliaten (Ciliophora, Protista) aus Abwasserverrieselungsflächen. Diplomarbeit Freie Universität Berlin.
- 52 Schaefer M. (1991): Fauna of the European temperate deciduous forest. In: E. Röhrig and B. Ulrich (eds.): Ecosystems of the World 7. Temperate Deciduous Forests, pp. 503–525. Elsevier, Amsterdam, London, New York, Tokyo.
- 53 Sommer G. (1951): Die peritrichen Ciliaten des Großen Plöner Sees. Arch. Hydrobiol. 44, 349–440.
- 54 Song W. (1990): Morphologie und Morphogenese des Bodenciliaten *Periholosticha wilberti* nov. spec. (Ciliophora, Hypotrichida). Arch. Protistenkd. 138, 221–231.
- 55 Song W. and Wilbert N. (1988): *Parabakuella typica* nov. gen., nov. spec. (Ciliata, Hypotrichida) aus dem Edaphon eines Standortes in Qingdao, China. Arch. Protistenkd. 135, 319–325.
- 56 Song W., Packroff G. and Wilbert N. (1988): Morphologie und Infraciliatur von *Dileptus orientalis* sp. n., einem Bodenciliaten aus Qingdao, China. Acta Protozool. 27, 271–277.
- 57 Varga L. (1935a): Die Protozoen und ihre Verteilung im Waldboden von Tharandt. Zentbl. Bakt. ParasitKde. 93, 128–137.
- 58 Varga L. (1935b): Daten zur Kenntnis der Protozoenfauna des Waldbodens von Eberswalde (Deutsches Reich). Zentbl. Bakt. ParasitKde. 93, 32–38.
- 59 Wanner M., Dunger W., Schulz H.-J. and Voigtländer K. (1998): Primary immigration of soil organisms on coal mined areas in Eastern Germany. In: V. Pižl and K. Tajovský (eds.): Soil Zoological Problems in Central Europe, pp. 267–275. České Budějovice.
- 60 Wenzel F. (1953): Die Ciliaten der Moosrasen trockener Standorte. Arch. Protistenkd. 99, 70–141.
- 61 World Conservation Monitoring Centre (1992): Global biodiversity: status of the earth's living resources. Chapman and Hall, London.