

Progress in Taxonomy of Planktonic Freshwater Ciliates ¹

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Abstract

Most ecological papers on planktonic protozoa lack reliable identifications and modern nomenclature. The present review, which summarizes some recent progress in the taxonomy of planktonic freshwater ciliates, should encourage ecologists and project leaders to pay more attention to species identification, for the benefit of the reliability of their own results and of our general scientific knowledge. The following genera and species are treated in some detail and mostly figured: *Actinobolina radians*, *A. smalli*, *A. vorax*, *Askenasia acrostomia*, *A. chlorelligera*, *A. volvox*, *Astylozoon enriquesi*, *A. fallax*, *A. faurei*, *Codonella cratera*, *Coleps hirtus*, *C. spetai*, *Disematostoma buetschlii*, *D. tetraedricum*, *Halteria bifurcata*, *H. grandinella*, *Hypotrichidium conicum*, *H. tisiae*, *Marituja pelagica*, *Meseres corlissi*, *Mesodinium acarus*, *M. pulex*, *Nassula ornata*, *Obertrumia aurea*, *O. georgiana*, *Ophrydium eutrophicum*, *O. naumanni*, *O. versatile*, *Pelagohalteria viridis*, *Pelagostrombidium fallax*, *P. mirabile*, *Pelagotrichidium faurei*, *Pseudobalanion planctonicum*, *Pseudostrombidium planctonicum*, *Rhabdoaskenasia minima*, *Rimostrombidium lacustris*, *R. velox*, *Stenosemella lacustris*, *Stentor amethystinus*, *S. niger*, *Stokesia vernalis*, *Strombidium pelagoviride*, *S. viride*, *Tintinnidium fluviatile*, *T. pusillum*, *Tintinnopsis cylindrata*, *Urotricha faurei*, *U. furcata*, *U. pelagica*. A simple generic key to the oligotrich freshwater ciliates is provided.

Résumé

Progrès dans la taxonomie des ciliés planctoniques des eaux douces

La plupart des publications écologiques sur les protozoaires planctoniques manquent d'identifications fiables et d'une nomenclature moderne. La présente revue, qui résume certains progrès récents dans la taxonomie des ciliés planctoniques des eaux douces, devrait encourager les écologistes et les meneurs de projets à donner plus d'attention aux identifications spécifiques, au bénéfice de la fiabilité de leurs propres résultats et de la connaissance scientifique en général. Les genres et espèces suivants sont traités en détail et représentés pour la plupart : *Actinobolina radians*, *A. smalli*, *A. vorax*, *Askenasia acrostomia*, *A. chlorelligera*, *A. volvox*, *Astylozoon enriquesi*, *A. fallax*, *A. faurei*,

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Codonella cratera, *Coleps hirtus*, *C. spetai*, *Disematostoma buetschlii*, *D. tetraedricum*, *Halteria bifurcata*, *H. grandinella*, *Hypotrichidium conicum*, *H. tisiae*, *Marituja pelagica*, *Meseres corlissi*, *Mesodinium acarus*, *M. pulex*, *Nassula ornata*, *Obertrumia aurea*, *O. georgiana*, *Ophrydium eutrophicum*, *O. naumanni*, *O. versatile*, *Pelagohalteria viridis*, *Pelagostrombidium fallax*, *P. mirabile*, *Pelagotrichidium faurei*, *Pseudobalanion planctonicum*, *Pseudostrombidium planctonicum*, *Rhabdoaskensia minima*, *Rimostrombidium lacustris*, *R. velox*, *Stenosemella lacustris*, *Stentor amethystinus*, *S. niger*, *Stokesia vernalis*, *Strombidium pelagoviride*, *S. viride*, *Tintinnidium fluviatile*, *T. pusillum*, *Tintinnopsis cylindrata*, *Urotricha faurei*, *U. furcata*, *U. pelagica*. Une clé générique simple des ciliés oligotriches d'eau douce est fournie.

Introduction

The concept of the “microbial loop” stimulated many scientists and hydrobiologists to study ecological aspects of planktonic protozoa, mainly heterotrophic flagellates and ciliates (Arndt and Nixdorf, 1991; Fenchel, 1987). With few exceptions (e.g. Finlay *et al.*, 1988), the species involved were not or only very incompletely and/or superficially identified, either, as I assume, because most people prefer to avoid such a boring job or because they did not know that taxonomists have collected valuable information on planktonic protozoa during the last 20 years. I thus welcomed the invitation of the editor of this fascicule to compile some of the progress made in the taxonomy of planktonic freshwater ciliates. Space limitation did not permit detail, so I decided to treat such species as can be easily confused with others and those described after the still indispensable monographs by Kahl (1930-35). In spite of this and other shortcomings, I hope to encourage ecologists to pay more attention to species identification, for the benefit of the reliability of their own results and of our general scientific knowledge.

Thanks to Mag. Margit Palzenberger, Mag. Eric Strobl, and Andreas Zankl for technical assistance.

Benchmark literature

Unfortunately, a comprehensive, updated key to the planktonic ciliates is not available, and many species are still undescribed or insufficiently characterized. Thus, a few books and some hundred reprints are necessary to have a well-ordered and modern guide to the identification of planktonic ciliates. The following chronological compilation focuses on benchmark publications; miscellaneous papers are mentioned in the taxonomic section.

Taxonomic methods for studying ciliated protozoa were treated in detail by Dragesco and Dragesco-Kernéis (1986), Foissner (1991) and Lee and Soldo (1992). Bibliographic guides to the ecology of free-living protozoa were compiled by Finlay and Ochsenein-Gattlen (1982) and Fenchel (1987).

Fauré-Fremiet (1924): The first detailed study on planktonic ciliates. Still indispensable for its detailed descriptions and excellent figures.

Gajewskaja (1933): A large, beautifully illustrated guide to the ciliates found in Lake Baikal. Many new species are described; few of them are mentioned in the later literature, although it is quite reasonable to assume that most occur also in other lakes.

Kahl (1930-35): These monographs, which include the results of Fauré-Fremiet (1924) and Gajewskaja (1933), are still indispensable for their completeness and detailed keys to species. "The Kahl" is, however, now rather outdated, *i.e.* species number has at least doubled since his time. An updated treatise is in progress (see below; Foissner, 1993 and Matthes *et al.*, 1988).

Sommer (1951): A comprehensive guide to peritrichs found in Lake Plön. Many new species are described.

Bick (1972): An updated, though rather incomplete and not very attractively illustrated guide to the planktonic ciliates. Also contains useful ecological data.

Corliss (1979): Still the only comprehensive text-book on morphology and taxonomy of ciliated protozoa. Truly outstanding and indispensable. Suprafamilial taxa are thoroughly characterized, all known genera are figured but not described.

Curds (1982) and Curds *et al.* (1983): A valuable generic key to the freshwater ciliates. All genera are depicted by at least one line drawing and described in detail. Literature to relevant species descriptions is indicated.

Maeda and Carey (1985) and Maeda (1986): An illustrated guide to the species of oligotrichine ciliates. Species and their synonyms are depicted by line drawings and described in fair detail; they are, however, not critically evaluated.

Small and Lynn (1985): This guide is widely used by ecologists. It contains a rather biased introduction to recent ciliate systematics and depicts some common genera, mostly only silver impregnated cells. It is, however, not a guide to species, as some ecologists apparently assume. This may be due to the unfortunate inclusion of some new genera and species which all are poorly described.

Dragesco and Dragesco-Kernéis (1986): An outstanding guide to the ciliates known from tropical Africa. 267 taxa, including many planktonic species, are described in detail and illustrated by 1136 beautiful line drawings. Short notes on ecology and related literature are given to each species. Recently supplemented with species from the coast of Lake Tanganyika (Dragesco and Dragesco-Kernéis, 1991).

Matthes *et al.* (1988): An updated key to the suctorians and mobile peritrichs. All species, but not their synonyms, are figured by line drawings and briefly described. A very helpful, though sometimes too simplistic, compilation.

Foissner *et al.* (1991, 1992, 1994; the last volume IV is in preparation): An indispensable guide to 350 common ciliates found in running waters and in the plankton of reservoirs and lakes. Each species is described monographically, *i.e.* the taxonomic, faunistic, and autecologic literature is thoroughly reviewed and the morphology is documented by many line drawings, light micrographs of living and silvered specimens, and by scanning electron micrographs. Keys and descriptions are designed to enable live identification. The four volumes comprise about 2000 pages and 5000 figures.

Foissner (1993): An updated version of Kahl's monograph on colpodid ciliates, some of which (*e.g.* *Bursaridium*) are widespread in lake plankton. 170 species are

recognized and illustrated by 2900 figures including many scanning electron micrographs. Synonymy is discussed, nomenclatural problems are solved, detailed morphological, ecological, and faunistic descriptions and reliable keys are provided. Users can thus determine species without referring back to the original literature. Ecologists and cell biologists will find detailed descriptions of all known colpodid species and synonyms.

