The New Higher Level Classification of Eukaryotes with Emphasis on the Taxonomy of Protists


Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada, and Center for Ultrastructural Research, Department of Cellular Biology, University of Georgia, Athens, Georgia 30602, USA, and Bigelow Laboratory for Ocean Sciences, West Boothbay Harbor, ME 04575, USA, and Department of Pathobiology, Ontario Veterinary College, University of Guelph, Guelph, ON N1G 2W1, Canada, and Wadsworth Center, New York State Department of Health, Albany, New York 12201, USA, and Biologie des Protistes, Université Blaise Pascal de Clermont-Ferrand, F63 172 Aubière cedex, France, and Natural Resources Canada, Geological Survey of Canada (Atlantic), Bedford Institute of Oceanography, PO Box 1006 Dartmouth, NS B2Y 4A2, Canada, and Department of Biology, University of Louisiana at Lafayette, Lafayette, Louisiana 70504, USA, and Department of Biology, Duke University, Durham, North Carolina 27708-0338, USA, and Biological Faculty, Herzen State Pedagogical University of Russia, St. Petersburg 191186, Russia, and Department of Biology, Colorado State University, Fort Collins, Colorado 80523, USA, and Centre for Biodiversity and Conservation Biology, Mycology Section, Royal Ontario Museum, Toronto, ON M5S 2C6 and Department of Botany, University of Toronto, Toronto, ON M5S 3B2, Canada, and Department of Biochemistry, Dalhousie University, Halifax, NS B3H 4J1, Canada, and Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269, USA, and Center for Forest Mycology Research, USDA Forest Service, Forest Products Laboratory, Lurillo, Puerto Rico, and Department of Integrative Biology, University of Guelph, Guelph, ON N1G 2W1, Canada, and Royal Botanic Garden, Edinburgh, EH3 5LR, United Kingdom, and The Academy of Natural Sciences, Philadelphia, Pennsylvania 19103, USA, and Medical Technology Program, Department of Microbiology and Molecular Genetics, Michigan State University, East Lansing, Michigan 48824-1030, USA, and Department of Phylogeny, Københavns Universitet, Copenhagen DK-1353, Denmark, and Department of Plant Biology, University of Georgia, Athens, Georgia 30606, USA, and George Mason University, PWI campus, Manassas, Virginia 20110, USA, and Department of Plant Biology, University of Illinois, Urbana, Illinois 61801, USA, and Department of Invertebrate Zoology, St. Petersburg State University, 199034 St. Petersburg, Russia, and Department of Biological Sciences, University of Arkansas, Fayetteville, Arkansas 72701, USA, and Department of Oceanography, University of British Columbia, Vancouver, BC V6T 1Z4, Canada

ABSTRACT. This revision of the classification of unicellular eukaryotes updates that of Levine et al. (1980) for the protozoa and expands it to include other protists. Whereas the previous revision was primarily to incorporate the results of ultrastructural studies, this revision incorporates results from both ultrastructural research since 1980 and molecular phylogenetic studies. We propose a scheme that is based on nameless ranked systematics. The vocabulary of the taxonomy is updated, particularly to clarify the naming of groups that have been repositioned. We recognize seven clusters of eukaryotes that represent the basic groupings or traditional “kingdoms.” The multicular lineages emerged from within monophyletic protist lineages: animals and fungi from Opisthokonta, plants from Archaeplastida, and brown algae from Stramenopiles.

Key Words. algae, amoebae, ciliates, flagellates, fungi, microbiology, microorganisms, parasites, plankton, protozoa, systematics, taxonomy.

SINCE the previous classification proposed by the Society of Protozoologists (Levine et al. 1980), there have been many changes to our understanding of relatedness among phylogenetic lineages of eukaryotes. Many traditional groups are no longer valid and have been abandoned (see Hausmann, Hülsmann, and Radek 2003 for a recent historical review of classification schemes proposed since then). In particular, the classical scheme of Bützchi (1889), which divided Protozoa into Sarcodina (amoeboid organisms), Sporozoa (a parasitic group), Mastigophora (flagellated species), and Infusoria (ciliates), was abandoned decades ago by protists. It is, unfortunately, still used by non-protistologists. Despite some initial controversies, data from modern morphological approaches, biochemical pathways, and molecular phylogenetics are generally complementary. This has resulted in a classification scheme that we believe will have some stability in the near term.
The proposed classification scheme recognizes taxa that are considered to be evolutionarily related and the remaining paraphyletic taxa are identified. The highest ranking groups recognized have been summarized recently by Simpson and Roger (2002, 2004). Molecular phylogenies group eukaryotes into seven clusters: (1) the Opisthokonta, grouping the animals, fungi, choanoflagellates, and Mesomycetozoa; (2) the Amoebozoa, grouping most traditional amoebae, slime moulds, many testate amoebae, some amoeba-flagellates, and several species without mitochondria; (3) the “Excavata,” grouping oxyymonads, parasalids, diplomonads, jakobids, and several other genera of heterotrophic flagellates, and possibly including the Euglenozoa and Heterolobosea; (4) the Rhizaria, grouping the Foraminifera, most of the traditional “Radiolaria,” and the Cercozoa with filose pseudopodia, such as many amoeba-flagellates and some testate amoebae; (5) the Archaeplastida, grouping the Glaucophyta, red algae, green algae, and Plantae; (6) the Alveolata, grouping the ciliates, the dinoflagellates, and the Apicomplexa; and (7) the Stramenopiles, grouping the brown algae, the diatoms, many zoospores, and the ophalids, among others. The Cryptophyceae–Haptophyta–Stramenopiles–Alveolata may also form a distinct cluster known as the Chromalveolata. The chromalveolates are particularly interesting because they are derived from the symbiosis of a phagotrophic heterotrophic eukaryote with a photosynthetic red algal eukaryote. The plastid was secondarily lost in several lineages of stramenopiles and alveolates (Delwiche et al. 2004).

Several terms, highlighted below in bold, were identified as being problematic or requiring clarification. Others are no longer recognized as formal taxa, but remain useful terms. We recommend that they be spelled without capitalization. They include algae (phototrophic protists), zoospores (an eclectic mix of heterotrophic and saprotrophic groups), and protosporae (predominantly non-filamentous heterotrophic species). One must recognize that many species in these groups are mixotrophic and cannot exclusively be considered as autotrophic or heterotrophic. This also weakens the usefulness of terms such as phytoplankton and zooplankton. There are numerous examples that blur the boundary between autotrophs and heterotrophs: some heterotrophs retain their prey’s plastids; other heterotrophs form symbioses with photosynthetic species; and many photosynthetic species are also phagotrophic and osmotrophic. There are also cases of secondary photosynthetic species; and many photosynthetic species are also phagotrophic and osmotrophic. There are also cases of secondary photosynthetic species; and many photosynthetic species are also phagotrophic and osmotrophic. There are also cases of secondary photosynthetic species; and many photosynthetic species are also phagotrophic and osmotrophic. There are also cases of secondary photosynthetic species; and many photosynthetic species are also phagotrophic and osmotrophic.

In cases where several terms were in popular use to describe the group, unless its composition was substantially modified. In these cases, we have used a newer term and its appropriate authorship. The rules followed to establish this new taxonomy were few and simple. We have used the older name that describes each group, unless its composition was substantially modified. In these cases, we have used a newer term and its appropriate authorship. In cases where several terms were in popular use to describe the same taxon, we often used the older term, emended if necessary; the other terms, whether synonymous or not, are placed in brackets. In cases where ranks were created to include a single lower rank, the higher ranks were eliminated as superfluous. Therefore, in several instances, we have placed in brackets ranks of the
Table 1. Highest ranks of the eukaryotes with the next two ranks as presented in Table 2.

