ORDER RAPHIDOMONADIDA
HEYWOOD & LEEDALE, 1983
by
PETER HEYWOOD and GORDON F. LEEDALE

Raphidomonads are biflagellated motile or palmelloid unicells lacking cell walls. Cells are ovoid to almost spherical, occasionally pyriform, occasionally lanceolate. They are often flattened dorsoventrally with a furrow on the ventral surface. Chloroplasts are few (5) to many in number and contain chlorophylls *a* and *c*. An extensive Golgi apparatus often forms a ring over the anterior surface of the nucleus. Some species contain **extrusomes** (trichocysts or mucocysts). Interphase nuclei and mitotic chromosomes are comparatively large. Meiosis and fertilization have not been described. Cysts are known for some genera. No fossils have been reported.

Freshwater genera (*Gonyostomum, Merotricha*, and *Vacuolaria*) and marine genera (*Chattonella*, *Fibrocapsa*, *Heterosigma,* and *Olisthodiscus*) are recognized. Raphidomonads may be locally abundant, giving rise to blooms. The order Raphidomonadida was often termed the Chloromonadophyceae (or some variant of this name) in algal literature; in classifications of the Protozoa the group was usually the Chloromonadida. These names were inappropriate, since the genus *Chloromonas* is not included within the class or order. We proposed (Heywood and Leedale, 1985) that the order be named Raphidomonadida based upon the validation of the algal class name Raphidophyceae by Silva (1980). The group has been reviewed by Fott (1968) and by Heywood (1980, 1990). A useful taxonomic guide to the marine species has been provided by Fukuyo et al. (1990).

KEY CHARACTERS

1. Two flagella of unequal length arise from a shallow pit at or near the cell apex. The anteriorly directed flagellum is approximately as long as the cell and bears stiff, tubular hairs (Heywood, 1980) resembling mastigonemes of other "heterokont" algae (see 19 below). The posteriorly directed flagellum is up to twice the length of the cell and lacks appendages (Fott, 1968). Most raphidomonads contain an extensive flagellar root system, one part of which is a layered structure that appears to be characteristic of the order (Vesk and Moestrup, 1987).

2. During locomotion the flagellum that bears tubular mastigonemes projects anteriorly and beats rapidly. The other flagellum trails posteriorly and moves only occasionally.

3. Chloroplast-containing and color-less forms have been described (Fott, 1968); the latter are omitted here since evidence is lacking to warrant their inclusion in the order; some recent observations argue against such inclusion. Pigmented genera have many discoid or plano-convex chloroplasts up to 3 x 5 µm in size in the peripheral layer (termed "ectoplasm" by some authors). Pyrenoids are absent in *Gonyostomum, Merotricha,* and *Vacuolaria,* but are present in some of the marine species. Chloroplast lamellae consist of three thylakoids between which frequent interconnections occur; a girdle lamella is is present in most species, but absent in some species (Heywood, 1977; Mignot, 1976).

4. Chloroplasts may vary in color from bright green to yellow-green to yellow-brown. Chlorophylls *a* and *c* are present (Guillard and Lorenzen, 1972). In *Gonyostomum semen* and *Vacuolaria virescens* (freshwater species) the dominant carotenoids are diadinoxanthin, dinoxanthin, ß,ß-carotene, and heteroxanthin, while in *Chattonella japonica* and *Fibrocapsa japonica* (marine species) the dominant carotenoids are fucoxanthin, fucoxanthinol, ß,ß-carotene, and violaxanthin (Fiksdahl et al., 1984).

5. The chloroplast-containing raphidomonads are photoautotrophic; possibly some species also utilize heterotrophy.

6. Reserve food material appears to be oil, present as osmiophilic spheres in the cytoplasmic matrix and in the chloroplast stroma. Lipid-containing structures in *Heterosigma akashiwo* show diurnal changes (Wada et al., 1987). The major sterol of *Heterosigma akashiwo* and *Chattonella antiqua* is 24-ethylcholesterol (Nichols et al., 1987).