The species problem in “zoochlorellae” bearing ciliates

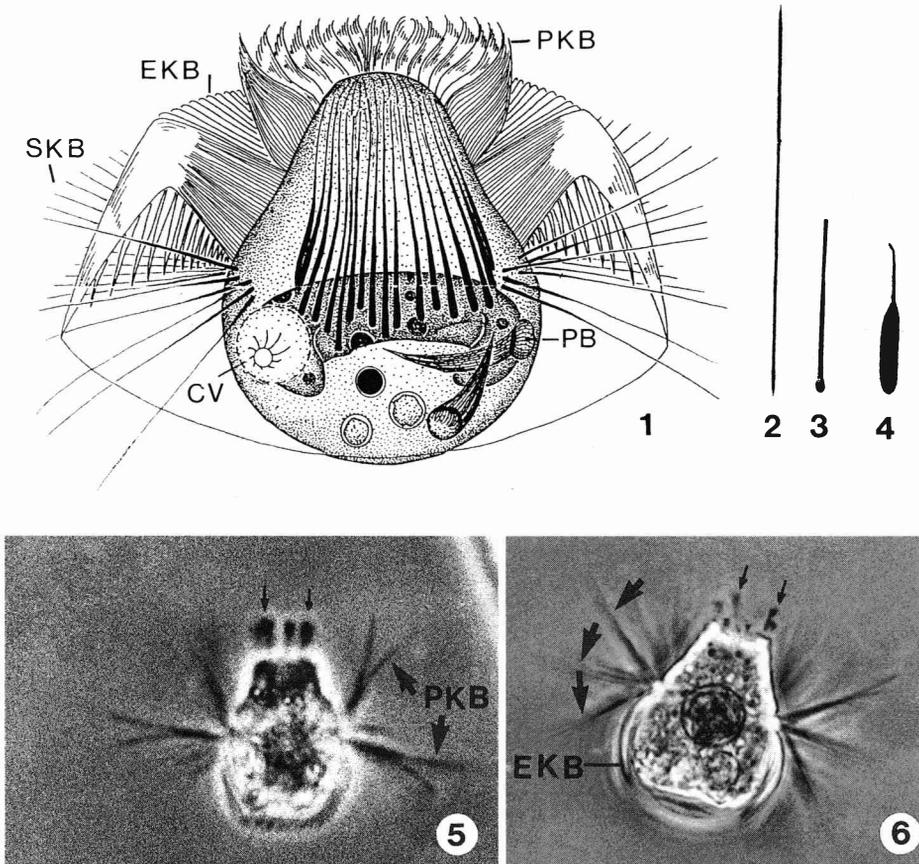
Rather many planktonic ciliates host green algae, mostly *Chlorella* (Christopher and Patterson, 1983; Finlay *et al.*, 1988; Reisser, 1986). It is widely assumed that such green populations are conspecific with apochlorotic strains. Certainly, green individuals often resemble apochlorotic congeners when superficially analyzed. However, closer examination often reveals more or less distinct morphological differences which are increasingly considered to be of significance at species level. Several examples are mentioned below, *e.g.* *Halteria grandinella* and *Pelagohalteria viridis* (differing even at genus level) as well as *Coleps hirtus* and *C. spetai* (differing in the structure of the armour plates).

Well-documented cases of green populations matching apochlorotic congeners exactly are not known to me. Christopher and Patterson (1983) report on a green and a colourless *Coleps hirtus*. From the figures provided, it seems that the symbiotic algae bearing, barrel-shaped population is *C. spetai*, whereas the colourless, cylindrical population belongs to *C. hirtus*. Klaveness (1984) also found morphological differences, though rather inconspicuous, between a green and an apochlorotic *Coleps*.

The integration of a symbiotic partner requires specific physiological and behavioural mechanisms [see Reisser (1986) for review] which can be considered, independently of morphological differences, as species characters. The zoochlorellae in *Paramecium bursaria*, for instance, release distasteful metabolites which repel a predator, *Didinium nasutum* (Berger, 1980). Certainly, the strength of association between algae and ciliates varies, and in some cases it might be weak and not associated with distinct morphological features. Generally, however, such differences become obvious if the species involved are thoroughly studied. I thus recommend that ecologists avoid lumping together green and colourless populations of a “species”.

Notes for the identification of some planktonic ciliates

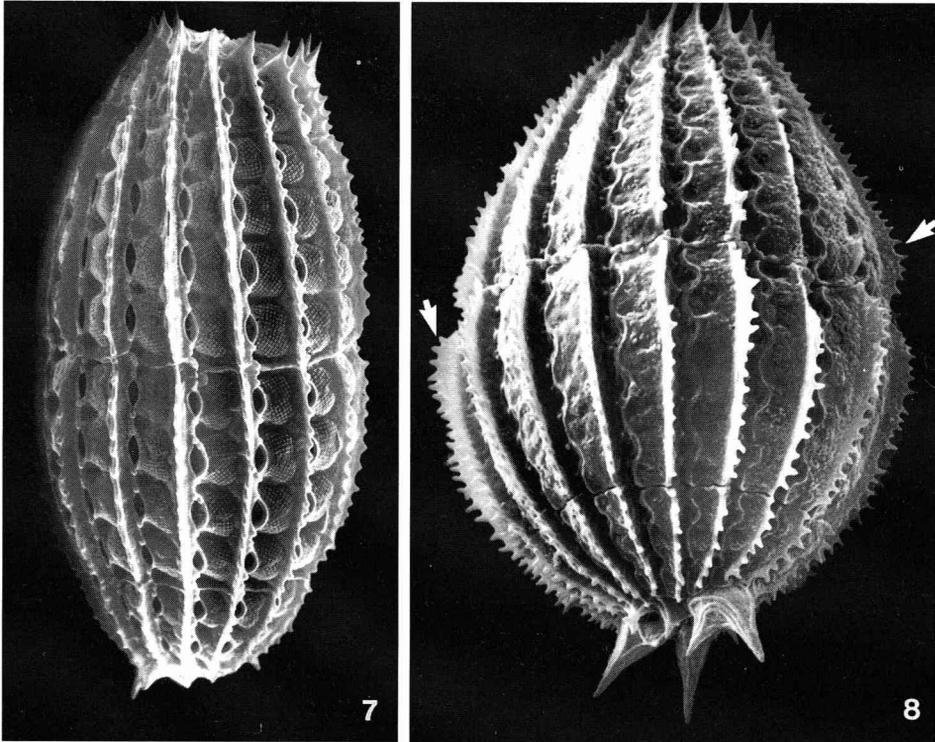
This section contains short descriptions of problematic or recently established species. Usually, the description focuses on a few main points and thus cannot replace the consultation of the references indicated. The material is arranged according to major systematic categories familiar to many plankton ecologists. Within these groups species are treated alphabetically.



Figs. 1-6. Planktonic, mesodiniid holotrichs from life (1-4, from Krainer and Foissner, 1990; 5, 6, from Tamar, 1987, 1992). These species, which belong to the haptorid order Cyclotrichida, are usually smaller than 50 μm and have a quick, jumping movement. Their ciliary pattern (\pm infraciliature) is basically similar but differs in details; *Mesodinium*, e.g., lacks the subequatorial kinety (ciliary) belt (SKB). **1-4:** Side view of *Askenasia volvox* (Fig. 1; length 40 μm), and extrusomes of *A. acrostomia* (Fig. 2), *A. chlorelligera* (Fig. 3), and *Rhabdoaskensia minima* (Fig. 4). These four species can be distinguished by the shape of the extrusomes, the number of contractile vacuoles, the presence/absence of symbiotic green algae, and details of the infraciliature. **5, 6:** *Mesodinium acarus* (Fig. 5; length 15-20 μm) and *M. pulex* (Fig. 6; length 20-30 μm) differ in size and “cirri” (PKB, thick arrows) which form 2 and 3 circlets, respectively. Thin arrows mark genus specific, retractable stylets in oral opening. CV = contractile vacuole, EKB = equatorial kinety (ciliary) belt, PB = pharyngeal basket of ingested ciliate, PKB = pre-equatorial kinety (ciliary) belt, SKB = subequatorial kinety (ciliary) belt.

Holotrichs

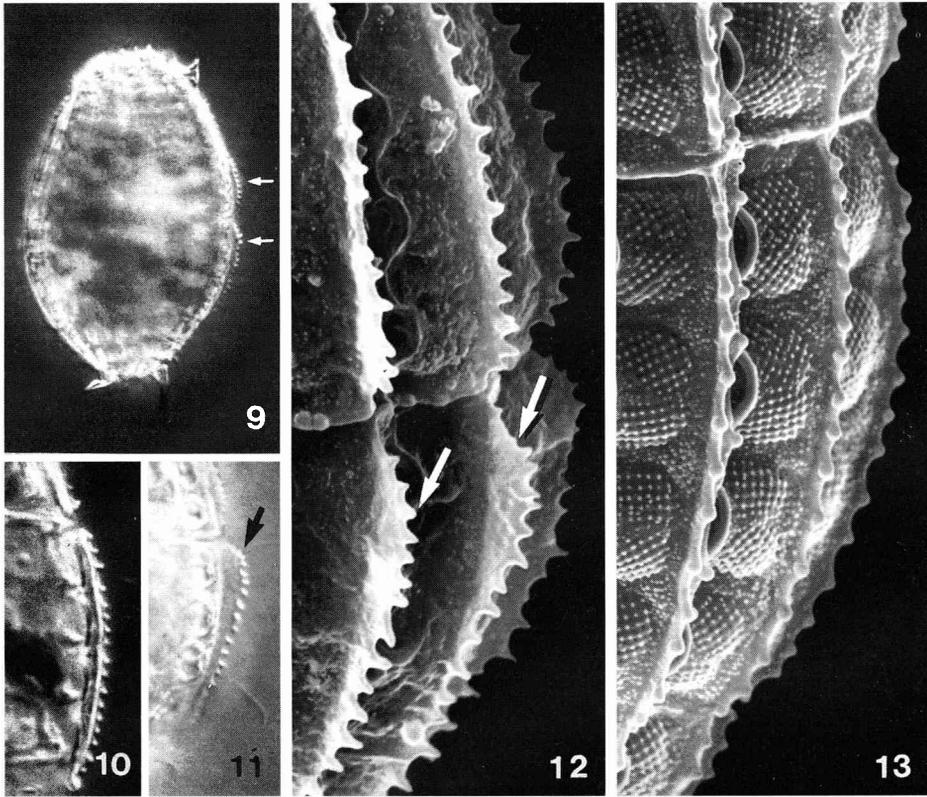
Under this time-honoured but outdated heading a few forms which are common in lake plankton and have been thoroughly redescribed during the last decade are discussed.



Figs. 7, 8. Scanning electron micrographs of planktonic, prostomate holotrichs (from Foissner *et al.*, 1994). **7, 8:** *Coleps hirtus* (Fig. 7; length 45 μm) and *C. spetai* (Fig. 8; length 60 μm) differ in symbiotic algae, size of cell and caudal processes, shape, and structure of armour plates, which are broadened wing-like in *C. spetai* (arrows). For further comparison see Figures 9-13.

