ORDER BICOSOECIDA
GRASSÉ 1926

By ØJVIND MOESTRUP

The bicosoecids form a well-defined group of heterotrophic heterokont flagellates. Recent studies on 18S rRNA (Leipe et al., 1995) have shown that *Cafeteria*, a primitive bicosoecid, is one of the most primitive heterokont protists and precedes both the oomycetes and the heterokont algae. Bicosoecids (sometimes erroneously spelled bicoecids or bikocoecids) are phagotrophic flagellates in fresh water and marine environments. Only three genera are known, comprising c. 45 described species. Most species are unicells but some form colonies. The great majority belongs to the genus *Bicosoeca*. Bicosoecids are biflagellate and the movements of the anterior hairy flagellum draws the swimming cell forward in the water. The smooth flagellum is usually directed posteriorly and may be used for attachment (Fig. 1). When attached, the movements of the hairy flagellum create a water current that draws water and food particles towards the peristome area of the cell (Figs. 1A, B). This area is supported by a broad band of microtubules, now known to be homologous with a flagellar root that serves in food uptake in other hetero- and mixotrophic heterokonts (Moestrup, 1995). In the light microscope, the peristome area may be visible as a lip-like structure. Cells of *Bicosoeca* are loricate and the cells attach to the inside bottom of the lorica with the smooth flagellum tip. *Cafeteria* and *Pseudobodo are* naked and freeswimming but may attach transiently to various surfaces, including the water film.

Key characters

1. Cells are biflagellate. The flagellar apparatus is diagnostic for the group and is described above.
2. Cells are phagotrophic and lack all traces of chloroplast, indicating that the ancestors of bicosoecids were heterotrophic rather than auto- or mixotrophic protists (comp. *Paraphysomonas*). Cells feed on bacteria or other eukaryotes.
3. Cells lack ejectile organelles. Freshwater species possess a contractile vacuole system.
4. The cell is surrounded by a lorica or naked (Figs 1-4).
5. Reproduction is by fission. Sexual reproduction is unknown.
6. Freshwater or marine species, very widely distributed, some species occur in tropical as well as temperate areas.
7. Diagnostic features used in species identification are cell size, shape, lorica shape and texture, single or colony-forming cells.

Bicosoecids were classified by Moestrup (1995) into two families, Bicosoecaceae and Cafeteriaceae, depending on the presence or absence of a lorica.

Key to the Genera

1. Cells naked, not surrounded by a lorica. 2
1´. Each cell living in a lorica.... ***Bicosoeca***

2. Smooth posterior flagellum attached to the surface directly..... ***Cafeteria***
2´. A thin thread of mucus extends from the tip of the posterior flagellum to the substrate ..... ***Pseudobodo***

Genus ***Bicosoeca*** James-Clark, 1866

Colorless cells attached by the tip of the posterior flagellum to the bottom of an organic lorica of various shapes and textures. Some lorica types are very thin and almost transparent, whilst others are thicker and variously ornamented. They may be stalked (Figs. 1A-D, 2) or unstalked (Fig. 1E), and species may be

free-swimming or attached, e.g. attached to diatoms or other protists.

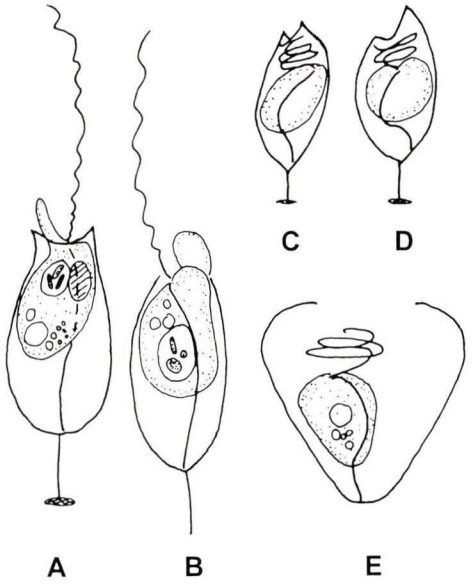

Fig. 1. *Bicosoeca* spp. A-D. *B. mignotii.* A,B. Undisturbed cells. C,D, Cells that have withdrawn into the cell with the hairy flagellum coiled up. E. *B. planctonica,* a planktonic species with stalkless lorica. x2000. (from Vørs, 1992)

Cell shape more or less rounded. The front flagellum is directed out of the lorica when the cell is undisturbed or swimming. When disturbed, the flagellum retracts and coils up rapidly on the anterior end of the cell (Figs 1C-E), and the cell withdraws to the bottom of the lorica. In some species, the daughter cells settle on the parent lorica and colonies develop. Species of *Bicosoeca* phagocytize bacteria or eukaryotic algae (Moestrup & Thomsen 1976). Nearly 40 known species, mostly in fresh water. See Preisig et al. (1991).