7. No eyespots are present.

8. No flagellar swellings have been observed.

9. All species are monads. Cells are ovoid to almost spherical, occasionally pyriform, occasionally lanceolate. They are often flattened dorsoventrally with a furrow on the ventral surface. Some species (e.g. *Vacuolaria virescens*, q.v.) may be variable in shape (Fott, 1968; Spencer, 1971). The variable size and morphology of *Chattonella,* which made species recognition problematic, has led to the use of monoclonal antibodies for identification (Hiroishi et al., 1988).

10. A cell wall is absent, but some species secrete mucus and form palmellae (Heywood, 1980).

11. A contractile vacuole occurs in freshwater genera (*Gonyostomum, Merotricha*, and *Vacuolaria*), but is absent in the marine genera. The contractile vacuole may reach 10 µm diameter; it lies between the nucleus and the region of flagellar insertion. In *Vacuolaria virescens* a large Golgi body occurs between the anterior surface of the nucleus and the contractile vacuole; it is thought to be involved in osmoregulation (Heywood, 1978b).

12. The nucleus is large (to 20 µm long) and contains one or more nucleoli; interphase chromatin occurs as distinct fine threads (Heywood, 1980; Hovasse, 1945). Chromosome numbers are large: 97 ± 2 in *Vacuolaria virescens* and 65-75 in *Gonyostomum semen* (Heywood, 1980); chromosome length at metaphase varies from 1 to 12 µm. In *Vacuolaria virescens* kinetochores are present, attached to spindle microtubules; the latter form around the flagellar basal bodies and enter the nucleus at prophase through polar gaps in the nuclear envelope (Heywood, 1978a). Condensation of chromosomes, dispersion of nuclei, and formation of a metaphase plate of chromosomes resemble similar events in the "classical mitosis" of other organisms. Peculiar features of mitosis in *Vacuolaria virescens* are that Golgi bodies and contractile vacuoles occur near the poles of the mitotic nucleus and the original nuclear envelope remains intact until telophase, by which time a new nuclear envelope has begun to form around the daughter nuclei (Heywood, 1978a).

13. Asexual reproduction is by binary fission. Possible sexual reproduction has been reported for *Chattonella marina* (Subrahmanyan, 1954). Microfluoro-metric studies of *Chattonella antiqua* and *Chattonella marina* suggest a diplontic life cycle in which meiosis precedes encystment (Yamaguchi and Imai, 1994).

14. Some species form cysts, probably in response to nutrient depletion (Nakamura and Umemori, 1991). In *Chlorella antiqua,* silicon predominates in the cyst wall with magnesium and aluminum also being present (Meksumpun et al., 1994).

15. Extrusomes (trichocysts or mucocysts) occur in most (but not all) species. The rod-shaped trichocysts of *Gonyostomum* can discharge mucilaginous threads for distances in excess of 100 µm. The spherical mucocysts of *Vacuolaria* secrete mucilage around the cell.

16. Freshwater species frequently occur in the plankton, among aquatic plants or immediately above the benthic muds of bogs, ponds, and lakes, the pH of which ranges from 4.0 to 7.0. *Chattonella*, *Fibrocapsa, Heterosigma,* and *Olisthodiscus* occur in marine environments.

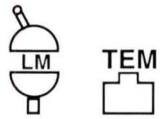
17. Diel vertical migrations between lower layers at night where inorganic nutrients are more abundant and euphotic zones during the day, have been observed in both freshwater (Cronberg et al., 1988) and marine (Watanabe et al., 1988) species. In *Heterosigma akashiwo*, phosphate taken up at night in deeper water was accumulated as polyphosphate and subsequently used for photophosphorylation in the photic layer (Watanabe, 1988).

8. Raphidomonads may occur in large numbers causing mortality to marine organisms (Subrahmanyan, 1954) or health

problems to bathers (Cronberg et al., 1988). Red tides of raphidomonads may be controlled by viruses (Nagasaki et al., 1994) or by heterotroph predation (Nakamura et al., 1992).