Actinobolina spp.: Three species have been described which differ in size, ciliary pattern, and symbiotic algae: *Actinobolina radians* Stein, 1867 (50-125 μm , ciliary rows distinctly spiralled); *A. vorax* Wenrich, 1929 (60-200 μm , ciliary rows almost meridional); *A. smalli* Holt *et al.*, 1973 (42-55 μm , ciliary rows slightly spiralled, with symbiotic green algae).

Askenasia volvox (Eichwald, 1852): Easily confused with three other species recently described by Krainer and Foissner (1990). *Askenasia volvox*: no symbiotic algae but sometimes greenish by ingested algae, single contractile vacuole, extrusomes needle-shaped, rostrum (anterior body portion) arched (Fig. 1); *A. chlorelligera*: with symbiotic green algae, single contractile vacuole, extrusomes pin-shaped (Fig. 3), rostrum truncated; *A. acrostomia*: without symbiotic algae, four contractile vacuoles, extrusomes rod-shaped with pointed ends (Fig. 2), rostrum tapered; *Rhabdoaskenasia minima*: without symbiotic algae, single contractile vacuole, extrusomes conspicuously club-shaped (Fig. 4), rostrum truncated. Detailed morphological and ecological description and key to all known genera and species in Krainer and Foissner (1990).



Figs. 9-13. Light and scanning electron micrographs of planktonic, prostomate holotrichs (from Foissner *et al.*, 1994). *Coleps hirtus* (Figs. 10, 13; overview Fig. 7) and *C. spetai* (Figs. 9, 11, 12; overview Fig. 8) differ not only in the absence/presence of symbiotic algae but also in the structure of the armour plates, which are broadened wing-like in *C. spetai* (arrows).

Coleps hirtus (Müller, 1786): Possibly often confused with the green *C. spetai* Foissner, 1984b, which is more distinctly barrel-shaped and has symbiotic algae. Furthermore, the armour plates of *C. spetai* have wing-like broadened marginal ridges (cp. Figs. 8, 9, 11, 12 with 7, 10, 13). Other characters, like the shape of the armour windows and the ciliary pattern are very similar in both species. *Coleps spetai* is widespread in the plankton of eutrophic lakes and also not identical with *C. hirtus* var. *lacustris* Fauré-Fremiet, 1924, which, like *C. hirtus*, lacks symbiotic algae and “wings”. There might be further, not yet described, *Coleps* species with symbiotic algae. Detailed description of the morphology and ecology of common species in Foissner *et al.* (1994).

Mesodinium pulex (Claparède and Lachmann, 1859) and *M. acarus* Stein, 1863: These tiny and fast-moving ciliates are not easy to study and details of their ciliary pattern are still unknown. However, Tamar (1992, and literature cited therein) undertook excellent living observations and suggested identifying these species by size

(usually 15-20 μm versus 20-30 μm) and “cirri”, which form 2 and 3 circlets, respectively, in *M. acarus* and *M. pulex* (Figs. 5, 6). *Mesodinium fimbriatum* Stokes, also redescribed by Tamar (1971), is possibly a junior synonym of *M. acarus* (Kahl, 1930). *Mesodinium rubrum* (Lohmann, 1908), which causes spectacular red tides in marine environments, has a different ciliary pattern and belongs to the genus *Myrionecta* Jankowski, 1976 (Krainer and Foissner, 1990).

Obertrumia aurea (Ehrenberg, 1833): Easily confused with *O. georgiana* (Dragesco, 1972) and *Nassula ornata* Ehrenberg, 1833, which, however, have distinct trichocysts (cp. Figs. 14, 19, 21 with 15-18, 20). *Obertrumia aurea* (formerly in the genus *Nassula*) is possibly the sole nassulid common in lake plankton. It may develop heavy blooms under eutrophic conditions and feeds on various filamentous cyanobacteria (e.g. *Oscillatoria rubescens*) making the cells dark (Fig. 19). Detailed descriptions of the morphology and ecology in Canter *et al.* (1990), Foissner *et al.* (1994), and Thomas (1941).

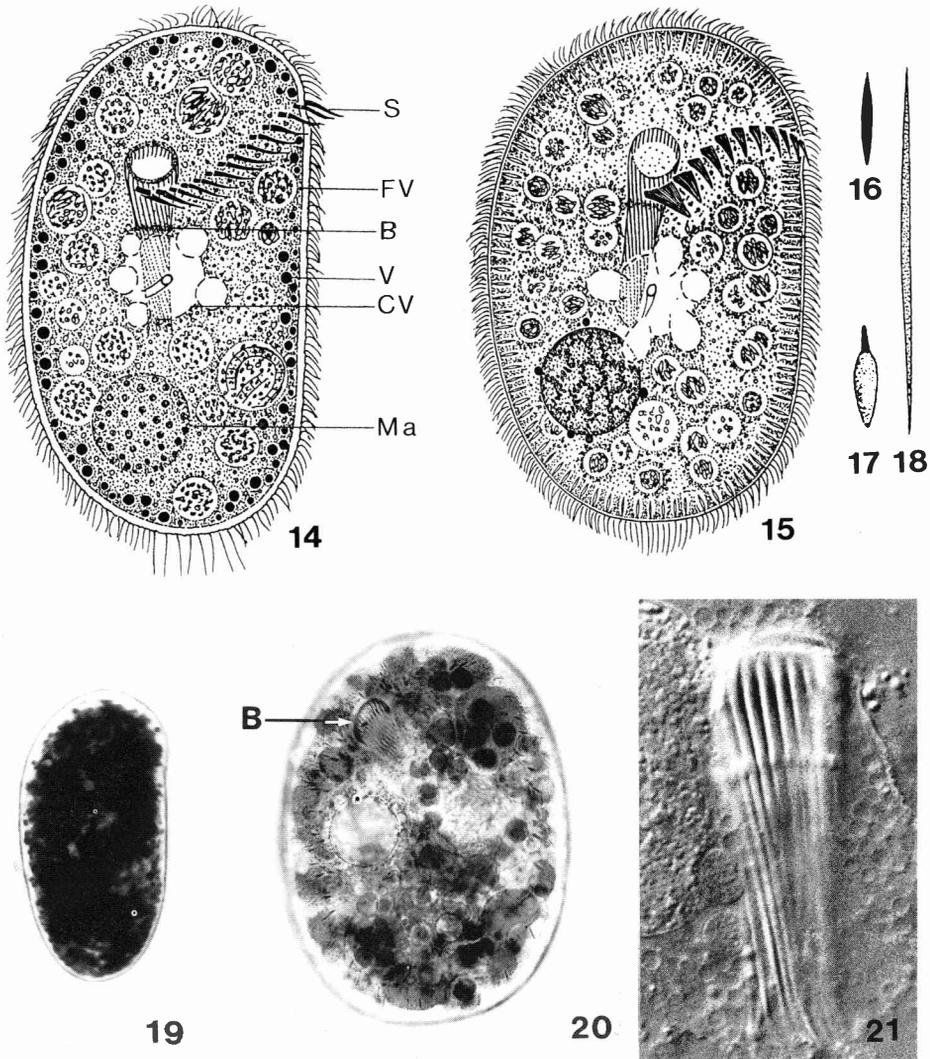
Pseudobalanion planctonicum Foissner *et al.* (1990): Easily confused with *Urotricha* spp., which have a smaller oral opening and much shorter oral flaps (cp. Figs. 22, 25). This small (about 20 \times 15 μm) species is, as recent data indicate, widespread in the lake plankton; very likely, it has often been misidentified as *Urotricha* sp.

Urotricha spp.: Many species have been described; some are common in the plankton of lakes. Unfortunately, a reliable identification is very difficult because no newer revision is available. There is, however, one species which is easily recognized by its two caudal cilia, viz. *U. furcata* Schewiakoff, 1892 (Fig. 22); detailed descriptions in Foissner and O'Donoghue (1990) and Foissner *et al.* (1990). See Dragesco *et al.* (1974), Foissner (1984a), Song Weibo and Wilbert (1989), and Wilbert (1986) for descriptions and redescriptions of species having a single elongated cilium or more than two caudal cilia (Figs. 23, 24).