Bicosoeca mignotii Moestrup, Thomsen & Hibberd (Fig. 1A-E). Cells 3-4 μm long and 5-7 μm wide. Lorica elongate ovoid, transparent and delicate. Lorica chamber 10-15 μm long, 5-7 μm wide, with a 5-10 μm-long stalk that attaches to a substrate by a small disc. Anterior end of the lorica divided into two opposing beak-like parts. Lorica apparently amorphous, the stalk fibrous. Very common freshwater species, in the plankton or attached. Known from the inner Baltic, Denmark, and England but almost certainly much more widely distributed (Vørs 1992).

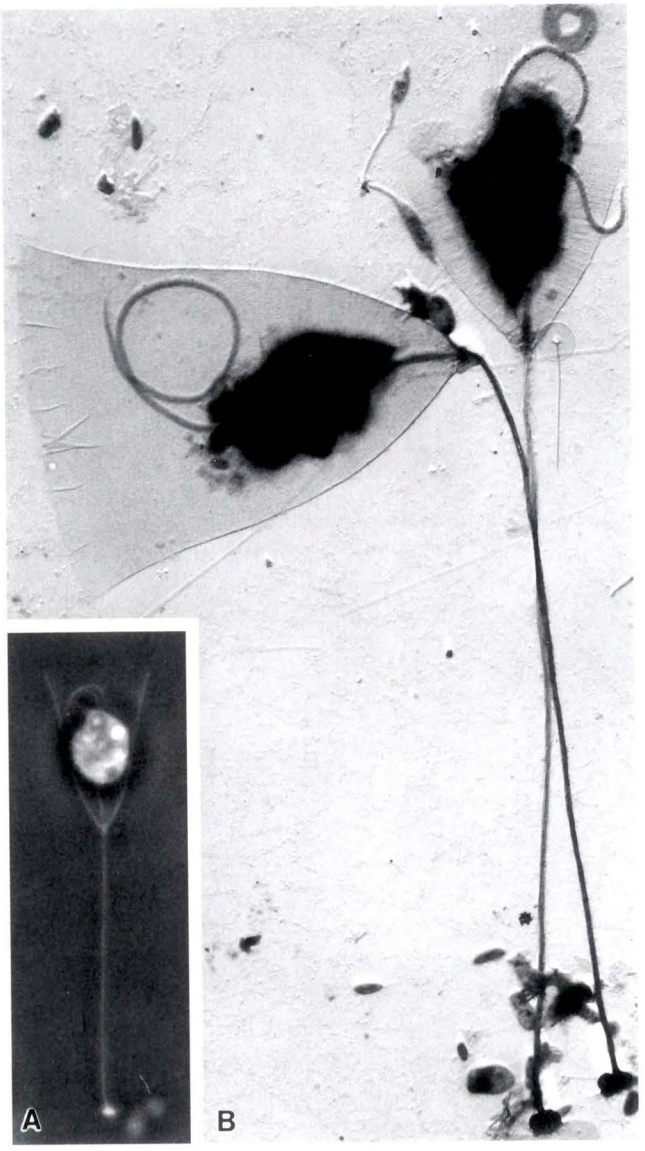

Fig. 2. *B. petiolata,* a species with very long-stalked, bell-shaped lorica. The cell on the right in Fig. 2B has only half completed formation of its lorica. A, anoptral contrast, x1000. B. shadowcast whole mount, x27,000. (Original photographs courtesy of H. A. Thomsen).

Genus ***Cafeteria***
Fenchel and Patterson, 1988

Colorless cells with the two flagella inserted subapically (Fenchel and Patterson 1988). Cells may swim with the hairy flagellum projecting forwards, or they may attach with the tip of the smooth flagellum. Four described species from temperate and tropical plankton and marine sediments. One species with a distinct furrow used in food uptake (Larsen and Patterson,1990.) See Larsen and Patterson, (1990) for a description of all four species).

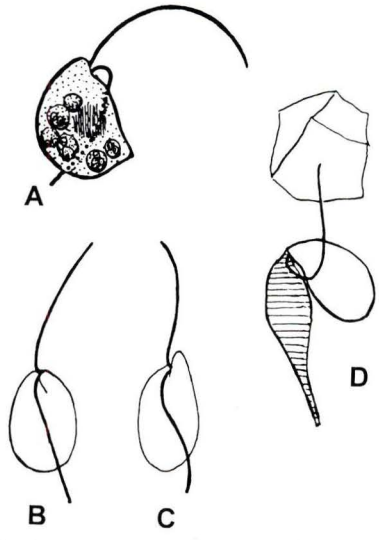

Fig. 3. *Cafeteria roenbergensis.* A. Feeding cell. B.C. Swimming cells. D. Beat envelope of anterior flagellum. x3000. (From Larsen and Patterson, 1990)

Cafeteria roenbergensis Fenchel and Patterson (Fig. 3). Cells D-shaped, cordiform or spherical, sometimes distorted by ingested food particles, mostly 3-6 μm long, compressed laterally. Larger cells occur occasionally (Larsen & Patterson 1990). Anterior flagellum 5-8 μm long, posterior flagellum c. 5 μm. The posterior flagellum passes in a shallow groove and the tip of the flagellum is often attached to a piece of debris or other surface when undisturbed. In swimming cells, the posterior flagellum trails loosely behind the cell. *Cafeteria* is easily grown in culture on a diet of bacteria. It is widely distributed and probably generally overlooked or misidentified.