<table>
<thead>
<tr>
<th>Monophyletic clusters</th>
<th>First rank</th>
<th>Second rank, examples</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Amoebozoa</strong></td>
<td>Acanthamoebidae</td>
<td>Dicyostelium, Myxogastria, Protostelia</td>
</tr>
<tr>
<td></td>
<td>Entamoebida</td>
<td><em>Cochliopodium</em>, <em>Dactylopodia</em>, <em>Thecamoebida</em>, <em>Vanellida</em></td>
</tr>
<tr>
<td></td>
<td>Eumycetoza</td>
<td><em>Leptomyxida</em>, <em>Testacea</em></td>
</tr>
<tr>
<td></td>
<td>Mastigamoebae</td>
<td><em>Tubulinida</em></td>
</tr>
<tr>
<td></td>
<td>Stereomyxida</td>
<td><em>Tubulinida</em></td>
</tr>
<tr>
<td></td>
<td>Tubulinea</td>
<td><em>Tubulinida</em></td>
</tr>
<tr>
<td><strong>Opisthokonta</strong></td>
<td>Fungi</td>
<td><em>Ascomycota</em>, <em>Basidiomycota</em>, <em>Chytridiomycetes</em>, <em>Glomeromycota</em>, <em>Microsporidia</em>, <em>Urediniozymycetes</em>, <em>Ustilaginozymycetes</em>, <em>Zygomycota</em></td>
</tr>
<tr>
<td></td>
<td>Mesomycetoza</td>
<td><em>Apheleida</em>, <em>Capsaspora</em>, <em>Corallomyctium</em>, <em>Ichthyospora</em>, <em>Ministeria</em>, <em>Nuclearidae</em></td>
</tr>
<tr>
<td></td>
<td>Choanomonada</td>
<td><em>Acanthoecidae</em>, <em>Monosigidae</em>, <em>Salpingoecidae</em></td>
</tr>
<tr>
<td></td>
<td>Metazoa*</td>
<td><em>Porifera</em>, <em>Phacozoa</em>, <em>Mesozoa</em>, <em>Animalia</em></td>
</tr>
<tr>
<td></td>
<td>Haplosporidia</td>
<td>Subdivisions uncertain</td>
</tr>
<tr>
<td></td>
<td>Foraminifera</td>
<td><em>Acantharia</em>, <em>Polycystinea</em>, <em>Taxopodida</em></td>
</tr>
<tr>
<td></td>
<td>Radiolaria</td>
<td><em>Acantharia</em>, <em>Polycystinea</em>, <em>Taxopodida</em></td>
</tr>
<tr>
<td><strong>Archaeplastida</strong></td>
<td>Glaucothyta</td>
<td>Subdivisions uncertain</td>
</tr>
<tr>
<td></td>
<td>Rhodophyceae*</td>
<td><em>Charophyta</em>, <em>Chloroendrakes</em>, <em>Chlorophyta</em>, <em>Mesostigma</em>, <em>Prasinophytae</em></td>
</tr>
<tr>
<td></td>
<td>Chloroplastida</td>
<td><em>Mesostigma</em>, <em>Prasinophytae</em></td>
</tr>
<tr>
<td><strong>Chromalveolata</strong></td>
<td>Alveolata</td>
<td><em>Apicomplexa</em>, <em>Ciliophora</em>, <em>Dinofzoo</em></td>
</tr>
<tr>
<td></td>
<td>Cryptophyceae</td>
<td><em>Cryptomonadales</em>, <em>Goniomonadales</em></td>
</tr>
<tr>
<td></td>
<td>Haptophyta</td>
<td><em>Pavlovophyceae</em>, <em>Pynmesiophyceae</em></td>
</tr>
<tr>
<td></td>
<td>Stramenopiles</td>
<td><em>Actinophryidae</em>, <em>Bacillariophyta</em>, <em>Botildomonas</em>, <em>Bicosoeida</em>, <em>Chrysophyceae</em>, <em>Dictychophyceae</em>, <em>Eustigmatales</em>, <em>Hypochytriales</em>, <em>Labyrinthulomycetes</em>, <em>Opalinata</em>, <em>Pelagophyceae</em>, <em>Peronosporomycetes</em>, <em>Phaeothamniophyceae</em>, <em>Phaeophyceae</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Pinguiochrysidales</em>, <em>Raphidiophyceae</em>, <em>Schizocladia</em>, <em>Syrnulares</em>, <em>Xanthophyceae</em></td>
</tr>
<tr>
<td><strong>‘Excavata’</strong></td>
<td>Fornicata</td>
<td><em>Carpediemonas</em>, <em>Eophyra</em></td>
</tr>
<tr>
<td></td>
<td>Malawimonas</td>
<td><em>Cristamonadida</em>, <em>Spirotrichonymphida</em>, <em>Trichomonadida</em>, <em>Trichonymphida</em></td>
</tr>
<tr>
<td></td>
<td>Parabasalia</td>
<td><em>Oxymonadida</em>, <em>Trinastix</em></td>
</tr>
<tr>
<td></td>
<td>Preaxostyla</td>
<td><em>Jakobi</em>, <em>Histionidae</em></td>
</tr>
<tr>
<td></td>
<td>Jakobida</td>
<td><em>Jakobi</em>, <em>Histionidae</em></td>
</tr>
<tr>
<td></td>
<td>Euglenozoa</td>
<td><em>Euglenida</em>, <em>Diplonemida</em>, <em>Kinotoplasta</em></td>
</tr>
<tr>
<td></td>
<td>Heterolobosea</td>
<td><em>Acrasidae</em>, <em>Gubereellidae</em>, <em>Vahlkampfiidae</em></td>
</tr>
</tbody>
</table>

*Clades with multicellular groups.

traditional codes of nomenclature, where they were no longer necessary. In this scheme, monotypic taxa are represented by the genus only and each receives the highest rank within its group. The presence of taxonomic endings that conveyed hierarchical information in the traditional codes are, in this classification, considered an accident of history and the endings are not intended to carry any hierarchical meaning. The formal names provided in this classification, with the genera they cluster, were based on accepted monophyly according to the information available. In some instances, the term used required significant modification, and these were emphasised by “emend.” Where a new term was introduced in this classification, it was identified with “Adl et al. 2005” as the authority, or by the submitting author (e.g. Mann in Adl et al., 2005). They are to be cited as emended in this publication. The descriptions provided are not intended to substitute for formal diagnoses. They are provided primarily to identify common morphological features, such as synapomorphies and apomorphies, within monophyletic lineages.

This classification (Table 2) provides formal names within a modern framework, in lieu of the imprecise, informal, sometimes redundant or parallel vocabulary that has accumulated. When referring to a rank in this nameless-rank system, the position of the organism referred to should be followed by two or three higher ranks placed in brackets, highest rank first. For example, to clarify the position of *Paramecium*, it could be written as *Paramecium* [Alveolata: Ciliophora], or to locate the genus more precisely as *Paramecium* [Ciliophora: Oligohymenophora: *Peniculida*].

While this revised classification of protists is proposed by the International Society of Protistologists, it should be noted that it is the work of a committee that worked in collaboration with specialists from many societies (phycologists, mycologists, parasitologists, and other protistologists), and that many experts were consulted on issues as needed. However, it should not be assumed that all contributors agreed on all points. The final synthesis is, nonetheless, a classification that we recommend as the basis for future revisions.

Table 2. Classification of the higher ranks of the protists and multicellular groups. The authority to whom the name is attributed appears immediately after the taxon name. In the square brackets following are commonly used other names for the group and their taxonomic authority. References to the recent literature can be found in Appendix 1 under the major monophyletic clusters. If the taxon description has been emended herein, the authority name is followed by “emend. Adl et al., 2005”. Finally, notation is made of some features of the group as follows: (M)—monotypic group; (P)—paraphyletic group; and (R)—ribogroup, usually based on molecular phylogenetic analyses of rRNA genes. Throughout this table, reference to flagellum refers to the eukaryotic flagellum or cilium. ~

**AMOEBOZOA** Lu¨he, 1913, emend. Cavalier-Smith, 1998

Amoeboid locomotion generally with non-eruptive morphologically variable pseudopodia (lobopodia); sub-pseudopodia common in some groups; cells “naked” or testate; tubular cristae, often branched (ramicristate), secondarily lost in some; usually uninucleate, rarely binucleate, sometimes multinucleate; cysts common, morphologically variable; cell inclusions (parasomes and trichocysts) of diagnostic value in some; flagellate stages if present, rarely bikont, usually with one kinetid bearing a single flagellum.

- Tubulinea Smirnov in Adl et al., 2005 (R)
  - Naked or testate amoeboid organisms; for locomotion and phagocytosis produce broad pseudopodia never pointed at their tips (lobopodia); locomotion based on actino-myosin cytoskeleton; cytoplasmic microtubules, if present, are rare and never arranged in bundles; without trilaminar cytoplasmic centrosomes; without known flagellate stages; glyocalyx variable between genera, often prominent, sometimes with glycostyles, microscales or cuticle.

- Tubulinida Smirnov in Adl et al., 2005 (R)
  - Without theca; sub-cylindrical monopodium or pseudopodia; without flattened locomotive morphology; non-adhesive uroid. Amoeba, Cashia, Chaos, Deuteramoeba, Glaceria, Hartmannella, Hydramoeba, Nolandella, Parachoae, Polychaos, Saccamoeba, Trichamoeba.

  - Locomotive form generally a flattened reticulate or highly branched sheet; Leptomyxa is reticulate and multinucleate; most active locomotive form sometimes sub-cylindrical; sub-pseudopodia rare, never fuscate; with adhesive uroid; uninucleate, sometimes multinucleate; glyocalyx thin and amorphous; cysts common, double walled, without pores. Flabellula, Gephyroamoeba, Leptomyxa, Parafabellula, Rhizamoeba.

- Testacealobosia De Saedeleer, 1934
  - Test outside cell membrane encloses cell, with one (rarely more) distinct opening; although sex has not been conclusively demonstrated, meiosis has been reported in at least one species. Note 1.

- Arcellinida Kent, 1880
  - Test outside cell membrane, with single distinct opening and composed of organic matrix, which may be encrusted with mineral particles (silt) or other mineral debris, such as diatom shells; encystment inside test. Arcella, Centropyxis, Diffugia.

- Incertae sedis Testacea
  - Trichosphaerium Möbius, 1889 [Trichosidae] (M)
  - Multinucleate with synchronous divisions by closed mitosis; two life phases—with calcite spicules in one phase and outer layer fibrillar overlay from within and embedded spicules in the other phase; multiple semi-permanent openings for pseudopodia (described as tactile dactylopods). Trichosphaerium.

- Incertae sedis Tubulinea: Echinamoeba.

- Flabellinema Smirnov in Adl et al., 2005 (P)
  - Flattened locomotive amoebae, without sub-cylindrical pseudopodia; the locomotive form is never altered; cytoplasmic flow poly-axial or without pronounced axis.

- Dactylopodida Nerad and Smirnov in Adl et al., 2005 (R)
  - Flattened locomotive form an irregular triangle with broad hyaline margin; hyaline sub-pseudopodia finger like (i.e. dactylopodia) emerge from the edge of the hyaline cytoplasm; uninucleate with central nucleus; parasomes in Neoparamoebae and Paramoebae; cell coat variable, consists of microscales, hexagonal or pentagonal glycostyles, or fibrous. Korotnevella, Mayorella, Neoparamoeba, Paramoeba, Pseudoparamoeba, Vexillifera. Other possible genera: Boveella, Dactylosphaerium, Oscillogonium, Podostoma, Strioliatua, Subalamoeba, Trienanamoeba.

- Vannellida Bovee, 1979 (R)
  - Flattened, fan shaped to spatulate in locomotion; frontal area of the hyaloplasm occupying up to half of the area of the cell; posterior granuloplasm accumulated in a “hump” often raised off the substratum; single nucleus, with vesicular or peripheral nucleoli; single-walled cysts in some species; cell coat a layer of hexagonal prismatic structures (Platyamoeba), with short glycostyles (Clydonella, Lingulamoebae) or pentagonal glycostyles, with or without simple filaments (Vannella). Clydonella, Lingulamoeba, Platyamoeba, Vannella. Other possible genera: Discamoeba, Pessonella, Unda.