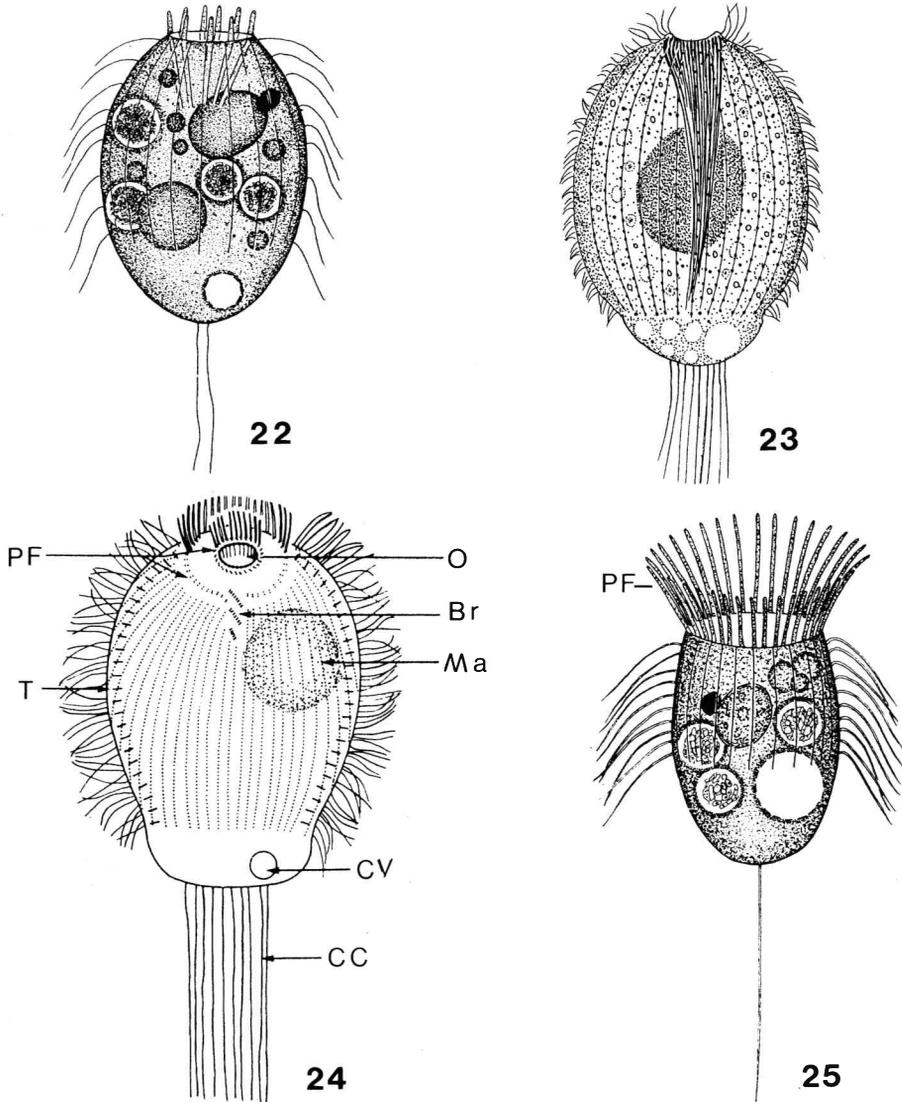
Hymenostomes and scuticociliates

The common larger forms, like *Marituja*, *Stokesia* and *Disematostoma*, have been restudied with modern methods. The small, planktonic “scuticos” (e.g. *Cyclidium*, *Dexiotricha*), which often become abundant under microaerobic conditions are still poorly known.

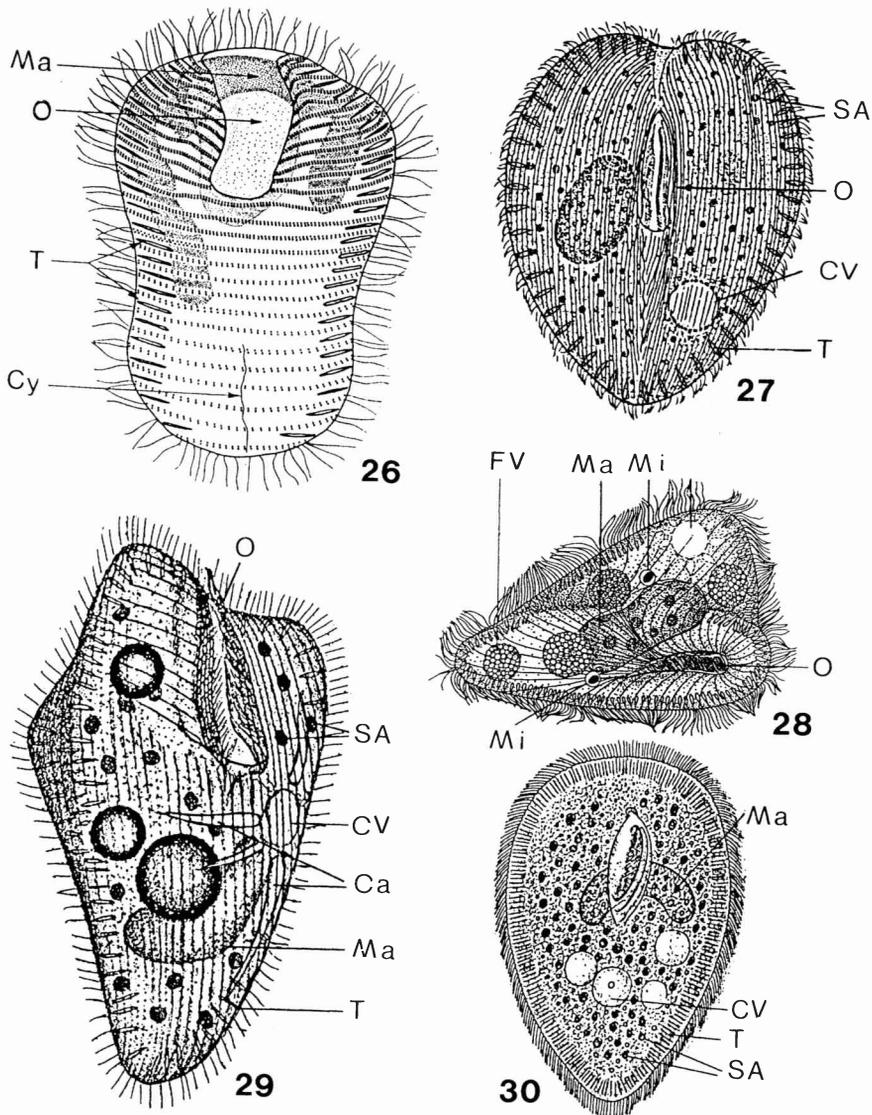
Marituja pelagica Gajewskaja, 1928: This curious species, originally assumed to be endemic to Lake Baikal, has since been found in several other lakes (Fig. 26). Its size and shape resemble *Stokesia vernalis*, *Disematostoma tetraedricum*, and *D. buetschlii*, all of which, however, bear symbiotic green algae. *Stokesia vernalis* is easily identifiable by its cap-like lateral appearance (Figs. 27, 28). According to Krainer (pers. comm.), *Stokesia vernalis* populations without symbiotic algae occur; possibly they belong to another species. *Disematostoma tetraedricum* (Fig. 29) and *D. buetschlii* (Fig. 30) differ in the shape of the anterior body portion. Detailed descriptions of the morphology and ecology of these four species are found in Fauré-Fremiet (1924), Foissner *et al.* (1994), Krainer (1994), Martin-Gonzalez *et al.* (1990), Packroff and Wilbert (1991), Roque (1961), and Wilbert (1972).



Figs. 14-21. Planktonic, nassulid holotrichs from life (14-16, 18-21, from Foissner *et al.*, 1994; 17, from Dragesco, 1972). *Obertrumia aurea* (Figs. 14, 19, 21; length 200 μ m) can become very abundant during blooms of *Oscillatoria rubescens*, which is grasped with the feeding basket (Figs. 14, 21) and makes well-fed cells dark at low magnification (Fig. 19). It is easily distinguished from *O. georgiana* (Fig. 17) and *Nassula ornata* (Figs. 15, 16, 18, 20; length 250 μ m) by its more slender shape and the absence of trichocysts. The trichocysts of *N. ornata* (Figs. 16, 18, resting and exploded) are fusiform, those of *O. georgiana* amphoral (Fig. 17). B = feeding basket, CV = contractile vacuole, FV = food vacuole, Ma = macronucleus, S = synhymenium (adoral organelles), V = blue vacuoles.



Figs. 22-25. Planktonic, prostomate holotrichs, composites from live and silver impregnated specimens (22, 25, from Foissner *et al.*, 1990; 23, from Dragesco *et al.*, 1974; 24, from Wilbert, 1986). **22:** *Urotricha furcata* is about 30 μm long and has two caudal cilia. **23, 24:** *Urotricha faurei* (Fig. 23) and *U. pelagica* (Fig. 24) both are about 50 μm long and have many caudal cilia; however, *U. faurei* lacks trichocysts and is, according to Krainer (1994), a junior synonym of *U. multisetosa* Wang and Nie. **25:** *Pseudobalanion planctonicum* is about 20 μm long and has a single caudal cilium as well as long perioral flaps which form a conspicuous corona. Br = brosse (adoral organelles), CC = caudal cilia, CV = contractile vacuole, Ma = macronucleus, O = oral basket opening, PF = perioral flaps, T = trichocysts.



Figs. 26-30. Planktonic hymenostomes from life (from Foissner *et al.*, 1994 and Krainer, 1994).

26: *Marituja pelagica*, composite from live and silver impregnated specimens, length 100 μm . This species has circular ciliary rows and lacks symbiotic algae. **27, 28:** *Stokesia vernalis* is about 150 μm long and easily recognizable by its cap-like lateral appearance and the symbiotic green algae. **29:** *Disematostoma tetraedricum* is about 120 μm long and easily identified by the four humps at the anterior end and the symbiotic green algae. **30:** *Disematostoma buetschlii* is about 150 μm long and has an obovoid shape and symbiotic green algae. Ca = canals of the contractile vacuole (CV), Cy = cypotype, FV = food vacuole, Ma = macronucleus, Mi = micronucleus, O = oral opening, SA = symbiotic algae, T = trichocysts.

Peritrichs

Peritrichs occur in three forms in the plankton, viz. either truly stalkless (e.g. *Astylozoon*) or stalked but free-swimming (e.g. *Vorticella mayeri*, *Epistylis rotans*, *Ophrydium* spp.), or attached to other planktonic organisms, especially to diatoms and colonies of bluegreen algae. The attached peritrichs (mostly vorticellids) often occur in masses, but are poorly known. The morphology and ecology of the truly stalkless and the euplanktonic taxa are extensively treated in Foissner (1975, 1977, 1978) and Foissner *et al.* (1992). Attached species were revised, although very briefly, by Warren (1986, 1987). I thus restrict discussion to a few forms which are possibly often confused.