19. Ultrastructural and biochemical evidence suggests that the closest relative of the raphidomonads are members of the algal division Heterokontophyta *sensu* Leedale (see van den Hoek, 1978) which also have heterokont flagella, tubular mastigonemes, chlorophylls *a* and *c*, three-thylakoid lamellae in the chloroplasts, and other common features. In this book those organisms are represented by the Chrysomonadida (q.v.) (and Heterochlorida), but they also include several major algal groups such as the diatoms and brown seaweeds.

ARTIFICIAL KEY TO SELECTED GENERA



1. Freshwater forms, contractile vacuole present..... 2
1′. Brackish or marine forms, contractile vacuole absent..... 4

2. Cells with rod-shaped trichocysts..... 3
2′. Cells with spherical mucocysts but lacking rod-shaped trichocyst ..... ***Vacuolaria***

3. Trichocysts mainly in swollen anterior region of cells; flagella arise on lateral surface immediately below this region..... ***Merotricha***
3′. Trichocysts around cell periphery (but may be locally dense at cell anterioand/or posterior); flagella arise near cell apex ..... ***Gonyostomum***

4. Flagella arise at or near cell apex 5
4′. Flagella arise sub-apically to laterally on ventral surface..... 6

5. Prominent rod-shaped trichocysts predominantly present at cell posterior ..... ***Fibrocapsa***
5′. Mucocysts if present and conspicuous are not predominantly grouped at the cell posterior ..... ***Chattonella***

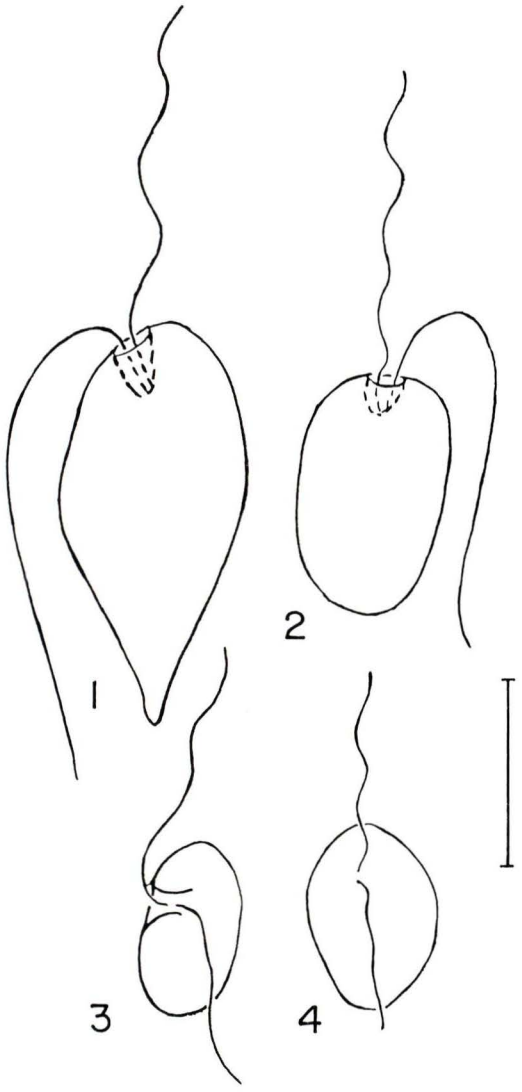
6. Chloroplasts are yellowish-brown to brown; during swimming, cell rotates helically ..... ***Heterosigma***
6′. Chloroplasts are yellowish-green to green; during swimming, cell moves without rotation ..... ***Olisthodiscus***

Genus ***Chattonella*** Biecheler, 1936

Cell shape is variable both within and between species; cells are frequently obovate, but vary from globose to lanceolate, with the latter often possessing a distinct caudus; 2 flagella, about the same length as the cell; many chloroplasts, often present as a single layer below the plasmalemma, give the cell a yellow-brown color; pyrenoids present in some species; some species form cysts; mucocysts present in some species; contractile vacuole absent; saline, periodically abundant, causes red tides; synonymous with *Hornellia* (Subrahmanyan, 1954). See Biecheler (1936); Fukuyo et al. (1990); Mignot (1976).
TYPE SPECIES: *Chattonella subsalsa* Biecheler, 1936 (Fig. 6). Cell 30-50 x 15-25 µm; brackish and marine habitats, often rich in organic matter (Mignot, 1976); may reach high densities; 6 other species have been recognized by Fukuyo et al, (1990): *C. antiqua, C. globosa, C. marina* (synonymous with *Hornellia marina* Subrahmanyan), *C. minima, C. ovata,* and *C. verruculosa.*

