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RESIDUAL HETEROTROPHIC STRAMENOPILES

by DAVID J. PATTERSON

The stramenopiles are a large group of protists which are defined by reference to a synapomorphy—tripartite, tubular hairs (Patterson, 1989). The composition of the group was indicated elsewhere (Patterson, 1994) and is upgraded to include genera described subsequent to 1994 as follows:

Stramenopiles
- Bicosoecales
- Slabyrinthulids
  - *Diplophrys*
  - Labyrinthulids
  - Thraustochytrids
- Sloomycetes
  - Oomycetes
  - Hyphochytridiomycetes
- Slopalines
  - Proteromonadidae
  - Opalinidae
- Stramenochromes
  - Core chrysophytes
    - Chromulinales
    - Hibberdiales
    - Hydrurales
    - Pelagophytes
    - Chrysomeridales
  - Axodines
    - Dictyochales
    - Pedinellales
    - Rhizochromulinales
  - Synurids
  - Xanthophytes
  - Raphidophytes
  - Eustigmatophytes
  - Brown algae
  - Diatoms
  - Parmales
  - *Commation*
  - *Developayella*
  - *Ollicola*
  - *Pendulomonas*
  - *Reticulosphaera*
  - *Siluania*

The group contains organisms with a diverse array of organizational types from the fungus-like oomycetes to the multicellular, massive brown algae. It includes autotrophs such as diatoms and chrysophytes as well as mixotrophs and heterotrophs. *Reticulosphaera* is an amoeboid autotroph, but there is dispute as to whether it is a member of this taxon. The group has some compositional overlap with the chrysophytes, chromophytes, heterokonts, or chromists — but not to a level that might regarded as sufficient to regard the stramenopiles as being identical with any of these (despite assertions by some to the contrary). The principal difference between this taxon and the others named is its definition by a single synapomorphy. The classification given above seeks to ensure that all taxa are monophyletic. Consequently, it differs from alternative groupings (heterokonts, chrysophytes, chromists) not only in concept, but

from alternative groupings (heterokonts, chrysophytes, chromists) not only in concept, but also in composition, hierarchical structure, and our present inability to rank its members.

Many stramenopiles have plastids, such that the grouping that contains the core chrysophytes has intuitively been regarded as algal (e.g. Cavalier-Smith, 1989). Comparisons of sequences and explicit analyses (Leipe et al., 1994, 1996; Williams, 1991), however, suggest that the ancestral stramenopiles were heterotrophs and that definitions that are dependent on plastids will only define a subset of this group.

In this book, various subsets of the stramenopiles have been included in other chapters; however, as criteria of monophyly have not been applied, the coverage has been incomplete. This chapter therefore serves to include organisms which are stramenopiles but have not been included elsewhere.

KEY CHARACTERS

Stramenopiles are identified by having tripartite hairs which are usually attached to the anterior flagellum. The presence of these hairs can be inferred from the flow of fluid which flows from tip to base of beating flagella. Some stramenopiles (e.g. opalines) have secondarily lost the hairs, and their membership of the group must then be determined by characters derived within the group (e.g. a double gyre in the transitional region of the flagellum).

Genera and species are distinguished on the number and disposition of the flagella, motility, and cell shape. Within this group, one subset is distinguished because the cell attaches to the substrate by the tip of the flagellum.

KEY TO GENERA

1. Taxa covered elsewhere in this text. See appropriate chapters
1'. Taxa not covered elsewhere in this text..... 2

2. Cells with two or no flagella.....3
2'. Cells always with a single flagellum ***Siluania***

3. Cells attaching to substrate via the distal tip of recurrent flagellum 4
3'. Cells not attaching by tip of recurrent flagellum but may attach using some of the distal length of the flagellum 6

4. Cell within lorica ..... ***Bicosoeca***
4'. Cells aloricate 5

5. Recurrent flagellum long; cell with apical collar; cell attaching indirectly by a strand of mucus ..... ***Pseudobodo***
5'. Recurrent flagellum short, no mucus strand, no collar..... ***Cafeteria***

6. Cell flattened and gliding, flagella normally absent..... ***Commation***
6'. Cell with active flagella 7

7. Attached cells attach by distal section of recurrent flagellum..... ***Pendulomonas***
7'. Both flagella active in attached cells, cells attached by cytoplasmic strands ..... ***Developayella***

ORDER BICOSOECIDA

Cells bearing two flagella that insert anterio-laterally; one flagellum attaching to the substrate or lorica either directly or indirectly (via a thread of mucus). Anterior flagellum creates currents of water from which particles are ingested at a discrete ingestion area. Freshwater and marine. Three genera in two families: Bicosoecidae for the loricate taxa and the Cafeteriidae for the aloricate taxa.

Genus ***Bicosoeca*** James-Clark, 1867

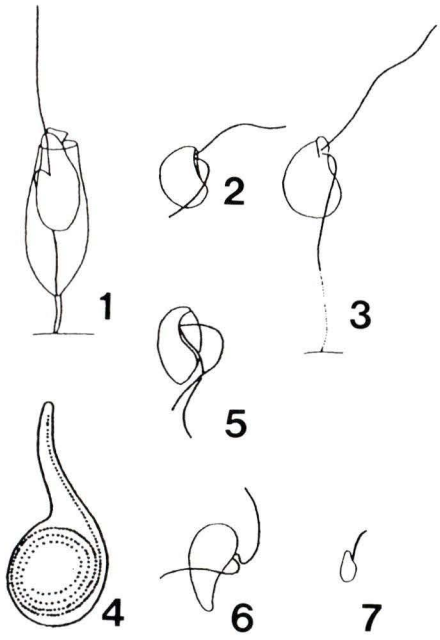
Biflagellated cells enclosed within an organic lorica, usually vase-shaped. Solitary or colonial; if colonial, may be arborescent or ball-shaped (Fig. 1). Lorica may attach directly to substrate or have stalk. Anterior margin of cell raised on one side to form a collar. This forms part of the ingestion area. Cells may retract into their lorica by action of the recurrent flagellum and anterior flagellum coils up. Sometimes incorrectly spelled *Bicoeca*. About 40 species, freshwater and marine. Reference: Preisig et al., 1990.