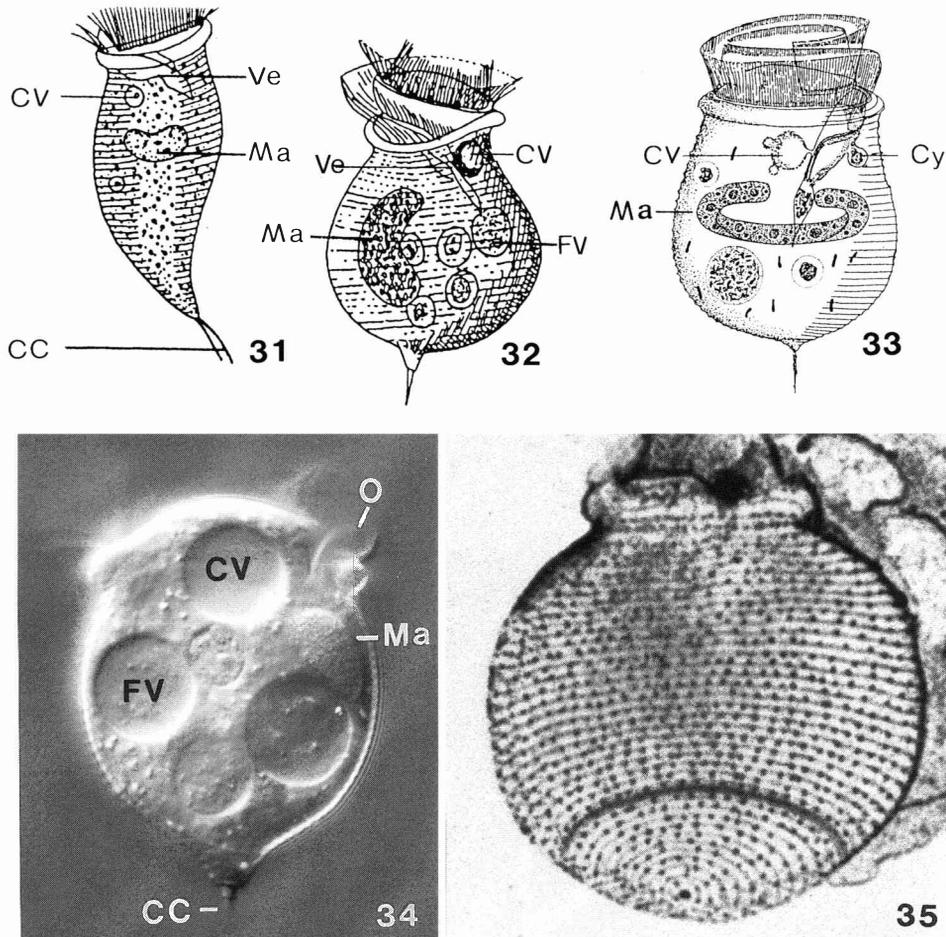
Astylozoon spp.: Species are differentiated according to cell and macronucleus shape and the location of the contractile vacuole. *Astylozoon fallax* Engelmann, 1862 and *A. faurei* Kahl, 1935, which have been recorded rather frequently from lake plankton, have a kidney-shaped macronucleus and the contractile vacuole located at the ventral or dorsal wall of the vestibulum (Figs. 31, 32). They thus differ clearly from *A. enriquesi* Foissner, 1977, which also occurs in the lake plankton, and has a semicircular macronucleus and the contractile vacuole at the dorsal vestibular wall (Figs. 33-35).

Ophrydium versatile (Müller, 1786): Easily confused with *O. eutrophicum* Foissner, 1979, which has a more elaborate oral apparatus, i.e. the peristomial ciliature winds around the peristomial disc in about 2 1/2 turns, as opposed to 1 1/2 turns in *O. versatile*. The anterior end of *O. eutrophicum* is thus set off head-like from the body, a feature which is easily recognizable even *in vivo* if cells are fully extended (cp. Figs. 36, 40 with 37, 38, 41). All other characters (size 250-600 µm, symbiotic algae, large colonies etc.) match those known from *O. versatile*. Another species, *O. naumanni* Pejler, 1962, is also stuffed with zoochlorellae and thus rather similar to *O. versatile*; however, it is distinctly smaller (about 50 µm only) and does not form large colonies. Further studies are necessary to prove whether *O. naumanni* is a distinct species or a juvenile or hunger form of *O. versatile*. Detailed morphological and ecological account of common species in Foissner *et al.* (1992).

Oligotrichs (Choreotrichs)

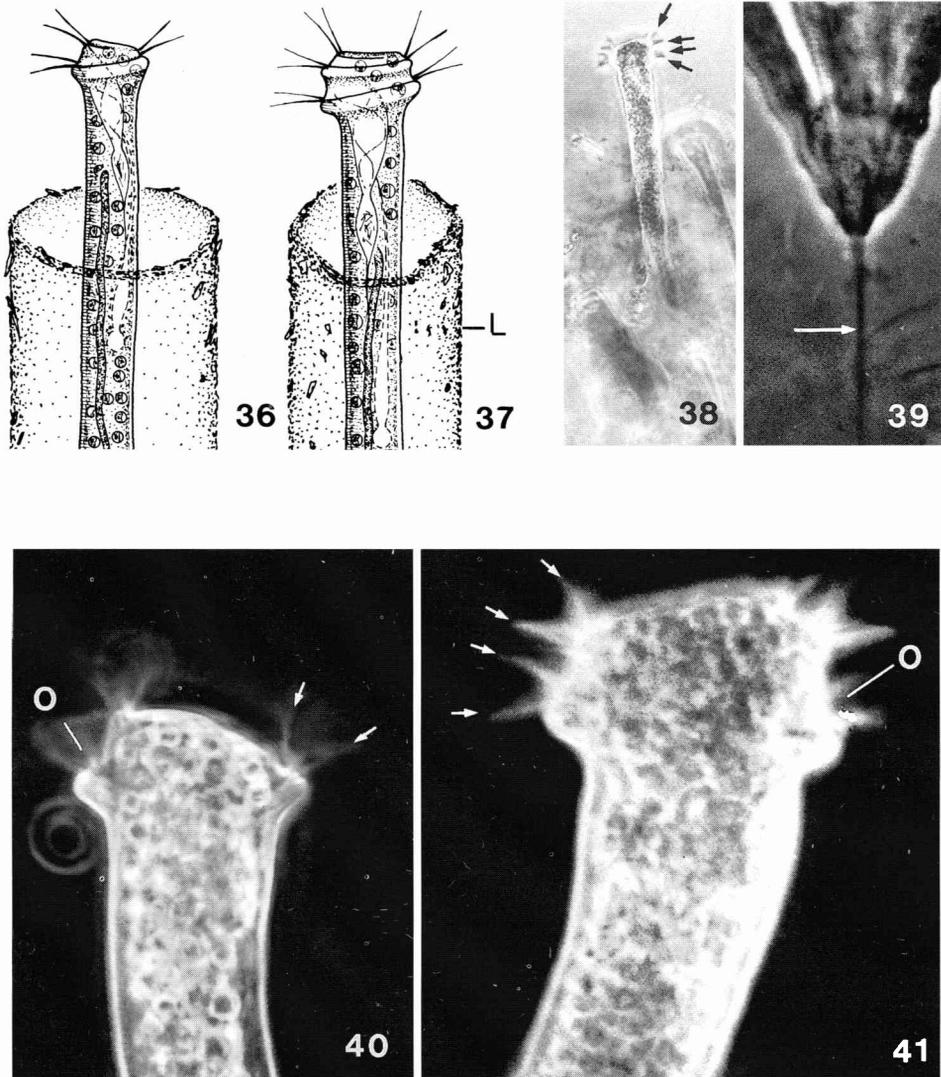
Oligotrichs are the dominant (in terms of number and biomass) and characteristic (in terms of species) component of the planktonic ciliate community, both in freshwater and marine environments. Foissner *et al.* (1991) thus referred to this community as "Oligotrichetea", in analogy to the system used by phytosociologists.

The name "Choreotrichida", introduced by Small and Lynn (1985), designates an artificial taxon (comprised of Tintinnina and Strobilidiina) and is thus superfluous; the taxa in question can be well included in the time-honoured oligotrichs (Petz and Foissner, 1992).



Figs. 31-35. Planktonic, stalkless peritrichs from life and after silver impregnation (from Foissner *et al.*, 1992). Members of the genus *Astylozoon* are mainly distinguished according to the shape of the macronucleus and the location of the contractile vacuole. **31:** *Astylozoon fallax* (length 90 μm) has a kidney-shaped macronucleus and the contractile vacuole is at the ventral wall of the vestibulum. **32:** *Astylozoon faurei* (length 60 μm) also has a kidney-shaped macronucleus but the contractile vacuole is at the dorsal wall of the vestibulum. **33-35:** *Astylozoon enriquesi* (length 60 μm) has, like *A. faurei*, the contractile vacuole at the dorsal vestibular wall, but the macronucleus is semicircular. A regular pattern of circular lines (silverlines) with attached granules (pellicular pores) is recognizable after silver nitrate impregnation (Fig. 35). CC = caudal bristles, CV = contractile vacuole, Cy = cypotype, FV = food vacuole, Ma = macronucleus, O = oral opening, Ve = vestibulum.

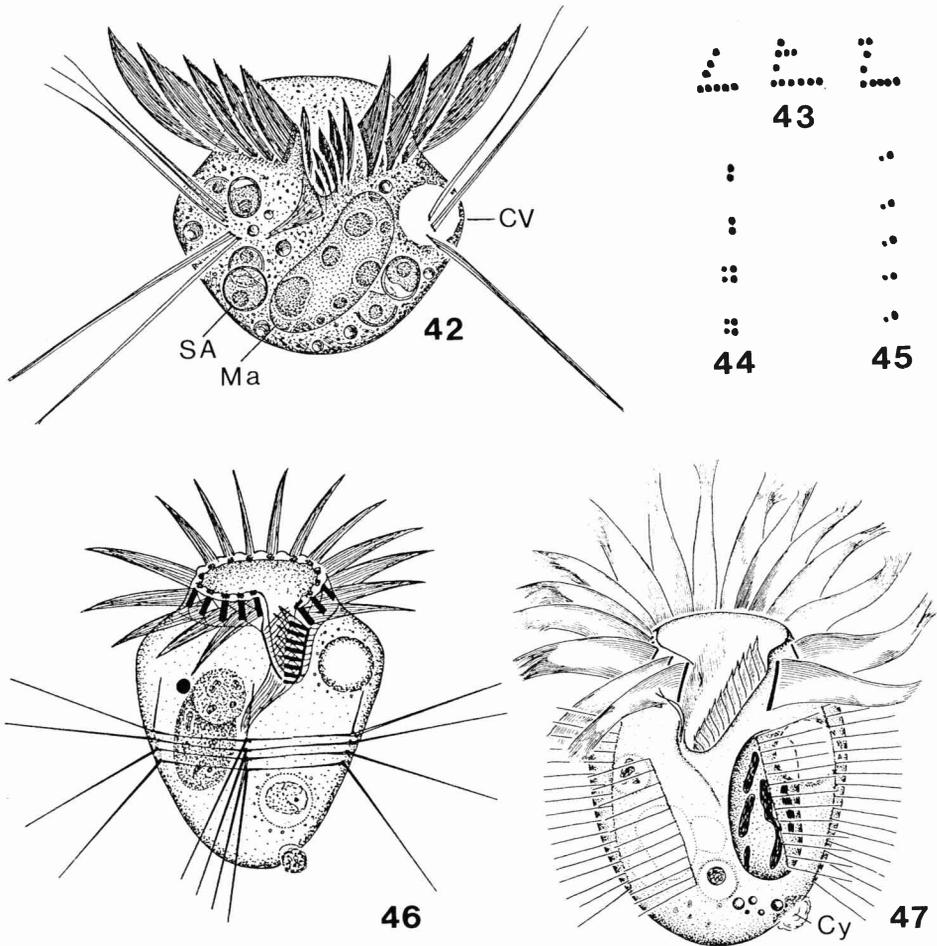
The freshwater oligotrichs comprise few genera most of which can be easily identified with the following key.