- Thecamoebida Schaeffer, 1926, emend. Smirnov and Goodkov, 1993 (P)
  - Locomotive form oblong with hyaline antero-lateral crescent, usually less than half the body length; without sub-pseudopodia; single nucleus (except Sappinia which has several pairs of closely adjacent nuclei); nucleus vesicular or with several peripheral nucleoli; dorsal surface wrinkled (Thecamoeba) or smooth (other genera); cell coat amorphous, glycostyles or fibrous. Dermamoeba, Paradermamoeba, Parvamoeba, Sappinia, Thecamoeba.

- Cochliopodida Hertwig and Lesser, 1874
  - Cells covered with a tectum comprised of elaborate microscales and with no distinct opening; cysts in some. Cochliopodium.


- Stereomyxida Grell, 1966 (P)
  - Branched plasmodial organisms with lobose pseudopodia; trilaminar centrosome. Corallomyxa, Stereomyxa.
- Acanthamoebidae Sawyer and Griffin, 1975 (R)
  Glycocalyx absent or extremely thin; sub-pseudopodia prominent, flexible, and tapering to a fine or blunt tip (acanthopodia); uninucleate; non-adhesive uroid; cysts of most species double walled, with operculate pores; centriole-like body present. *Acanthamoeba* (syn. *Comandonia*), *Balamuthia*, *Protopancanthamoeba*.

- Entamoebida Cavalier-Smith, 1993
  Flagellum and centrioles absent; mitochondrion, peroxisomes, and hydrogenosomes absent; mitosis closed with endonuclear centrosome and spindle; reduced Golgi dictyosome. *Entamoeba*.

- Mastigamoebidae Goldschmidt, 1907
  Amoeboid with several pseudopodia; sometimes body stiff without amoeboeid motion, depending on conditions; single flagellum directed forward, with stiff vibrating beat; single kinetosome with cone of microtubules extending to nucleus; uninucleate, some species multinucleate; large nuclei persist through division with intranuclear spindle; stages without flagellum occur; without mitochondria; cysts; occurring in microaerophilic to anaerobic habitats rich in dissolved nutrients. *Mastigella*, *Mastigamoeba*. Incertae sedis *Endolimax*, *Mastigina*.

- *Pelomyxa* Greef, 1874 [Pelobiontida Page, 1976] (M)
  Multiple cilia; anaerobic; lacking mitochondria, peroxisomes, and hydrogenosomes; with structural vacuoles; polymorphic life cycle with multinucleate stages; with symbionts. *Pelomyxa*.

- Eumycetoza Zopf, 1884, emend. Olive, 1975 [not Mycetoza de Bary, 1873]
  Producing amoeboid organisms, called slime moulds; amoebae of various types, all with acutely pointed sub-pseudopodia; tubular cristae; life cycle stages with uninucleate amoeboid flagellates; non-flagellate stages; uninucleate obligate amoeboflagellate (1–2 nuclei); obligate amoeba, and multinucleate (up to > 10 nuclei) obligate amoeba; trophic amoeboid state absent from some life cycles, other types of amoebae derived from modifications of amoeboid flagellate or derived from the obligate amoeba that develop following the amoeboidflagellate stage; with two (or one) kinetosomes, with at least two microtubular roots from the dorsal fibrils of the anterior kinetosome; sub-aerial fruiting body either a sporocarp, developing from a single amoeboid cell (myxomyctes and protostelids), or a sorocarp, developing from an aggregate of amoeboid cells (dictyostelids).

- *Protopistelia* Olive, 1975 (P)
  Sporocarps from single amoeba or nucleated fragment of a multinucleate obligate amoeba; sporocarp a hollow acellular stalk (length from < 5 to > 100 µm) that supports 1–8 spores; spores monolocular from cell division after the stalk has been secreted; trophic cells amoeboidflagellates only, amoeboidflagellates and obligate amoeba, or obligate amoebae only; flocc pseudopodia; at least three separate origins of obligate amoebae likely, all morphologically and ultrastructurally distinct. *Protostelium*, *Microglomus*, *Nematostelium*, *Protopistelia*, *Tychosporium*.

- *Myxogastria* Macbride 1899 [not Myxomycetes Link, 1833, emend. Haeckel, 1866]
  Trophic state a free-living, multinucleate, coenocytic, saprobic multinucleate obligate amoeba (plasmodium); under poor conditions plasmodium sometimes becomes a sclerotium; sporocarps (< 1 mm–ca 1 m) from multinucleate obligate amoeba, the plasmodium, or fragment of plasmodium; most with stalked sporangia but also sessile sporangia, plasmodiocytes, aethalial or pseudoaethalian; stalks when present acellular; meiosis in uninucleate spores with sculptured spore walls, with spores produced in masses; spores in some suspended by thread-like acellular capsulillium; haploid gametic amoeboid flagellates (in sexual species) germinate from spores to trophic state that may alternate between flagellated (swarm cell) and non-flagellated (myxamoeba) state, or dormant thin-walled microcysts; kinetid closely associated with nucleus, present until mitosis; anterior kinetosome with orthogonally attached posterior kinetosome; microtubule roots 1, 2, 3, 4, 5, and posterior parakinetosomal structure associated with kinetosome; suspended amoeboidflagellates twisted and oblong with distinct uroid; anteriorly directed flagellum and shorter recurved posterior flagellum in groove underlain by microtubule arrays 4, 5; mitosis centric and open. Plasmodium develops a from zygote in sexual species, directly from amoeboidflagellate in apomorphic species; small and unequipped with 8–100 nuclei (protoplasmidium) or large and veined network with 10–20 nuclei with thick gel-like cortex shuttle in veins (phaneroplasmidium) or thin transparent veins (aphanoplasmidium); mitosis in plasmodium intra-nuclear with non-centric poles; dormancy as sclerotia of many macrocysts or as sporocarps. Traditional groups may not represent monophyletic assemblages. *Arcyria*, *Badhamia*, *Barbrelly*, *Brefeldia*, *Comatrichia*, *Cribraria*, *Duclaea*, *Didera*, *Dydium*, *Echinostelium*, *Fugile*, *Lampromyces*, *Leocarpus*, *Lepidoderma*, *Lycogala*, *Macbrideola*, *Metatrichia*, *Perichaena*, *Physarella*, *Physarum*, *Sclerotium*, *Tychosporium*, *Willkommlangea*.

  Cellular slime moulds, with stalked fruiting bodies from aggregation of amoebae; sorocarps of stalks with terminal sorus of haploid spores; stalks (sorophores), acellular (*Acystostelium*), cellular, and unbranched to sparsely branched (*Dictyostelium*) or cellular with whorls of branches (*Polyphthorylium*); stalk cells forming cell wall and dying; spores usually ellipsoidal, occasionally reniform or spherical; trophic amoebae, non-flagellated, haploid, uninucleate; nucleus with reticulate peripheral nucleolus; microtubular cytoskeleton of amoeba radiating from lamellae discoid organelle near nucleus; amoebae of some species entering dormant stage as thin-walled microcysts; upon starvation, populations of amoebae becoming aggregation-competent, aggregating into a multicellular aggregation centre in response to a chemical attractant called an acrasin; acrasins vary according to taxon; aggregated cells differentiating directly into subaerial sorogens that become sorocarps, or migrating along the substrate as slugs, prior to differentiating into sorogens that culminate as sorocarps; stalks produced by both migrating slugs and sorogens in most species, although a few species have stalkless migration; stalk tubes secreted by inner ends of cells at least the anterior end of the slug/sorogen; in taxa with cellular stalks an anterior population of prestalk cells becomes enclosed in the stalk tube as the slug/sorogen advances, enlarging, secreting walls, vacuolating, and dying as mature stalk cells; remaining posterior prespore cells developing into spores suspended in a slime matrix; sexual zygote amoebae forming and acting as aggregation centres for haploid amoebae, which are ingested by the zygote; entire small aggregate secreting a thick wall and then becoming a dormant macrozyst once all the haploid amoebae are ingested; meiosis occurring when dormancy of macrozyst is broken; haploid amoebae germinating from macrozyst. Classical ranks are not monophyletic. *Acystostelium*, *Dictyostelium*, *Polyphthylium*. Incertae sedis *Coenoria*.
**Incertae sedis Eumycetozoa: Copromyxa, Copromyxella, Fonticula.**

**Incertae sedis AMOEBOZOA: Filamoeba, Gephyramoeba, Gocevia, Hartmannia, Janickia, Malamoeba, Malpigamoeba, Multicilia, Stygamoeba.**

Sessile feeding cells, solitary or colonial, often embedded in mucoid matrix with endogenous globules; cells ovoid with or two similar parallel flagella, emerging apically and surrounded by a cytoplasmic collar or asymmetric protrusion; vesicular tubular cristae; kinetosome microtubular rootlet tending to radial symmetry; forming rounded or branching colonies. **Note 2.**

**Phalanterium Stein, 1878**
Single kinetosome and cilium; cilium surrounded by a collar of cytoplasm, used in feeding; often colonial in a gelatinous matrix. **Phalanterium.**

**Spongomonadidae Karpov, 1990**
Biflagellated with asymmetrical cell projection at anterior. **Rhipidodendron, Spongomonas.**

**OPISTHOKONTA Cavalier-Smith, 1987, emend. Cavalier-Smith and Chao, 1995, emend. Adl et al., 2005**
Single posterior cilium without mastigonesmes, present in at least one life cycle stage, or secondarily lost; with pair of kinetosomes or centrioles, sometimes modified; flat cristae in the unicellular stage.

**Fungi Linnaeus 1753, emend. Cavalier-Smith, 1981, 1987**
Heterotrophic, not phagotrophic; often with walls and multiciliate hyphae; walls, when present, with β-glucan and usually chitin, at least in spore walls; AAA lysine biosynthesis pathway; mitochondrial and peroxisomes present, except in Microsporidia; flat cristae; plastids and tubular mastigonesmes absent.