Genus ***Fibrocapsa*** Toriumi & Takano, 1973

Cells ovate to obovate, slightly flattened; flagella arise from an anterior depression; anterior flagellum is approximately the same length as the cell, but the trailing flagellum is slightly longer; trichocysts predominantly grouped at posterior end; chloroplasts



Figs. 1-4. Diagram of marine raphidomonads to allow comparison of cell size, shape, and insertion of flagella; all at same magnification; scale bar=10 µm. Fig. 1. *Chattonella subsalsa* drawn from lateral surface to illustrate insertion of the flagella and structure of the caudus. Figs. 2-4 are drawn in ventral view to illustrate cell shape and insertion of flagella; Fig. 2. *Fibrocapsa japonica*. Fig. 3. *Heterosigma akashiwo*. Fig. 4. *Olisthodiscus luteus*. Figs. 1 and 3 are based on the illustrations in Table 3 of Hara and Chihara (1987); Fig. 2 is based on Fig. 1 of Hara and Chihara (1985); Fig. 4 is based on Fig. 1 of Hara et al. (1985).

forming a single layer below the plasmalemma are yellowish-green or brown. See Hara and Chihara (1985), Toriumi and Takano (1973).
TYPE SPECIES: *Fibrocapsa japonica* Toriumi & Takano, 1973 (Fig. 2). Cell 20-30 x15-17 µm; many rod- shaped trichocysts often grouped at posterior end can eject threads up to 300 µm in length; each chloroplast possesses a pyrenoid ; chloroplasts may be so tightly abutted at the cell periphery that they appear as one large reticulate chloroplast.

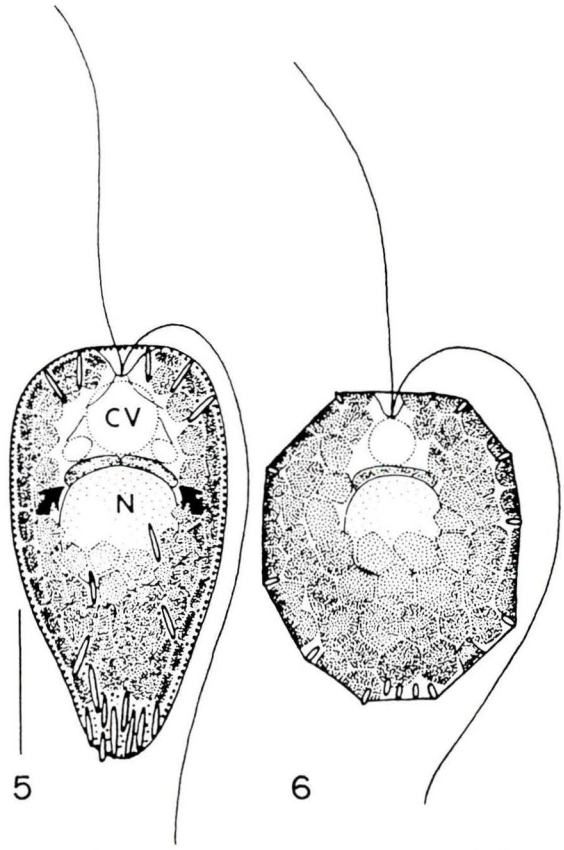


Fig. 5. *Gonyostomum semen*; ventral view, but trailing flagellum (usually over ventral surface) shown at side of cell; chloroplasts stippled; Golgi apparatus and vesicles arrowed between nucleus (N) and contractile vacuole (CV); group of trichocysts shown at posterior end of cell. x1000. Fig. 6. *Gonyostomum latum*, ventral view; organelles as Fig. 5. x1,000. Figs. 5-8 from Fott (1968) by permission of E. Schweizerbart'sche Verlagsbuchhandlung

Genus ***Gonyostomum*** Diesing

Cells obovate-lanceolate, obovate or almost spherical, flattened dorsoventrally with a furrow on the ventral surface, caudus short; rod-shaped trichocysts around cell periphery or concentrated at the 2 ends of the cell; flagella usually the same length as the cell, but the trailing flagellum may reach twice that length; many chloroplasts in a single layer in the cell periphery; frequently among aquatic plants in acidic bogs or pools. See Hovasse (1945).