Figs. 36-41. Semiplanktonic, stalked peritrichs from life (from Foissner *et al.*, 1992). These figures show *Ophrydium versatile* (Figs. 36, 39, 40; length 300-600 μm) and *O. eutrophicum* (Figs. 37, 38, 41; length 250-350 μm) which both form large, slimy colonies and have symbiotic algae. However, the peristomial ciliature of *O. eutrophicum* winds around the peristomial disc in about $2\frac{1}{2}$ turns, as opposed to $1\frac{1}{2}$ turns in *O. versatile*, giving the cells a cephalized appearance which is easily recognizable even at low magnification (Fig. 38). Two and four ciliary windings (arrows) are recognizable, respectively, because the ciliature consists of an adoral zone of membranelles which is accompanied by an undulating membrane; these form a V-shaped pattern in feeding cells. The stalk is very thin in both species (Fig. 39, arrow). L = mucilaginous lorica, O = oral opening.

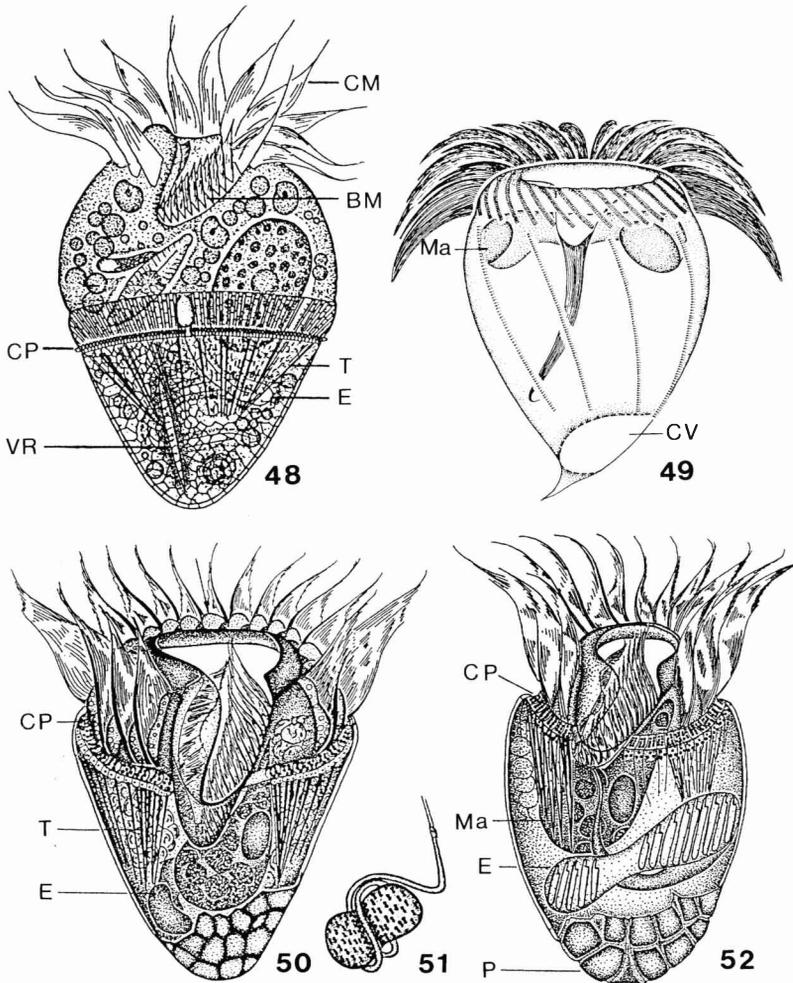
- 1 With mucous or firm, extracellular lorica about as long as cell Tintinnids (Figs. 53-55)
- Without extracellular lorica 2
- 2 Jumping bristle complexes or meridional rows of long cilia in middle third of cell 3
- Ciliary pattern different 5
- 3 Jumping bristle complexes with long (> 10 μm) cilia 4
- Simple meridional rows of long cilia in middle third of cell *Meseres* (Fig. 47)
- 4 Jumping bristle complexes composed of a short meridional row of paired and single, long (> 10 μm) cilia. Most species without symbiotic green algae *Halteria* (Fig. 46)
- Jumping bristle complexes composed of a short meridional and a short horizontal row of long (> 10 μm) cilia. Planktonic species with symbiotic green algae *Pelagohalteria viridis* (Fig. 42)
- 5 Many (≥ 10) ciliary rows with cilia of different length. Body very soft and usually barrel-shaped Tintinnids with lost lorica (Figs. 53-55)
- Usually less than 10 slightly spiralling ciliary rows near more or less distinct cortical ridges or single circumferential row at or above mid-body. All somatic cilia very small (< 5 μm) and of same size 6
- 6 Adoral zone of membranelles forms a closed circle at anterior end. At least 5 slightly spiralling ciliary rows near more or less pronounced cortical ridges. Without long, rod-shaped trichocysts (extrusomes) 7
- Adoral zone bipartite in large collar and small buccal membranelles. Single circumferential ciliary row with very short cilia. Extrusomes long and rod-shaped 8
- 7 Somatic ciliary rows extend to posterior end of body, forming distinct spiral at posterior pole *Strobilidium* [only one reliable species known, *S. caudatum*, which is semi-sessile and usually does not occur in the plankton of lakes; detailed description in Petz and Foissner (1992)]
- Somatic ciliary rows end subterminally, *i.e.* do not form a caudal spiral *Rimostrobilidium* (Fig. 49) [See Petz and Foissner (1992) for a detailed discussion of nomenclature. *Rimostrobilidium* Jankowski is an unfortunate name because it indicates that the genus belongs to the family Strombidiidae, although it is a member of the Strobilidiidae]
- 8 Circumferential extrusome and ciliary girdle at or near mid-body; single, inconspicuous postequatorial ciliary row. Collar and buccal adoral membranelles merge with each other *Strobilidium* (Fig. 48)
- Circumferential extrusome and ciliary girdle located supraequatorially, *i.e.* at level of buccal membranelles; no postequatorial ciliary row. Collar and buccal adoral membranelles separate *Pelagostrobilidium* (Figs. 50-52)

Halteria grandinella (Müller, 1773): Easily confused with the green *Pelagohalteria viridis* (Fromentel, 1876) Foissner *et al.*, 1988, which has symbiotic algae and more



Figs. 42-47. Ventral views of planktonic, halterioid oligotrichs, composites from life and silver impregnated specimens (42, 43, from Foissner *et al.*, 1988; 44, 46, from Foissner *et al.*, 1991; 45, 47, from Petz and Foissner, 1992). Halterioid genera are distinguished mainly by the arrangement of the somatic cilia (Figs. 43-45). **42, 43:** *Pelagohalteria viridis* (diameter 20-30 μm) has symbiotic green algae and was probably often misidentified as green *Halteria grandinella*. **44, 46:** *Halteria grandinella* (length 30 μm) has simpler bristle complexes than *P. viridis* and lacks zoochlorellae. **45, 47:** *Meseres corlissi* (length 80 μm) has long ciliary rows composed of simple, rather stiff cilia. CV = contractile vacuole, Cy = cytopogye, Ma = macronucleus, SA = symbiotic algae.

and differently arranged jumping bristles (cp. Figs. 42, 43 with 44, 46). Note that *H. grandinella* is sometimes also green-coloured, however, not by zoochlorellae but by ingested algae. Another green species is *H. bifurcata* Tamar, 1968, whose jumping bristles are curved and bifurcated and which moves more slowly than *H. grandinella* in a right-handed spiral. These characters are not easily recognized and one may hope that silver impregnation will reveal further differences to both *H. grandinella* and



Figs. 48-52. Ventral views of planktonic, strombidiid and strobilidiid oligotrichs, composites from live and silver impregnated specimens (48, from Foissner *et al.*, 1991; 49, from Foissner *et al.*, 1988; 50-52, from Krainer, 1991). **48:** *Strombidium viride* (length 60 μm) differs from *Pelagostrombidium* spp. by its more posteriorly located circumferential paratene (a ring containing short cilia and trichocysts), by having a ventral row of short cilia, and by the simpler neoformation organelle. **49:** *Rimostrombidium lacustris* (length 70-100 μm) differs from *R. velox* by the lack of symbiotic algae and less pronounced cortical ridges. **50-52:** *Pelagostrombidium fallax* (Figs. 50, 51; length 60 μm) and *P. mirabile* (Fig. 52; length 45 μm) are distinguished by the buccal adoral membranelles which extend at least half cell length internally in *P. fallax*. Members of this genus have a complicated neoformation organelle (Fig. 51) from which the oral apparatus of the posterior daughter cell originates during binary fission. BM = buccal adoral membranelles, CM = collar adoral membranelles, CP = circumferential paratene, E = embryonic body (part of the neoformation organelle), Ma = macronucleus, P = polysaccharide plates, T = trichocysts, VR = ventral ciliary row.