**Basidiomycota de Barry 1866, emend. Schaffer, 1975**
Mycelium present, but with a yeast state primarily in the Tremellomycetidae; basidia produced in a fertile layer with or without fleshly sporocarp; basidia whole or divided longitudinally, typically with four spores per basidium but ranging from one to eight; fusion of compatible mycelia of opposite mating types results in a dikaryotic mycelium in which nuclei of the parent mycelia remain paired but not fused; karyogamy quickly followed by meiosis, one or more mitotic divisions and migration of the nuclei into the developing basidiospores; asexual reproduction may occur through production of conidiospores or via spores produced on basidia from nuclei that have not undergone karyogamy and meiosis (secondary homothallism); cell wall with xylose; septa with swelling near pore; septal pore caps (parenthesomes—multilayered endoplasmic reticulum) usually present, elaborate in Tremellomycetidae; clamp connections present in hyphae or at base of basidia in some groups. Subdivisions not shown. **Agaricus, Auricularia, Boletes, Cantharellus, Dacrymyces, Fistulina, Gotaeria, Hypodonta, Jaapia, Lycoperdon, Laccaria, Polyporus, Phlebia, Russula, Tremella.**

**Urediniomycetes Swann and Taylor, 1995**
Mycelial or yeast states; many are plant pathogens (rusts), animal pathogens, non-pathogenic endophytes, and rhizosphere species; karyogamy typically in probasidium or teliospore, followed by meiosis in a separate compartment (metabasidia), but in some it occurs in the same compartment (holobasidia); holobasidia remain whole or fragment at septation after meiosis (phragmobasidia); metabasidia typically transversely septate with basidiospore borne laterally; cell wall with xylose; parenthesome pore caps absent but with microbodies at septal pores; septal pores occluded by a plug; centrosome multilayered. Subdivisions not shown. **Agaristostilbum, Ceoama, Melampsora, Rhodotorula, Uromyces.**

**Ustilaginomycetes Bower, Oberw, and Vánky, 1997**
Mycelial in the parasitic phase, and many with saprobic yeast or ballisticonidial states; plant parasites causing rusts and smuts; meiospores produced on septate or aseptate basidia; cell wall carbohydrates dominated by glucose; xylose absent; parenthesomes absent at septal pores; swellings absent at septal pores except in Tilletia; centrosomes globose, unlayered. Subdivisions not shown. **Malassezia, Tilletia, Ustilago.**

**Ascomycota Berkeley, 1857**
Sexual reproduction within asci (saccate structures); meiosis usually followed by mitosis to produce from one to over 1,000 ascospores, but usually eight; ascospore walls form inside ascus; mating types heterothallic, homothallic (selfing) or both; may reproduce sexually (teleomorph) or asexually (anamorph) only, or both sexually and asexually (holomorph); ascis cylindrical, fusiform, clavate or globose, persistent or evanescent, with or without a fruiting structure (ascoma, -ata); asci developing directly from ascogenous hyphae, from a crozier or from a single cell; asexual reproduction by conidiospores (mitosores) formed by fragmentation of vegetative hyphae (thallic), blastically from single cells, hyphae, or conidiofiores; vegetative body of single cells or tubular, septate filaments (hyphae); septa with simple pores, except for those associated with ascogenous hyphae and asci; cell walls lamellate with a thin electron dense outer layer and a relatively thick electron transparent inner layer, consisting of varying proportions of chitin and glucans; saprobes, endophytes, parasites (especially on plants) or lichen forming (hyphae). **Note 3.**

**Neolecta Sppegazzini, 1881** [Neol ectomycetes Eriksson and Winka, 1997]
Mycelium present, multinucleate; ascomata apothecial, stalked, fleshy; interascal tissue absent; cylindrical asci formed from binucleate cells that undergo karyogamy, meiosis and one mitotic division to produce eight cylindrically asci, thin walled, walls bluing in iodine, ascus apex truncate, slightly thickened below ascus wall, with wide apical slit, persistent; ascospores ellipsoidal to globose, hylame, aseptate; anamorph unknown; saprobic; found in wet mixed woodlands. **Neol ecta.**

**Taphrinomyxycotina Eriksson and Winka, 1997**
Mycelium present or absent; asci produced from binucleate cells; do not form croziers or interascal tissue; ascomata lacking, unicellular or dimorphic, dividing by fission or budding.

**Pneumocystis Delanoe and Delanoe, 1912** [Pneumocystidomycetes Eriksson and Winka, 1997]
Mycelium and ascomata absent; vegetative cells thin walled, irregularly shaped, uninucleate, dividing...
by fission; sexual reproduction initiated by fusion of two vegetative cells followed by karyogamy, cyst wall formation, meiosis, and in some, one mitotic division, to produce four to eight nuclei that are delimited by the cyst (ascus) vesicle; ascospore walls are deposited between the delimiting membranes; cyst walls rupture to release ascospores; extracellular parasite of mammalian lungs. *Pneumocystis.*

Schizosaccharomycetes Eriksson and Winka, 1997
Mycelium absent or poorly developed; ascomata absent; vegetative cells cylindrical, proliferating by mitosis followed by cell division to produce two daughter cells (fission); cell wall composition differs from that of species of Saccharomycetes; sexual reproduction initiated by fusion of two vegetative cells to form an ascus; karyogamy and meiosis occur within the ascus to produce four nuclei, which may or may not divide once again mitotically; ascospores aseptate, delimitated by enveloping membrane system (EMS), wall formed within bilayers of EMS, wall bluing in iodine, hyaline or pigmented; saprophytes in sugary plant exudates, fermentation positive. *Schizosaccharomyces.*

Taphrinomycetes Eriksson and Winka, 1997
Vegetative mycelium mostly absent; ascomata absent; interascal tissue absent; dikaryotic mycelium infects host and proliferates through host tissue; dikaryotic cells or mycelium develop directly into asci, often forming a palisade layer on the host; ascus globose or ellipsoid, eight-spored; ascospores hyaline, aseptate; birotrophic on angiosperms forming galls or lesions; cells bud from ascospores to form a yeast-like, monokaryotic, saprobic anamorph. *Taphrina.*

Saccharomycetes Eriksson and Winka, 1997
Mycelium mostly absent; ascomata absent; interascal tissue absent; dikaryotic mycelium infects host and proliferates through host tissue; dikaryotic cells or mycelium develop directly into asci, often forming a palisade layer on the host; ascus globose or ellipsoid, eight-spored; ascospores hyaline, aseptate; birotrophic on angiosperms forming galls or lesions; cells bud from ascospores to form a yeast-like, monokaryotic, saprobic anamorph. *Candida, Saccharomyces.*

Pezizomycotina Eriksson and Winka, 1997
Mycelium present; hyphae filamentous, septate; septa with simple pores and Woronin bodies; life cycle haploid with a dikaryotic stage immediately prior to sexual reproduction; ascomata disoid, perithecial, cleistothecial or occasionally lacking; antheridium (male sex organ) present or absent; ascogonium (female sex organ), ascogenous hyphae and crosiers present; the penultimate cell of the crosier, in which meiosis and usually one mitotic division occur, becomes the ascus; ascii fissitunicate or do not fissitunicate, cylindrical, clavate or saccate; ascii frequently with ascospore discharge mechanism; ascospores (usually eight) surrounded by enveloping membrane system; ascospore morphology and pigmentation varied; asexual state present or absent, produced from vegetative hyphae in a thallic or blastic manner; mitospores (conidiospores) varied in morphology and pigmentation.

Arthoniomycetes Eriksson and Winka, 1997
Ascomata usually apothecial, occasionally closed with an elongated poroid opening; peridium thin or thick walled; interascal tissue of branched paraphyses in a gel matrix; ascii thick walled, fissitunicate, bluing in iodine, with or without a large apical dome; ascospores aseptate or septate, sometimes becoming brown and ornamented; anamorphs pycnidial; forming crustose lichens with green algae, lichenicolous or saprobic on plants. *Arthonia.*

Dothideomycetes Eriksson and Winka, 1997
Ascomata variable (apothecial, perithecial, cleistothecial), formed lygenously from stromatic tissue (ascolocular); interascal tissue present or absent, of branched paraphyses or pseudoparaphyses; ascii cylindrical to saccate, thick walled, fissitunicate, rarely with apical structures; ascospores mostly septate or muriform, colourless to dark brown; anamorphs hyphomycetous or coelomycetous; saprobic, plant parasites, coprophilous or lichen forming. *Dothidea.*

Chaetothyriomycetes Eriksson and Winka, 1997
Mycelium usually superficial of brown narrow hyphae; ascomata perithecial, often formed beneath a subiculum, spherical or flattened with or without a papilla, sometimes setose; papilla with a periphysate ostiole; interascal tissue of short apical paraphyses; hymenium usually bluing in iodine; ascii fissitunicate, saccate; ascospores hyaline or pale, transversely septate or muriform; anamorphs hyphomycetous; epitrophic or biotrophic on leaves. *Chaetothyrium.*

Eurotiomycetes Eriksson and Winka, 1997
Ascomata cleistothecial, sometimes absent; peridium thin, membranous or hyphal; interascal tissue absent; ascii not fissitunicate, clavate or saccate, often evanescent; ascospores aseptate, with equatorial ornamentation; anamorphs hyphomycetous, important industrially and medically (*Aspergillus, Penicillium*); saprobic, pathogenic on animals. *Eurotium, Talaromyces.*

Pezizomycetes Eriksson and Winka, 1997
Ascomata apothecial or cleistothecial, usually visible with unaided eye, leathery or fleshy, carotenoids (bright colours to dark) sometimes present; interascal tissue present (paraphyses); ascii not fissitunicate, usually elongated, cylindrical (more or less globose in cleistothecial species), thin walled, lacking obvious apical wall thickening or apical apparatus, with operculum or vertical slit (except in cleistothecial species), forcibly discharging ascospores except in cleistothecial species; ascospores usually ellipsoid or globose, aseptate, hyaline to darkly pigmented, smooth or ornamented; anamorphs...
hyphomycetous, where known; saprophages on soil, dead wood or dung; some species hypogeous and mycorrhizal. Ascomycetes, Helvella, Morchella, Peziza, Sarcoscypha.

**Laboulbeniomycetes** Engler, 1898
Myelium absent except in Pyxidiophorales; cellular thallus hyaline to dark, with basal haustorium present; ascomata perithecial, frequently surrounded by complex appendages, translucent, ovoid, thin walled; interascal tissue absent; asci few and basal, not fissitunicate, clavate, thin walled, evanescent, maturing sequentially, usually with four ascospores; ascospores two celled, hyaline, elongate, one end modified as attachment to host; anamorphs hyphomycetous, spermatial; ectoparasitic on insects, some may be coprophilous. Laboulbenia, Pyxidiophora.