TYPE SPECIES: *Gonyostomum semen* Diesing, (Fig. 5). Cell 40-90 µm long; many rod-shaped trichocysts often grouped at ends of cell; grown on defined medium at pH 5.5-5.8 (Heywood, 1980); division stages observed during the dark period in laboratory cultures (Heywood, 1980); during unfavorable conditions may be present as cysts (Cronberg et al., 1988); frequently collected, usually from acidic bogs, pools, and lakes; diurnal movement occurs in natural populations (Cronberg et al., 1988), cells being near the surface in early hours of daylight; 3 other species have been recognized (Fott, 1968): *G. intermedium*, *G. latum* (Fig. 2) and *G. ovatum*

Genus***Heterosigma*** Hada, 1968

Cell shape variable, from approximately spherical to ovoid, somewhat compressed dorsoventrally; flagella arise from separate pits in a furrow running from near the apex along the ventral side; both flagella approximately the same length as the cell; the beat of the anterior flagellum causes cell to rotate helically while swimming; discoid chloroplasts, 10-30 per cell, in peripheral layer, yellowish-brown to brown in color; mucocysts present. See Fukuyo et al. (1990); Hara and Chihara (1987); Vesk and Moestrup (1987).

TYPE SPECIES: *Heterosigma akashiwo* (Hada) Hada, 1968 (Fig. 3). Cell 10-22 x 8-15 µm; only species of the genus; was maintained in some culture collections as *Olisthodiscus luteus*; other synonyms: *Heterosigma inlandica, Chattonella inlandica, Chattonella luteus.*

Genus***Merotricha*** Mereschkowsky, 1879

Cells appear elliptical in front view; anterior end of cell enlarged into a distinctive convex structure containing a group of trichocysts; flagella inserted laterally below this region; bright green discoid chloroplasts occur in cell periphery except for the cell anterior where the trichocysts occur.

TYPE SPECIES: *Merotricha bacillata* Mereschowsky, 1879 (Fig. 7). Cell 40-50 x 18-25 µm; only species of the genus; trailing flagellum overlooked in original description but subsequently described by Skuja (1934) as *M. capitata,* which is almost certainly synonymous with *M. bacillata* (Fott, 1968); no accounts of laboratory culture, biochemistry, or ultrastructure; from acidic bogs and ponds (Skuja, 1934; Graffius, 1966).

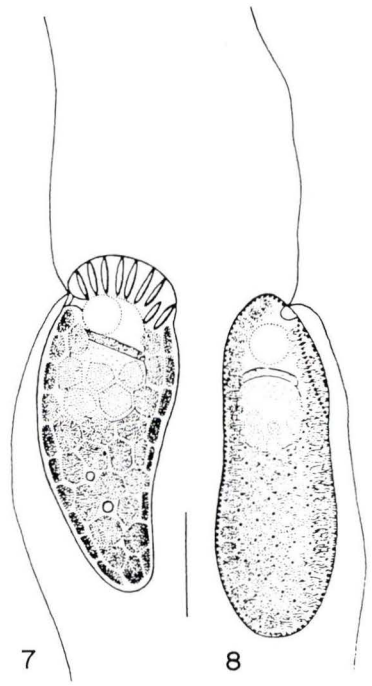


Fig. 7. *Merotricha bacillata*, side view; organelles as Fig. 1; distinctive anterior region contains battery of trichocysts. x1000. Fig. 8. *Vacuolaria virescens*, side view; organelles as Fig. 1; peripheral cytoplasm contains small, spherical mucocysts between the chloroplasts. x1000.