P. viridis, some of whose bristles are also bifurcated; Krainer (1994) synonymizes *H. bifurcata* Tamar with *H. minuta* Gelei. Possibly also easily confused with *Meseres corlissi* Petz and Foissner, 1992, which, like *H. grandinella*, lacks symbiotic algae, but has meridional ciliary rows whose cilia are not fused to jumping bristles (Fig. 47). Detailed morphological and ecological account of common species in Foissner *et al.* (1988, 1991) and Petz and Foissner (1992).

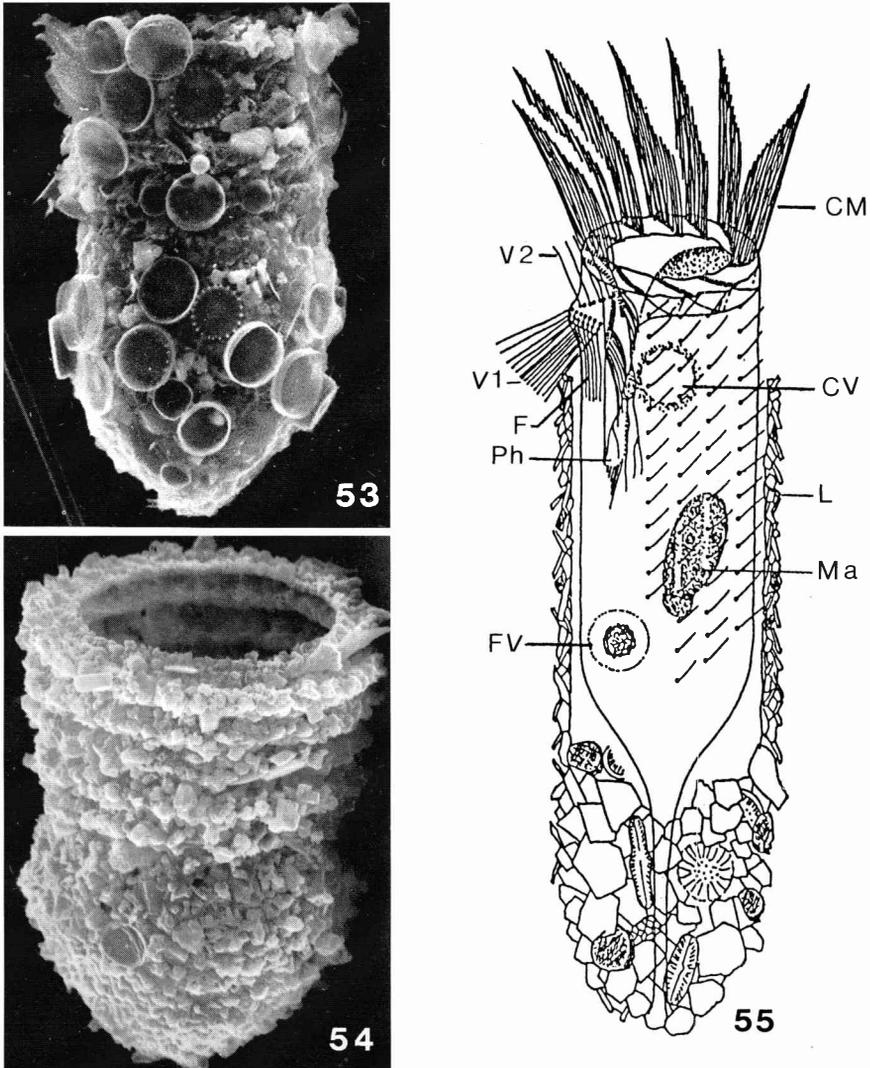
Pelagostrombidium mirabile (Penard, 1916) and *P. fallax* (Zacharias, 1895): Easily confused with *Strombidium* spp., which have the circumferential paratene (the girdle formed by the cilia and extrusomes) located in mid-body and a simpler oral anlage, *i.e.* lack the potato-shaped embryonic body (Fig. 51). *P. mirabile* (Fig. 52): 45 × 30 μm, slender conical to ovoid, greenish-grey to orange-yellow. Polysaccharide plates usually square. 12-15 buccal membranelles extending a third of cell length internally; *P. fallax* (Fig. 50): 60 × 50 μm, plump conical to almost globular, reddish-brown. Polysaccharide plates polygonal. 19-22 buccal membranelles extending at least half cell length internally. Detailed description of the morphology and ecology in Krainer (1991).

Rimostrombidium velox (Fauré-Fremiet, 1924): This green species, which is still insufficiently known, is easily confused with *R. lacustris* Foissner *et al.*, 1988 (Fig. 49), which, however, lacks zoochlorellae, but often appears greenish by ingested algae, has less pronounced cortical ridges, and is larger (70-100 × 50-70 μm versus 30-50 × 53 μm). Several other species of this genus occur rather frequently in the lake plankton, *e.g.* the small (20-30 × 15 μm) *R. humile*. See Foissner *et al.* (1988, 1991) and Krainer (1994) for a detailed account on the morphology and ecology of *R. lacustris* and *R. humile*.

Strombidium pelagicum Krainer, 1991 [now *S. pelagoviride* because of preoccupation; Krainer (1993)]. This species is considered by Foissner *et al.* (1991) as a junior synonym of *S. viride* Stein or of *S. viride pelagica* Kahl. The differences indicated by Krainer are small and concern meristic characters (*e.g.* number of collar membranelles) which the early authors, lacking the advantage of silver impregnation, could not analyze in detail.

Strombidium viride Stein, 1867 (Fig. 48): Easily confused with *Pelagostrombidium* spp., which have the circumferential paratene (the girdle formed by the cilia and extrusomes) located supraequatorially, *i.e.* at level with the buccal adoral membranelles. Detailed description of the morphology and ecology in Foissner *et al.* (1991) and Krainer (1994).

Tintinnids (Figs. 53-55): See also *Codonella cratera* and *Tintinnidium fluviatile*. The fresh-water tintinnids are well known, *i.e.* have been investigated with modern methods. These studies showed that lorica characters are less important than the ciliary pattern of the cell which, unfortunately, is clearly recognizable only after protargol silver impregnation. The following fresh-water species were described or reinvestigated and reliably characterized by Blatterer and Foissner (1990), Foissner and O'Donoghue (1990), Foissner and Wilbert (1979), and Song Weibo and Wilbert (1989): *Tintinnidium fluviatile* (Stein), *T. pusillum* Entz, *T. semiciliatum* (Sterki) which is the "sessile *T. fluviatile*" mentioned by several authors and described also by



Figs. 53-55. Planktonic, tintinnid oligotrichs (from Foissner *et al.*, 1991). **53, 54:** Scanning electron micrographs of the lorica of *Codonella cratera* (length 40-80 μm) which is composed of diatom frustules, sand grains and other materials available in the water column. This species is easily identified, even if it is aloriccate and/or fixed, by its two macronuclear segments. Most other freshwater tintinnids need, however, protargol impregnation for reliable identification. **55:** *Tintinnopsis cylindrata*, composite from live and silver impregnated specimens, length 100 μm . This is the sole, reliably described freshwater tintinnid having a firm, cylindroid lorica made of foreign particles (sand grains, diatom frustules, etc.). CM = collar adoral membranelles, CV = contractile vacuole, F = fibres, FV = food vacuole, L = lorica, Ma = macronucleus, Ph = pharynx, V1 + V2 = ventral organelles.

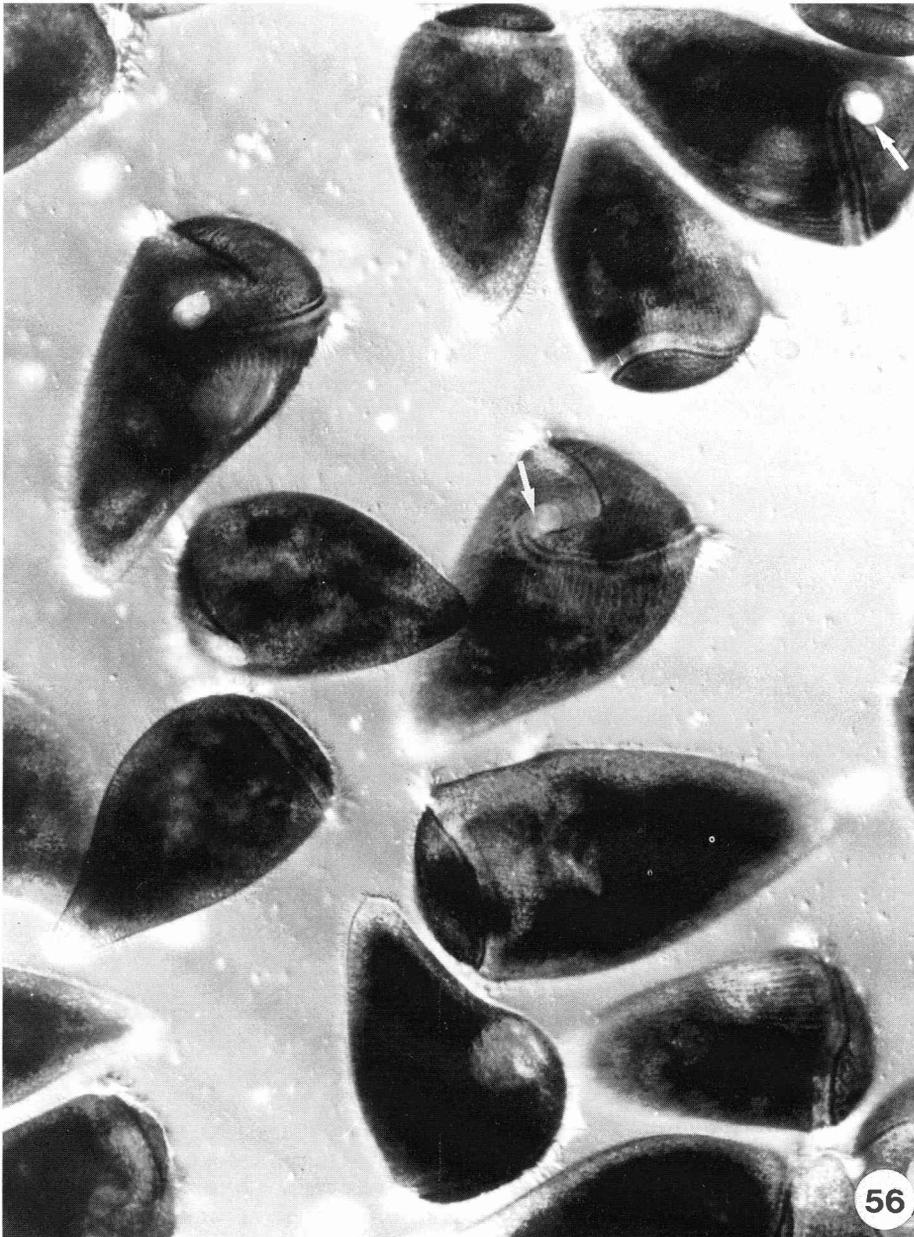


Fig. 56. A bloom of *Stentor amethystinus* (length 300-500 μm), a planktonic heterotrich ciliate (from Foissner *et al.*, 1992). Arrows mark oral opening. This species is easily confused with *S. niger* which, however, lacks symbiotic green algae.