TYPE SPECIES: *Bicosoeca lacustris* James-Clark, 1867.

Genus ***Cafeteria*** Fenchel & Patterson, 1988

Genus of marine flagellates, attached by the tip of the shorter recurrent flagellum (Fig.

2.) Food ingested in ventral depression or posteriorly. Very common in marine habitats. Several species. *Acronema* (Teal et al., 1998) cannot be clearly distinguished from this genus. Cosmopolitan type species. References: Preisig et al., 1990; Teal et al., 1998.
TYPE SPECIES: *Cafeteria roenbergensis* Fenchel & Patterson, 1988



Figs. 1-7. 1. *Bicosoeca lacustris*. (after Mignot, 1974) 2. *Cafeteria roenbergensis*, original. 3. *Pseudobodo tremulans*, original. 4. *Commation esposianum.* (after Thomsen & Larsen, 1993) 5. *Developayella elegans.* (after Tong, 1995) 6. *Pendulomonas adriperi.* (after Tong, 1997) 7. *Siluania monomastiga* (original). Scale=10 μm.

Genus ***Pseudobodo*** Griessmann, 1913

Genus of marine flagellates, attaching usually by a thin strand of mucus arising from the tip of the shorter recurrent flagellum. With a raised collar around part of the antero-lateral margin of the cell (Fig. 3). Common in marine habitats. Probably two species, type species: *P. tremulans* Griessmann, 1913 is cosmopolitan. Reference: Preisig et al., 1990.

Other genera

Genus ***Commation*** Thomsen & Larsen, 1993

Gliding circular or ovoid cell, usually flattened, with proboscis, the single (hairy) flagellum occasionally emerging at the base of the proboscis (Fig. 4). Move by gliding involving the secretion of mucus. Phagotrophic and marine, described from Antarctic waters. Two species, type species *C. esposianum* Thomsen & Larsen, 1993. Reference: Thomsen and Larsen, 1993.

Genus ***Developayella*** Tong, 1995

Free swimming naked stramenopiles with 2 flagella which insert into a considerable depression on the right anterior ventral face of the cell (Fig. 5.). One flagellum is held in an arc in front of the swimming cells and bears hairs; the other is smooth and attached along the base of the depression. Stationary cells attach by means of cytoplasmic strands and when stationary, both flagella are directed posteriorly, the anterior flagellum sweeps up and down slowly, the posterior flagellum beats rapidly. Marine (estuarine). Monotypic, type species: *D. elegans* Tong, 1995. Reference: Tong, 1995.

Genus ***Pendulomonas*** Tong, 1997

Comma-shaped cells with 2 equal flagella. May swim or may attach to the substrate using the distal third of the recurrent flagellum (Fig. 6). Anterior flagellum used to generate feeding current, but posterior part of the cell may be extended to form a feeding cup. Marine, described from south of England. One and type species, *P. adriperis* Tong, 1997. Reference: Tong, 1997

Genus ***Siluania***
Karpov, Kersanach & Williams, 1998

Freshwater stramenopile with one short anterior flagellum with tripartite hairs. Small. With small apical cytostome (Fig. 7). One and type species, *S. monomastiga* Karpov, Kersanach & Williams, 1998. Reference: Karpov et al., 1998.

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ORDER SLOPALINIDA

Patterson, 1989

BY

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Slopalines embrace seven genera of endocommensal flagellates occurring mostly in the posterior regions of the intestines of cold-blooded vertebrates. Most opalines have been described from Anura. The order comprises two families, the Opalinidae and the Proteromonadidae. The Opalinidae consist of five genera and about 400 species which have been described in amphibia, reptiles, freshwater and marine fish, and in a few invertebrates. The group has been most recently reviewed by Delvinquier and Patterson (1993).

The Proteromonadidae consist of two genera. There is only a few species of *Karotomorpha* (from amphibia). There are several species of *Proteromonas* occurring mainly in reptiles and more rarely in amphibia and mammals. The opalines have been more extensively studied than proteromonads (Kulda and Nohyková, 1978; Metcalf, 1923, 1940; Wessenberg, 1978; Delvinquier and Patterson, 1993). The relationships among genera of slopalines is illustrated in Fig. 1.

The surface of opalines is covered with rows (kineties) of flagella. As a result, they were first considered to be ciliates, and Metcalf (1923, 1940) referred to them as Protociliates; however, they lack a number of the pecularities of the ciliates such as dimorphic nuclei and were transferred from the ciliates to the Sarcomastigophora by Corliss and Balamuth (1963). With the recognition of the polyphyly of the Sarcomastigophora, they have been segregated as an independant group. Opalines and proteromonads are placed together because they have a similar and distinctive structure of the flagellum and because in both families the cell surface is underlain by a cortex of evenly spaced microtubules. In the opalines and *Karotomorpha*, these take the form of ribbons. In *Proteromonas*,