**Lecanoromycetes** Eriksson et al., 2001
Ascomata apothecial, discoid, perithecial or elongated, sometimes stalked or immersed, occasionally evanescent; interascal tissue of simple or branched paraphyses swollen at the apices, often with a pigmented or iodine staining epithelium; hymenial gel often present; asci not fissitunicate, thick walled, with a thickened, cap-like apex, often with an internal apical ocular chamber, ascus walls and thickened apex often stains blue with iodine; ascospores one to several septate, occasionally, multinucleate or with an interascal apparatus variable; asci not fissitunicate, with or without apical structures, cylindrical, clavate or globose, persistent or evanescent; ascospores with or without at least one dark cell with germ pore, varied in shape and colour, with or without gelatinous sheaths or appendages; saprobic or parasitic on plants, coprophilous, fungi-colous or lichenicolous. Neurospora, Sordaria.

**Microsporidia** Balbiani, 1882
Obligate intracellular parasites, usually of animals; without mitochondria and peroxisomes; spores with inner chitin wall and outer proteinaceous wall; without kinetosomes, centrioles or cilia; centrosomal plaque; extrusive specialized polar tube for host penetration; sexual, asexual or both. Subdivisions for host penetration. Amblyospora, Encephalitozoon, Buxtehuieda, Caudospora, Corythidiopsis, Desportesia, Encephalitozoon, Enteroctozoan, Glugea, Hessea, Metchnikovella, Nosema, Spraguea, Vairimorpha.

**Glomeromycota** Schüssler et al., 2001 [Glomales Morton and Benny, 1990; Glomomyctes Cavalier-Smith, 1998] Filamentous; primarily endomycorrhizal, arbuscular, sometimes with vesicles; without cilia; asexual spores outside host (chlamydospores, azygospores); with or without centrioles or cilia; centrosomal plaque; extrusive specialized polar tube for host penetration; sexual, asexual or both. Subdivisions for host penetration. Amblyospora, Encephalitozoon, Buxtehuieda, Caudospora, Corythidiopsis, Desportesia, Encephalitozoon, Enterocytozoan, Glugea, Hessea, Metchnikovella, Nosema, Spraguea, Vairimorpha.

**Zygomyctes** Fischer, 1892, emend. Benjamin, 1979, emend. Benny et al., 2001 Primarily filamentous, without septa (coenocytic), or septa occurring irregularly when present; lacking cilia; sexual reproduction by thick-walled zygospore, formed at the junction between complementary hyphae; endospores formed by internal cleavage of sporangia, except in Entomophthorales and some Zoopagales; septa associated with lens-shaped plug (lenticular cavity) in Dimargaritales, Harpellales, and Kickxellales.

**Dimargaritales** Benjamin, 1979
Hyphal regularly septate; septa containing a lenticular cavity; asexual reproduction by bisporous merosporangia; sexual reproduction by a zygospore, often ornamented; obligate haustorial parasites of fungi, especially Mucorales. Dimargaris, Dispora, Spinaulis, Tiegheimyces.

**Harpellales** Lichtwardt and Manier, 1978, emend. Benny et al., 2001 Endosymbiont of freshwater arthropods; basal cell attached to host, from which a filamentous thallus.
develops; hyphae septate, with or without branching; septa containing a lenticular cavity; asexual reproduction by lateral elongate monosporous trichospores; sexual reproduction by conical or biconical zygospores. *Harpella, Orphella, Smittium, Zygodogonas.*

- **Kickxellales Benjamin, 1979**
  Filamentous; hyphae possessing septa with a lenticular cavity; asexual reproduction by uninucleate sporangiola (merosporangia) produced on a sporocarpus; saprobic or mycoparasitic, isolated from soil and dung. *Coe-mansia, Dipspacomyces, Kickxella, Lindera, Martensella, Martensiomycetes, Pseudactynol, Spireomyces.*

- **Zoopagales Benjamin, 1979**
  Filamentous, hyphae coenocytic or septate; parasites of soil fungi, invertebrates and ameobae; asexual reproduction by conidia or merosporangia; sexual reproduction by globose zygospores with apposed suspensors. *Amoebophillus, Piptochaethus, Rhopalomyces, Sigma-ideomyces, Stylopogas.*

- **Basidiobolus Eidam, 1886**
  Filamentous; without cilia; uninucleate cells; sporophores with sub-sporangial vesicle; asexual reproduction by a forcibly discharged conidium; hyphae septate with uninucleate cells; sexual reproduction by thick-walled zygospore; possessing a centriole-like nuclear-associated organelle; isolated from soil and insectivorous animal dung. *Basidiobolus.*

- **Mucorales Schröter, 1897 (P?)**
  Filamentous fungi; generally saprotrophic, with exceptions; septa absent except in older hyphae; with plasmodesmata at septal plates; asexual reproduction with one to many spores in merosporangia, sporangiola, or sporangium; reproduction by zygospore, typically with opposed suspensors. Traditional subdivisions artificial. *Chaetocladium, Choeneophyta, Morterella, Mucor, Phycomyces, Phialobolus, Syncephalestrum, Thammidiurn.*

- **Endogonales Benjamin, 1979, emend. Morton and Benny, 1990**
  Filamentous, hyphae coenocytic; saprobic and ectomycorrhizal; zygospores with apposed suspensors produced in a subterranean sporocarp. *Densospora, Endogone, Pteridiospora, Selerogone, Youngiomyces.*

- **Entomophthorales Schröter, 1897**
  Filamentous, primarily without septa; mostly parasites of insects, mites, and spiders; sexual reproduction by thick-walled zygospore, strictly homothallic, where known; asexual reproduction by conidia formed by blastosporogenesis; conidia forcibly discharged and often form second conidia. *Conidiobolus, Com-pletoria, Entomophthora, Meristacrum, Neozygitas.*

- **Chytridiomycetes de Barry, 1863, emend. Sparrow, 1958, emend. Cavalier-Smith, 1981**
  Ciliated cells in at least one life cycle stage; both uni- and multiciliated; point of insertion varying, but the flagellum always posteriorly directed; main cell wall polysaccharides, chitin and β-1,3-1,6-glucan; AAA lysine biosynthesis pathway; glycogen storage product.

- **Blastoscladiales Petersen, 1909**
  Unciliated cells, with nuclear cap of ribosomes and cone-shaped nucleus, with the narrow end close to the kinetosome with root of 27 microtubules in sets of three; microtubules extend from kinetosome to nuclear cap, covering both nucleus and cap; without rumposome or electron opaque material in kinetosome transition zone; when present, dormant kinetosome is reduced in size and positioned at a right angle from the kinetosome.

- **Blastocladiaceae Petersen, 1909**
  Monocentric and/or polycentric with bipolar germination. *Allomyces, Blastocladi, Blastocladiella, Blastocladiopsis, Microallomyces.*

- **Catenariaeae Couch, 1945**
  Filamentous and polycentric with monocentric germination. *Catenomyces, Catenophyta, Catenaria.*

- **Coelomycetaceae Couch, 1945**
  Obligate parasites of insect larvae with an alternate gametophyte generation on copepods. *Coeleomyces.*

- **Physodermataeae Sparrow, 1952**
  Obligate parasites of angiosperms in marsh and aquatic habitats; two types of thalli: 1) monocentric and epibiotic or 2) polycentric and endobiotic. *Physoderma, Urophylaxis.*

- **Sorochytrium Dewel, 1985 [Sorochytriaceae Dewel, 1985] (M)**
  Single species that parasitizes tardigrades; life cycle with endobiotic, eucarpic, polysporangiate thallus on live hosts, and extramatrical, polycentric thallus on dead hosts or in culture. *Monoblepharidales Schroeter, 1893, emend. Barr, 2001*

- **Monoblepharaeidae Schroeter, 1893, emend. Barr, 2001**
  In the motile cell, the kinetosome root with two parts, a striated disk partially extending around the kinetosome and microtubules extending out into the cytoplasm from the proximal end of the kinetosome; dormant kinetosome parallel; with an electron-opaque plate in the kinetosome transition zone; a non-fenestrated rumposome present. Note 4.

- **Gonapodyaceae Sparrow, 1960**
  Sex anisogamous. *Gonapodya.*

- **Monoblepharidaceae Fischer 1892, emend. Molli-cone and Longcore, 1999**
  Sex oogamous with a small male gamete fertilizing an oogonium. *Monoblepharella, Monoblepharis.*

- **Oedogoniomyces Barr, 1990**

- **Spizellomyctaeae Barr, 1980**
  Cell with nucleus either closely associated with the kinetosome or connected by its root; ribosomes dispersed in the cytoplasm; rumposome absent; dormant kinetosome at an angle to the ciliated kinetosome; without electron-opaque material in the kinetosome transition zone. Note 5.
Spizellomyctecatae Barr, 1980
Monocentric with endogenous thallus development. Gaertneriomycetes, Karlingiomycetes, Kochiomycetes, Spizellomyctecatae, Triparticular.

Olpidiaceae Schroeter, 1889
Monocentric with exogenous thallus development. Caulochytrium, Entophlyctis, Olpidium, Rhizophylyctis, Rozella.

Neocallimastigaceae Li, Heath, and Packer, 1993
Obligate anaerobes of the rumen and hindgut of herbivores; species multiciliated; ribosomes aggregated mostly in the cell interior; with hydrogenosomes, without mitochondria; dormant kinetosomes absent in all species; complex electron-opaque saddle-like structure partially surrounding the kinetosome and extending to the plasma membrane; kinetosome root composed of an irregularly arranged array of microtubules that extend from a spur on the kinetosome into the cytoplasm; in the posterior portion of the cell, the posterior dome lying, connected to the spur on the kinetosome by some of the root microtubules. Anaeromycymes, Caecomyces, Cyllamyces, Neocallimastix, Orpinomyces, Pirymyces.