Maskell as *T. fluviatile* var. *emarginata* (i.e. *T. fluviatile* and *T. semiciliatum* are valid species, whereas *T. fluviatile* var. *emarginata* is a junior synonym of *T. semiciliatum*), *Tintinnopsis cylindrata* Kofoid and Campbell, *Codonella cratera* (Leidy), and *Stenosemella lacustris* Foissner and O'Donoghue. About 20 other tintinnids have been described from, or reported to occur in freshwater. However, I am convinced that most, if not all, are junior synonyms of the species mentioned above or misidentifications. Typical examples are *Tintinnopsis amphora*, *T. amphora acuminata*, and *T. ovalis* recorded by Pollinger and Kimor (1967) from Lake Tiberias. These species are testate amoebae of the genus *Diffugia*!

Codonella cratera (Leidy, 1877): Several *Codonella* species and varieties have been described from freshwater, based on differences in lorica structure and shape. However, the investigations by Bernatzky *et al.* (1981) indicate that such differences are caused by the habitat and the age of the lorica (Figs. 53, 54). I think that this genus contains only one freshwater species, viz. the common *C. cratera*, originally described by Leidy (1877) as testate amoeba. Detailed descriptions of the morphology, morphogenesis, and ecology in Bernatzky *et al.* (1981), Foissner and Wilbert (1979), Foissner *et al.* (1991), and Petz and Foissner (1993).

Tintinnidium fluviatile (Stein, 1863), *Tintinnidium pusillum* Entz, 1909, and *Tintinnopsis cylindrata* Kofoid and Campbell, 1929: These common planktonic freshwater tintinnids need protargol silver impregnation for reliable identification. However, the lorica of *T. fluviatile* is usually larger (150 x 35-70 μm) than in the other species, and the lorica of *T. cylindrata* (40-150 x 20-30 μm) is usually made of foreign particles (sand grains, diatom frustules; Fig. 55), whereas it consists of a mucous substance in the other species. Detailed morphological and ecological description as well as key to Laurasian freshwater species in Foissner and Wilbert (1979), Foissner *et al.* (1991), and Petz and Foissner (1993).

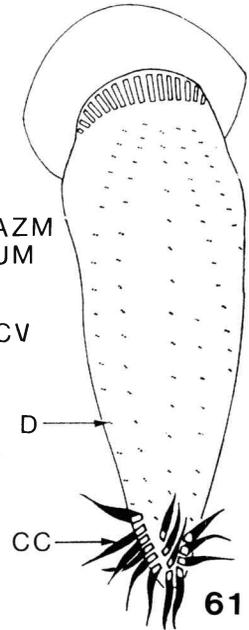
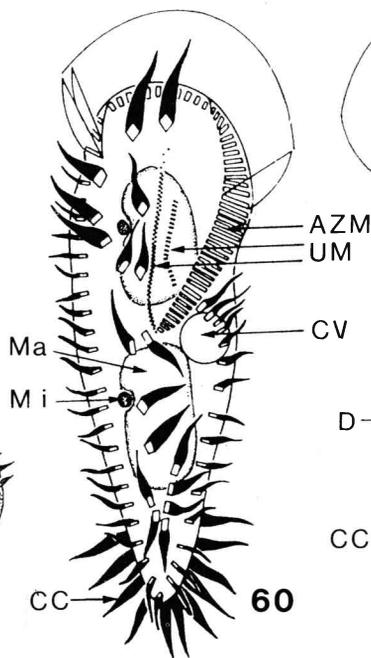
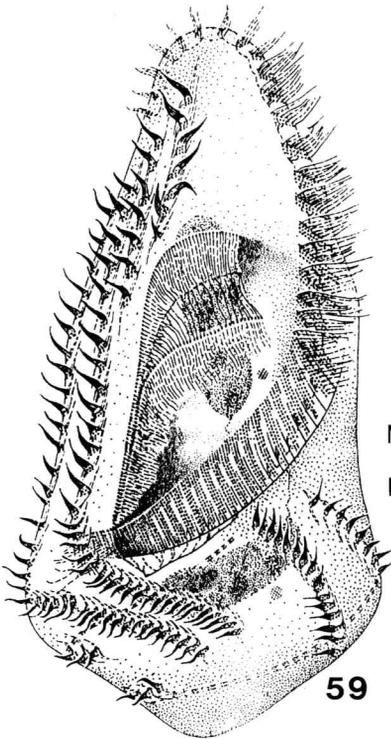
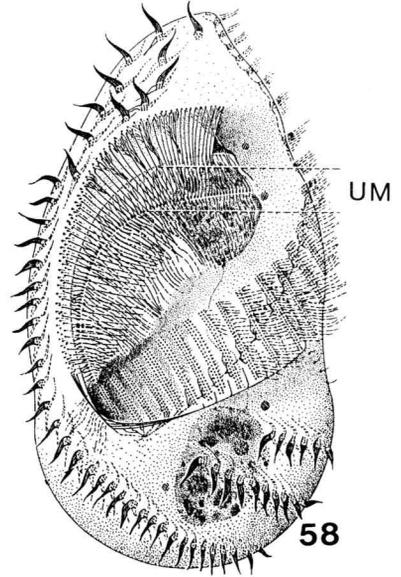
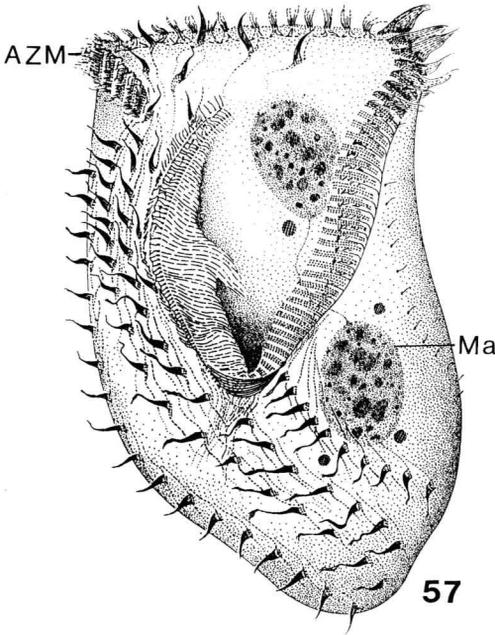
Heterotrichs

Heterotrichs are represented in the plankton mainly by the genus *Stentor*, which often causes heavy blooms in small lakes used for recreation. The genus is in urgent need of revision. Common species from Europe and Africa are treated in detail in Dragesco and Dragesco-Kernéis (1986), Foissner *et al.* (1992), and Nilsson (1986).

Stentor niger (Müller, 1773): Easily confused with *S. amethystinus* Leidy, 1880, which has violet granules and green symbiotic algae in the cortex, as opposed to *S. niger*, which has rusty brown granules and lacks zoochlorellae. All other characters are very similar in both species, especially their black appearance at low (< x 100) magnification (Fig. 56).

Hypotrichs

Few euplanktonic hypotrichs are known. Most remarkable are the genera *Pelagotrichidium* and *Hypotrichidium* because of their beauty and complicated cirral



Figs. 57-61. Ventral views of planktonic hypotrichs, composites from live and silver impregnated specimens (57-59, from Tuffrau, 1972; 60, 61, from Wilbert, 1986). **57:** *Pelagotrichidium faurei* (length 280 µm) differs from *Hypotrichidium* spp. by the arrangement of the cirral rows and the more elaborate adoral zone of membranelles. **58, 59:** *Hypotrichidium tisiae* (Fig. 58; length 125 µm) and *H. conicum* (Fig. 59; length 140 µm) differ in the number of somatic cirral rows and adoral membranelles as well as in the shape of the body and buccal field. **60, 61:** Ventral and dorsal view of *Pseudostrombidium planctonicum*, length 200 µm. This large hypotrich is easily identified by its numerous caudal cirri which form a posterior tuft. AZM = adoral zone of membranelles, CC = caudal cirri, CV = contractile vacuole, D = dorsal ciliary rows, Ma = macronuclear segments, Mi = micronucleus, UM = undulating membranes.

pattern (Figs. 57-59). Species distinction is difficult and Foissner *et al.* (1991) discuss the possibility of all described *Hypotrichidium* species belonging to a single species, *H. conicum* Ilowaisky, 1921. Detailed descriptions of European and African species in Dragesco and Dragesco-Kernéis (1986), Foissner *et al.* (1991), and Tuffrau (1972). *Pseudostrombidium planctonicum* (Figs. 60, 61) is possibly easily confused with *Stylonychia* spp., which, however, have only three long caudal cirri.

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