Genus ***Olisthodiscus*** Carter, 1937

Cells discoid in ventral view; pronouncedly flattened dorsoventrally with dorsal surface concave and ventral surface convex, giving a structure resembling a saddle or a turtle's carapace; flagella arise from a shallow groove on the ventral surface; anterior flagellum somewhat longer than the cell, trailing flagellum is shorter, being of the same length as the cell or less; the beat of the anterior flagellum causes cell to move forward smoothly, without rotation; discoid chloroplasts, 5-13 in number with 6 being common, in peripheral layer, yellowish-green in color; mucocysts absent. See Fukuyo et al. (1990); Hara et al. (1985).

TYPE SPECIES: *Olisthodiscus luteus* Carter, 1937 (Fig. 4). Cell 15-25 long x 10-16 wide by 5-7 µm thick; only species of the genus; has been confused with *Heterosigma akashiwo*, which has similar size, shape, and environment, but the chloroplasts of *Olisthodiscus* are greener, and it swims without rotating.

Genus ***Vacuolaria*** Cienkowsky, 1870

Cell shape variable both between and within species, from almost spherical to oblong-cylindrical; cell dimensions also variable; flagella approximately the same length as the cell; many chloroplasts, not restricted to a single layer; spherical mucocysts occur at cell periphery. See Spencer (1971), Heywood (1977, 1978a,b).

TYPE SPECIES: *Vacuolaria virescens* Cienkowsky, 1870 (Figs. 4,5). Cell 30-85 x 18-25 µm; var. *minuta* only 19-23 x 17-19 µm (Fott, 1970); cell shapes vary in single natural collection (Spencer, 1971) or in single laboratory culture; spherical mucocysts occur near cell periphery and are involved in formation of palmelloid stages; species maintained in culture (Guillard and Lorenzen, 1972; Heywood, 1990) and several ultrastructural investigations made (Schnepf and Koch, 1966; Mignot, 1967; Heywood, 1977, 1978a,b); some aspects of chloroplast biochemistry also studied (Guillard and Lorenzen, 1972); occurs in ponds, bogs, and lakes usually rich in vegetation (Poisson and Hollande, 1943; Graffius, 1966; Spencer, 1971) and usually of pH 4.0-6.5, but also reported from slightly alkaline environments (Graffius, 1966); related species, *V. viridis* , pear-shaped with broad cell anterior (Fott, 1968, 1970) though Spencer (1971) thinks this is synonymous with *V. virescens* ; Fott (1968, 1970) described. *V. penardii* , a species in which chloroplasts are absent from the cytoplasm immediately below the cell membrane.

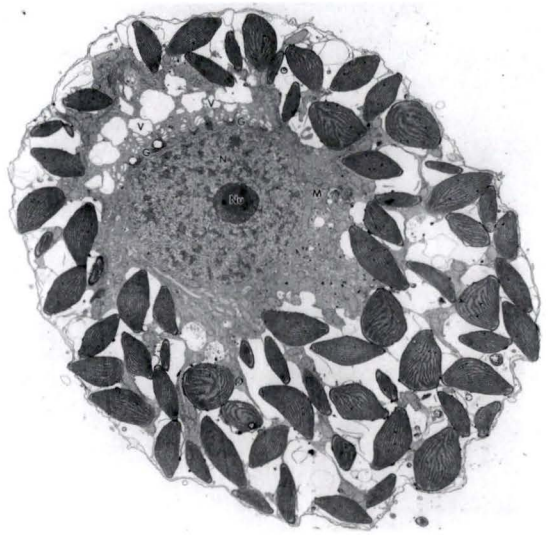


Fig. 9. *Vacuolaria virescens*; EM longitudinal section showing many chloroplasts in cell periphery, not in a single layer; nucleus (N) with nucleolus (Nu) lies in anterior half of cell surrounded by characteristic zone of cytoplasm including mitochondria (M) and Golgi bodies (G); Golgi vesicles (V) empty into the contractile vacuole. x3000. (from Heywood [1977] by permission of *J. Phycol.*)

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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