Chytridiales Cohn, 1879, emend. Barr, 2001 (P)
Monociliated, occasionally with multiple cilia; cell shape varying from globose to subglobose or elongate, some amoeboid just before encystment; with lipid globule partially enclosed by a microbody, either fenestrated (rumposome) or non-fenestrated, sometimes associated with mitochondria; compact grouping of ribosomes partially or wholly surrounded by endoplasmic reticulum; nucleus not connected to the kinetosome pair; usually with 2–16 microtubules in the root, extending from the kinetosome to the rumposome; series of fibres connect kinetosome pair. Allochytridium, Asterophlyctis, Catenochytridium, Chytridium, Cladochytrium, Chytromycetes, Endochytrium, Entophlyctis, Lacustromyces, Nephrochrytrium, Nowakowskiiella, Obelidium, Phylcotricha, Physocladia, Podochytrium, Polychytrium, Polyphagus, Rhizocloasmatis, Rhizophylyctis, Rhizophydium, Septochytrium, Synchytrium. Note 6.

Mesomyxozoea Mendoza et al., 2002; emend. Adl et al., 2005 [not Choanozoono Smith, 1981] (R) (P) Usually flat cristae (exceptions e.g. Aphelidea, Ichthyophonidae); at least one life cycle stage with spherical cells, posteriorly monoflagellated or amoeboid; some with parasitic spherical, non-flagellated stages and endospores; trophic stages with cell wall in some.

Aphelidea Gromov, 2000
Intracellular phagotrophic parasites of algae with complex life cycle: amoeboid cell invades host through apophysa of spore, attached to host cell surface; characteristic central food vacuole with excretory body; cell division leads to flagellate and amoeboid dispersal cells released from host; tubular cristae. Amoebophedilidium, Aphelidium, Pseudophedilidium.

Corallochytrium Raghu-Kumar, 1987 (M)
Spherical single cells 4.5–20.0 μm in diameter; binary fissions releasing numerous elongated amoeboid cells; marine saprotrophic usually recovered from coral reefs in the Indian Ocean. Corallochytrium limacisporum.

Capsaspora Hertel et al., 2002 (M)
Amoeboid 3.0–7.0 μm in diameter; single nucleus one-third to one-half size of cell, with central nucleolus; without flagellated stages; flat cristae; long, straight, unbranched pseudopodia, called “feeding peduncles”; without mucous sheath; capable of penetrating tegument of trematode larvae; cell wall with chitin, elastin or collagen. Capsaspora owczarzaki.

Ichthyosporea Cavalier-Smith, 1998 [Mesomyxozoea Mendoza et al., 2002]
Single-celled trophic organisms (some with hyphal, multinucleated filaments, Ichthyophonidae); flat cristae but some may have tubular cristae; if present, single flagellum; without collar or cortical alveoli; some species form only elongate amoeboid cells; most animal parasites, some free living and saprotrophic (Sphaeroforma, LKM51 isolate); chitin reported but controversial.

Rhinosporideaceae Mendoza et al., 2001 [Dermocystidae Cavalier-Smith, 1998] (R)
If present, posterior flagellum; flat cristae; when parasites of animals, spherical phenotypes with several 2–20 μm endospores that are eventually released and become mature cells with endospores to continue the parasitic cycle. Amphibiosporidium ranae, Dermocystidium, Rhinosporidium seeberi, Sphaeroforma desrens.

Ichthyophonidae Mendoza et al., 2001 [Ichthyophonidae Cavalier-Smith, 1998; Amoebidiidae Reeves, 2003] (R) Parasites of fish, arthropods, and insects, or free living and saprotrophic; usually with flat cristae but Ichthyophonidae with tubular cristae; some characteristic amoeboid cells, but in others amoeboid cells absent or unreported; monoflagellated stage only in Pseudoperkinsus tapetis, but controversial. Amoebidium parasiticum, Anurofeca richardi, Ichthyophonidae, Pseudoperkinsus tapetis, Psorospermium haecelli, Sphaeroforma arctica, Isolate LKM51, Isolate Ikaite un-c53.

Marine isolates known only; <5 μm with equally spaced, unbranched filopodia radiating from spherical bodies; flat cristae; flagellum has been suggested but controversial. Ministeria.

Nucleariida Cavalier-Smith, 1993
Amoeboid with rounded body, from which elongated filopodia extend; flat cristae. Nuclearia.

Choanomonad Kent, 1880
Phagotrophic with collar of microvilli around a single flagellum; radial symmetry; solitary or colonial; flat cristae; central filament in kinetosome transition zone. This group is traditionally divided into three groups based on the presence or absence of a cellulose theca or lorica of siliceous strips. Note 7.


Salpingoecidae Kent, 1880
Cellulose theca. Salpingoeca, Steleasoma.
**Acanthoecidae Norris, 1965**  
Loric of siliceous strips. *Bicosta, Stephanoeca*.

**Metazoa Haeckel, 1874**  
Multicellular; cells typically held together by intercellular junctions; extracellular matrix with fibrous proteins, typically collagen, between two dissimilar epithelia (except in Mesozoa and Placozoa); sexual with production of an egg cell that is fertilized by a smaller, often monociliated, sperm cell; phagotrophic and osmotrophic; without cell wall.

**Porifera Grant, 1836** [Parazoa Sollas, 1884] (P?)  
Cells without walls; flat crista; sexual species, mostly hermaphroditic, releasing mononucleated sperm or producing amoeboid egg cells at different times; zygotes forming ciliated dispersal larvae that resemble blastulae; sessile adult; asexual reproduction by gemmules; differentiation of larva to a variety of cell types, including choanoocytes, amoeboid cells, and digestive secretary cells; cell types transformable into other types as necessary; cells more or less independent; supporting matrix typically with collagen-IV, secreted by amoeboid cells; without mesoderm, nervous tissue, desmosomes, localised gonad, or glandular digestive cells.

**Silicispongia Schmidt, 1862** [Silicea Bowerbank, 1864]  
Usually with matrix of siliceous spicules.

**Hexactinellida Schmidt, 1870**  
Siliceous spicules triaxonic, hexactinic; cells forming extensive multinucleate syncytium, with some differentiated cells; electrical conductance across body; non-contractile body; larvae (poorly known) with medial region of ciliated cells. *Euplectella, Farrea, Hyalonema, Monoraphis, Lophocalyx, Spermarella*.

**Demospongiae Sollas, 1885**, emend. Borchelli et al., 2004  
Spongin and siliceous spicules in matrix; except in **Myxospongiae**; spicules not triaxonic; with hollow triangular canal and four rays, not perpendicular; larva with outer mononucleated cells, except at posterior pole; one family (Cladorhizidae) with external digestion, by amoeboid cell aggregation, of captured crustacean prey. *Aplysina, Axinella, Cacospongiosis, Chondroschia, Cliona, Euprosopis, Halisarca, Hippopongia, Oscarella, Plakina, Spongilla, Suberites*. Excludes Homoscleromorpha.

**Homoscleromorpha Lévi, 1973**, emend. Borchelli et al., 2004 (R)  

**Calcispongia Johnston, 1842** [Calcarea Bowerbank, 1864]  
Calcium carbonate spicules; larvae with outer mononucleated cells, larger at posterior; invagination of anterior cells at attachment of posterior to substrate.

**Calcinea Hartman, 1958**, emend. Borchelli et al., 2004 (R)  
Unambiguous characters congruent with molecular phylogenies unclear. *Clathrina*, *Murrayona*.

**Calcanea Hartman, 1958**, emend. Borchelli et al., 2004 (R)  
Unambiguous characters congruent with molecular phylogenies unclear. *Grantiopsis-Paralarilula, Vos-macropsis-Sycetta*, includes Heteropiidae, Staur-orthophidae, Minchinellidae.

**Placozoa Grell, 1971** (M)  
Two layers of epithelial cells, with a middle layer of syncytial contractile fibrous cells, and undifferentiated cells; with digestive glandular cells; belt desmosomes (zonulae adherentes) connecting adjacent cells; without extracellular matrix; collagen fibres absent; without endoderm, ectoderm, mesoderm or nerve cells; cilia of ventral cells with two orthogonal kinetosomes with 1–2 lateral and one vertical fibrillar rootlets; egg cell and non-ciliated sperm in mid-layer; asexual binary division of body possible. *Trichoplax*.

**Mesozoa van Beneden, 1877** (P)  
Multicellular with pluriciliated cells in epithelium; gap junctions, septate junctions and two types of adherens junctions present—(1) maculae adherentes like and (2) zonulae adherentes like; double-stranded cilia; cytoskeleton with rootlet horizontal, pointing anterior; without digestive tissues; only osmotrophic endoparasites known; sexual with testes and egg cells; without gastrulation; without basal membrane or extracellular matrix; tubular crista.

**Orthonecida Giard, 1880**  
Epithelial cells in rings of alternating pluriciliated and non-ciliated cells; contractile cells, with differentiated testes and egg cells. *Ciliocincta, Rhopalura, Stoecharitum*.

**Rhombozoa Krohn, 1839**  
Pluriciliated epithelial cells surrounding a single non-ciliated, long central cell (axial cell); egg cells forming inside axial cell and fertilized by non-ciliated sperm; asexual reproduction by successive mitoses of an axoblast cell in the axial cell. *Dicyema, Dicyemmenae*.

**Animalia Linnaeus, 1758**, emend. Adl et al., 2005 [Eumetazoa Bütschli, 1910]  
Reproduction through an egg cell, usually fertilized by a mononucleated sperm cell with acrosome; embryonic development with blastula and gastrulation, with differentiation into endoderm, ectoderm, mesoderm, and neuroderm; tissues organized into organs that share tasks for the individual, unless secondarily lost; some secondarily reduced to small number of cells (e.g. *Myxozoa Grasse, 1970*); coordination of cells and tissues by membrane receptors that respond to ligands through elaborate signal transduction; characteristic cell–cell junctions with belt desmosomes (zonulae adherentes); basal lamina and extracellular matrix with collagen and other fibrous proteins (laminin, nidogen, and perlecan); heterotrophic nutrition with secretion of digestive enzymes and osmotrophy through a digestive tract; without cell wall; ectoderm completely surrounding body, and endoderm surrounding a digestive tract; sensory cells in epithelium; nervous tissue in organized network; epithelial actin–myosin-based contractile cells between endoderm–ectoderm. Subdivisions not shown.