Genus ***Pseudobodo*** Griessmann, 1913

As *Cafeteria*, but cells may attach to a substrate by a long thin thread of mucus which extends from the tip of the smooth flagellum (Larsen and Patterson, 1990). Swimming cells are hardly distinguishable from *Cafeteria*. Two species, both marine. In plankton and marine sediments. Distributed in both tropical and temperate areas.

Pseudobodo tremulans Griessmann (Fig. 4). Cell body rounded, 2.5-5.5 μm in diameter. Anterior flagellum 10-16 μm long, the smooth posterior flagellum 5-10 μm.

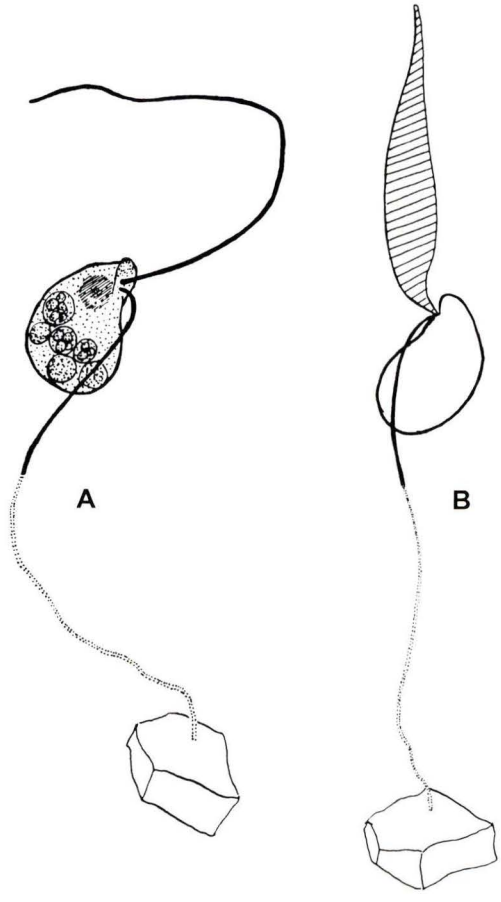

Fig. 4. *Psudobodo tremulans.* A. General aspect. B. Beat profile of hairy flagellum. x3000. (From Larsen and Patterson, 1990)

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CHRYSOMONADA (CLASS CHRYSOPHYCEAE PASCHER, 1914)

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This class is circumscribed here in the narrow sense, i.e. excluding organisms previously often assigned to the Chrysomonada but now referred to the Bicosoecida Grassé, 1926, Synurophyceae Andersen, 1987, Pelagophyceae Andersen & Saunders in Andersen et al., 1993, Chrysomerophyceae Cavalier-Smith in Cavalier-Smith et al., 1995, Phaeothamniophyceae Andersen & Bailey in Bailey et al., 1998, Silicoflagellata Lemmermann, 1901 (orders Dictyochales Haeckel, 1894/Pedinellales Zimmermann, Moestrup & Hällfors, 1984/Rhizochromulinales O'Kelly & Wujek, 1995), and Prymnesiophyceae Hibberd, 1976/Haptophyceae Christensen ex Silva, 1980 (=Prymnesiida/Haptomonadida). The chrysomonads comprise mainly single-celled and colonial flagellates, but amoeboid (rhizopodial), **plasmodial**, **palmelloid** (**capsoid**), coccoid, and **parenchymatous** forms also occur. In this chapter only genera with predominantly flagellate, amoeboid and plasmodial life forms are treated. About 100 such genera (including some 800 species) have been described, the 27 better known of which are surveyed in some detail below. The lesser known genera are only briefly indicated thereafter and have not been included in the "Artificial Key to Selected Genera".

Chrysomonads are mainly freshwater organisms, with only a few species reported from marine environments and a few from soil and snow habitats. They live in a wide range of freshwater environments from polar regions to the tropics, but most commonly occur in cold temperate lakes, ponds and bogs. Some species can form blooms causing taste and odor problems (see Nicholls, 1995).

Present knowledge on the Chrysomonada (Chrysophyceae) is summarized by Hibberd (1976), Pienaar (1980), Hibberd and Leedale (1985) and Kristiansen (1986, 1990). Detailed data from current research can also be found in the Proceedings of the International Chrysophyte Symposia (Kristiansen and Andersen, 1986; Kristiansen et al., 1989; Sandgren et al., 1995; Kristiansen and Cronberg, 1996). The most complete taxonomic account is that of Starmach (1985). See also Pascher (1913), Huber-Pestalozzi (1941), and Bourrelly (1957, 1968/1981). The heterotrophic taxa are reviewed