**RHIZARIA Cavalier-Smith, 2002**  
With fine pseudopodia (filopodia) varying as simple, branching, anastomosing, or supported by microtubules (axopodia).

**Cercozoa Cavalier-Smith, 1998**, emend. Adl et al., 2005 (R)  
Diverse clade lacking distinctive morphological or behavioural characters; biciliated and/or amoeboid, usually with filopodia;
most with tubular cristae; cysts common; kinetosomes connecting to nucleus with cytoskeleton; usually with microbodies and extrusomes.

  Amoeboid flagellates without cell wall; two heterodynamic flagella without mastigonemes; pseudopodia used for feeding; some species have complex life cycle including multinuclear and multigelollar plasmodium stage; cysts occur; kinesomes connected to the nucleus; tubular cristae; with microbodies and extrusomes.

- Cercomonadidae Kent, 1880, emend. Mylnikov and Karpov, 2004 [Cercobodoniidae Holland, 1942]
  Gliding cells with two flagella; posterior flagellum adhering to the cell; with transient filopodia. *Cercomonas, Eocercomonas, Helkesinastis, Neocercomonas*. **Note 8.**

  Rigid cells with two subapical non-adherent flagella but anterior flagellum sometimes absent; often gliding on posterior flagellum; phagocytosis with transient pseudopodia (e.g. *Heteromita* Dujardin, 1841, emend. Mylnikov and Karpov, 2004 (= *Bodomorpha* Holland, 1952 = *Sci- vianmons* Ekelund and Patterson, 1997); kinesome microtubular cone, absent. *Heteromita*. Incertae sedis: *Allantion, Cholamonas, Katabia, Protaspis, Sainouron.*

- Silicofiloidea Adl et al., 2005 [Imbricatea Cavalier-Smith and Chao, 2003]
  Secreted surface silica scales; tubular cristae.

- Thaumatomonadida Shirikina, 1987 [Thaumatostigmatidae Patterson and Zöllfer, 1991]
  Heterotrophs usually gliding cells that may swim also; with flattened cell body and with two heterodynamic flagella inserting subapically and/or ventrally; some unikont; with extrusomes; filopodia produced subapically or from ventral groove; cysts; multinucleate and multigelollar stages known; tubular cristae. Subdivisions unknown. *Allas, Gyromittus, Thaumatomonas, Thaumatostactis.*

- Euglyphida Copeland, 1956, emend. Cavalier-Smith, 1997
  Secreted silica plates bound by an organic cement into a test; tubular cristae. Subdivisions based on morphology.

- Euglyphidae Wallis, 1864
  Thin round to elliptical scales. *Assulina, Euglypha, Heteroglypha, Placosista, Pareuglypha, Sphenod- tia, Tracheuglypha, Trachelocorythion.*

- Trinematidae Hoogenraad and De Groot, 1940
  Test with bilateral symmetry; opening invaginated in some. *Corythion, Deharvengia, Pileolus, Play- fai-rina, Trinema.*

- Cyphoderididae de Saedeleer, 1934
  Scales circular to oval; test aperture angled, some with collar. *Campascus, Corythionella, Cyphoderia, Mess- ennviella, Pseudocorythion, Schaudivnula.*

- Paulinellidae de Saedeller, 1934
  Scales long, with length perpendicular to opening; with cyanelle. *Paulinella.*

- Incertae sedis Euglyphida: *Ampullatula, Euglyphidion, Heteroglypha, Matsakiaion.*

- Chlorarachniophyta Hibberd and Norris, 1984
  Amoeboid with plasids of secondary origin; plastid containing chlorophylls a and b, associated with a nucleomorph and surrounded by four membranes in total; usually reticulate pseudopodia with extrusomes; cell bodies often anastomosing; with a biflagellated dispersal stage. *Bigelowiella, Chlorarachnion, Cryptochloia.*

- Phytomyxea Engler and Prantl, 1897, emend. Cavalier-Smith, 1993 (includes Plasmodiophorida Cook, 1928, emend. Cavalier-Smith, 1993)
  Parasites or parasitoids of plants or stramenopiles; with amoeboid or plasmodial feeding cells producing biflagellate or tetraflagellate cells; some with specialized solid extrusome—‘‘satchel’’—for penetrating host cells; with distinctive cruciform mitotic profile due to elongate persistent nucleolus lying orthogonal to metaphase plate. *Plasmodiophora, Pongomyxa, Phagomyxa, Sorospheara, Spongospora.*

- Phaeodarea Haeckel, 1879 [Tripylea Hertwig, 1879]
  Central capsule with thickened, double-layered, capsular wall containing two kinds of pores or openings; large opening known as an “astropylum” or oral pore with a protruding mass of cytoplasm, and smaller, typically lateral openings, as “parapyleae”, with thinner protruding strands of cytoplasm; dense mass of darkly pigmented granular cytoplasm, the “phaeodium,” containing undigested debris, suspended in the extracapsulum; mineral skeletons, when present, composed of scattered spicules or hollow silica bars, joined by organic material; a wide variety of forms, including geodesic frameworks, spherical to polyhedral shells, or more solid, porous clam-shaped, bivalve shells.

- Phaeoconchia Haeckel, 1879
  Central capsule enclosed within bivalve lattice shell composed of dorsal and ventral boat-shaped valves, which are completely separated and rarely connected by a ligament on the aboral pole. *Conchellium, Concho- psis, Coelodendrum, Coelographis.*

- Phaeocystina Haeckel, 1879
  Central capsule suspended in the centre of the extracapsular cytoplasmic network; skeleton absent or incomplete, composed of numerous solitary, scattered pieces or spicules without organic connections. *Aula- cantha, Autographis, Cannoraphis.*

- Phaeogromia Haeckel, 1879
  Central capsule located eccentrically, aborally, in simple lattice shell typically provided with large shell opening placed on the oral pole of the main axis; capsule opening surrounded by ‘‘teeth’’ or by peculiar elongate extensions known as ‘‘feet’’, sometimes with elaborate branches. *Castanella, Challengeron, Haeckeliana, Medusetta, Tuscarora.*

- Phaeosphaeria Haeckel, 1879
  Central capsule located in the centre of a simple or double spherical lattice shell, not bivalve, with a simple shell opening, lacking ‘‘feet’’ or ‘‘teeth’’. *Aulosphaera, Cannosphaera, Sagospheara.*
• Nucleohelea Cavalier-Smith, 1993
Amorphous centrosome adjacent to nuclear envelope (axoplast); axopodial pseudopods supported by microtubules.

• Clathrulinidae Claus, 1874 [Desmothoracidida Hertwig and Lesser, 1874]
Extracellular capsule or lorica attached to substrate, with axopodia emerging from perforations; kinetocyst extrusomes along axopodia; tubular cristae; biciliated and amoeboid stages; can be colonial. Cienkowskia, Clathrula, Hedericyctis. Incertae sedis Servetia.

• Gymnosphaerida Poche, 1913, emend. Mikrjukov, 2000
Axopodia microtubules in irregular hexagonal prism; kinetocyst and other types of extrusomes along axopodia; tubular cristae; in some genera, cells attached to substrate with cytoplasmic stalk; free swimming as amoeboid or motile biciliated cells; one or more nuclei, often located in the amoeboid base of stalk when present; complex life cycle unresolved. Actinocoryne, Gymnosphaera, Hederiophrys. Incertae sedis Actinolophus, Wagnerella.

• Incertae sedis Cercozoa: Cryothecomonas, Gymnophrys, Lecythium, Massisteria, Metopion, Proleptomonas, Psuedodiffugia.

• Haplosporida Caullery and Mesnil, 1899
Plasmodial endoparasites of marine and sometimes freshwater animals; distinctive lidded spores; during spore development, spore wall produced inside of outer membrane of invaginated area; without polar capsules or polar filaments; spore anterior opening covered by hinged operculum; invaginated area; without polar capsules or polar filament, spore wall produced inside of outer membrane of Plasmodial endoparasites of marine and sometimes freshwater animals. Haplosporidium, Minchinia, Urosporidium.

• Foraminifera d’Orbigny, 1826
Filopodia with granular cytoplasm, forming branching and anastomosing network (reticulopodia); bidirectional rapid (∼10 μm/s) transport of intracellular granules and plasma membrane domains; tubular cristae; fuzzy-coated organelle of unknown function in reticulopodia; polymorphic assemblies of tubulin as (i) conventional microtubules in singly or in loosely organized bundles, (ii) single helical filaments, and (iii) helical filaments packed into paracrystalline arrays; majority of forms possess a test, which can be organic walled, agglutinated, or calcareous; wall structure in naked and single-chambered forms quite variable—for “naked” athalamids, such as Reticulomyxa, thicker veins vested with an amorphous, mucoid material; for thecate (soft-walled) species, such as members of the genus Allogromia, proteinaceous with little or no foreign material; for agglutinated species, foreign materials bound with an amorphous or fibrous organic matrix; for multi-chambered (polythalamous) forms, walls containing agglutinated material or mineralized with calcite, aragonite, or silica; life cycle often comprising an alternation of asexually reproducing amamont and sexually reproducing gamont; includes at least some Xenophyophorea Schulze, 1904, and some athalamids such as Reticulomyxa Nauss, 1949; previous subdivisions of single-chambered members no longer valid, but certain multi-chambered groups (e.g. rotaids and milioids) are monophyletic. Allogromia, Ammonia, Carpenteria, Cycloclypeus, Globigerinella, Lama, Lenticula, Nodogenerina, Textularia. Note 9.

• Gromia Dujardin, 1835
Test of organic material, brown and opaque, with single aperture; filopodia branched, with non-granular cytoplasm; filopodia Anastomose but not into a reticulum; multinucleate; flagellated dispersal cells or gametes. Gromia.

• Radiolaria Müller, 1858, emend. Adl et al., 2005
Cells with distinctive organic, non-living, porous capsular wall surrounding the intra-capsulum, which contains the nucleus or nuclei and cytoplasmic organelles; axopodia supported by internal microtubules, extending distally through the capsular wall pores and connecting to a frothy external layer, the extracapsulum; extracapsulum containing digestive vacuoles and in some cases algal and/or cyanobacterial symbionts; skeletons, when present, of amorphous silica (opal) or strontium sulphate (in Acantharia) and varying in shape from simple scattered spicules to highly ornate geometric-shaped shells, within and/or surrounding the central capsule; the siliceous skeleton is secreted within a specialized cytoplasmic envelope (cytokalymma) that dynamically determines the shape of the skeletal matter. Note 10.

• Polycystinea Ehrenberg, 1838, emend. Haeckel, 1887
Central capsule spherical to ovate with round pores in the capsular wall either distributed uniformly on the surface of a spherical capsular wall or localized at one pole of an ovate capsular wall; skeleton either absent or when present, composed of spicules or forming elaborate geometric-shaped, porous or latticed shells.

• Spumellaria Ehrenberg, 1875, emend. Haeckel, 1887, emend. Riedel, 1967
Central capsule typically spherical with uniformly distributed round pores in the capsular wall; skeleton either absent or when present, composed of spicules or forming latticed shells either single or multiple and concentrically arranged.

• Collodaria Haeckel, 1887
Skeletton either absent or when present, composed of scattered spicules within the extra-capsulum; solitary or colonial forms. Collopora, Collozoaum, Lamprozontium, Physisometum, Sphaerazoon, Siphonazoon, Thallassicolla.

• Sphaerellaria Haeckel, 1887
Skeleton a porous or latticed shell; skeleton single or multiple, and of various shapes: spherical, discoidal, quadrangular, trirgonal, or bilocular. Actinomma, Didymocystis, Euchiton, Hexacentrum, Hexaloniche, Hexastylus, Octodendron, Plegmosphaera, Saturnalis, Spongaster, Spongosphaera.

• Nassellaria Ehrenberg, 1875, emend. Haeckel, 1887
Central capsule ovate with pores localized at one pole; skeleton, when present, composed of a simple tripod, a sagittal ring without tripod or porous helmet-shaped “cephalis” enclosing the central capsule.

• Pleistellaria Haeckel, 1887
Skeleton absent or when present, simple tripod or sagittal ring. Lophospyris, Plagionium, Tetraplecta, Zygocecrus.

• Cyrtellaria Haeckel, 1887
Skeleton, a helmet-shaped “cephalis”, bilocular with sagittal construction, or multifilocal and segmented
with two or more constrictions, or simple without constriction and lobes. Botryostrobous, Callimira, Cornutella, Eucyrtidium, Lamprocyclas, Pterocanium, Spirocytis, Theopilum.

- Taxopodida Folt, 1883
  Axopodial pseudopods without kinetocysts, used for motility as oars; axopodial microtubules originate from depressions in nuclear envelope; microtubules in axoneme arranged in irregular hexagons; periplasm of siliceous tangential spicules, with external radial spicules. Sticholochne.

- Acantharia Haeckel, 1881, emend. Mikrjukov, 2000
  Cell surrounded by fibrillar capsule outside of cell membrane; axopodia, spicules, and amoeboid anastomosing dynamic network of irregular pseudopodia extending from the capsule; this outer network (ectoplasm) surrounded by fibrillar periplasmic cortex; inner cell region inside capsule (endoplasm) holding the organelles; axopodia, supported by microtubular arrays, with kinetocyst extrusomes and with a centroplast-centrosome at base of each spicule; 20 radial spicules of strontium sulphate merged at cell centre; spicule tips attached to contractile myonemes at periplasm; tubular cristae; often with algal symbionts in endoplasm, and captured prey in ectoplasm network; asexual reproduction involving consecutive mitotic and meiotic divisions that ultimately release 10^2–10^3 bicciliated isogametic cells; only marine isolates known.

- Arthracanthida Schewiakoff, 1926
  Thick capsule clearly demarcates pigmented endoplasm from ectoplasm; axopodia with hexagonal microtubule arrays; many nuclei in endoplasm; algal symbionts in all known species, except at reproduction; sexual reproduction without gamontocyst. Acanthometra, Daurataspis, Dictyacantha, Diploconus, Phractopelta, Phyllostaurus, Pleuraspis, Stauroacantha.

- Chaunocanthida Schewiakoff, 1926
  Pigmented endoplasm, clears towards periphery; many small nuclei in endoplasm; clear ectoplasm with periplasmic cortex; sexual reproduction in gamontocyst; small plaques synthesized in Golgi (lithosomes) forming the gamontocyst wall; lithophus stage prior to reproduction; hexagonal microtubular arrays in axopodia; contractile matrix at base of spicules. Amphiacon, Conacon, Gigartacan, Heteracon, Staurocon.

- Holocanthida Schewiakoff, 1926
  Pigmented endoplasm, clears towards periphery; many small nuclei in endoplasm; sexual reproduction in gamontocyst; with lithosomes forming the gamontocyst wall; dodecagonal microtubular arrays in axopodia. Acanthochaiusma, Acanthocholla, Acanthopelma.

- Symphyacanthida Schewiakoff, 1926
  Pigmented endoplasm, clears towards periphery; ectoplasm clear; single large central nucleus; outer endoplasm with anastomosing pseudopodia; capsule and periplasmic cortex visible with light microscopy; sexual reproduction in gamontocyst with lithosomes forming the gamontocyst wall. Amphilitum, Astrolonche, Pseudolithium.

**Note 11.**

  Flagella of swimming cells in pairs or multiples of two; stellate structure linking nine pairs of microtubules at basal body transition zone; thylakoids single or stacked; plastid with two membranes without periplastid endoplasmic reticulum; starch inside plastid; glycolate dehydrogenase present; cell wall, when present, of cellulose; cell division without phragmoplast.

- Ulvophyceae Mattox and Stewart, 1984 (P)
  Swimming cells with one or two pairs of flagella, without mastigomers; basal bodies with 4 microtubular rootlets in cruciate arrangement, and smaller roots of two sizes, alternating between two or more microtubules; flagella with scales and rhizoplasts; cell wall more or less calcified; cell division by furrowing with mitotic spindle closed, centric and persistent; phycoplast absent; thallus can be branched or unbranched, mono- or ditostromatic sheet (phyllose), or cushiony forms of compacted tubes; thallus often multinucleate and siphonous; free-living diplobiontic life cycle, iso- or heteromorphic. Acetabularia, Caulerpa, Chladosora, Codium, Pithophora, Pseudonochloris, Rhizoclonium.

**Note 11.**

- Rhodophyceae Thuret, 1855, emend. Rabenhorst, 1863, emend. Adl et al., 2005 [Rhodophyta Wettstein, 1901; Rhodoplantae Saunders and Hommersand, 2004].
  Without flagellated stages, and without centrioles, or flagella basal bodies, or other 9+2 microtubular structures—presence of polar rings instead; two-membraned simple chloroplasts lacking external endoplasmic reticulum, unstacked thylakoids with phycobilisomes, and chlorophyll a only; cytoplasmic carbohydrate reserve floridean starch; chromosomal and inter-zonar microtubules not converging towards polar rings, so spindle poles very broad; telophase spindle and nuclear envelope persisting with closed mitosis; mitotic nucleus surrounded by own envelope and perinuclear endoplasmic reticulum; cell wall of cellulose; cells in filamentous forms linked by pit plugs, formed between cells after incomplete cell division; sexual reproduction typically oögamous; triphasic life history common. Subdivisions of this group unknown at this time. Traditional subgroups are artificial constructs, and no longer valid. Bonnemaisonia, Ceramium, Eucheuma, Dasya, Dasyphloea, Gracilaria, Nemalion, Nizymenia, Porphyra, Rhodimenia, Rhodophysea, Sphaerococcus.

**Note 11.**

  Plastid with chlorophylls a and b; pyrenoid often present inside plastid; cell wall with cellulose usually present; with centrioles.

  Plastid in the form of a cyanelle; cyanelle distinct from the chloroplasts of other organisms in that like cyanobacteria it has a peptidoglycan wall between its two membranes; chlorophyll type a only, with phycobiliproteins and other pigments; flagellate and non-flagellate species or life cycle stages. Cyanophora, Glaucocystis, Gloeochaete.
Treboviophyceae Friedl, 1995 [Pleurastrophyceae Mattax et al., 1984; Microthamniales Melkonian, 1990] Swimming cells with one or two pairs of flagella, without mastigonemes; basal bodies with four microtubular rootlets in cruciate arrangement, including a multilayered structure, and a smaller root, alternating between two or more microtubules; basal bodies with prominent rhizoplast; cruciate, displaced counter-clockwise; counter-clockwise basal body orientation; closed mitosis with metacentric spindle, semi-closed mitosis, cytokinesis with phycoplast; asexual reproduction by autospores or zoospores; sexual reproduction reported: lichenose and autotrophy, Botryococcus, Chlorella, Chroicyctis, Coccomyxa, Microthamnion, Nannochloris, Oocystis, Pabia, Prasiola, Prototheca, Trebouxia.

Chlorophyceae Christensen, 1994 Swimming cells with one to hundreds of flagella, without mastigonemes; when two or four flagella, basal bodies with four microtubular rootlets in cruciate arrangement, alternating between two and more microtubules; basal bodies displaced clockwise or directly opposed; rhizoplast connects basal bodies and extends to nucleus; in colonial forms, basal bodies re-oriented to face outside of colony; closed mitosis; cytokinesis has phycoplast with microtubules, sometimes with furrowing, with formation of plasmodesmata cell–cell connections; haplobiontic life cycle; sexual reproduction by isogamy, anisogamy or oögamy; asexual reproduction by aplanospores, akinetes, or autosporic; osmotrophy and autotrophy. Prateacoccus, Chlamydomonas (P), Desmodesmus, Floydiella, Hydrodictyon, Oedogonium, Pediastrum, Sceneodesmus, Volvox. Incertae sedis: Carteria, Cylindrocapsa, Hafniomonas, Myxanastes, Treubaria, Trochiscia.

Chlorodendrales Fritsch, 1917 Pair of flagella, inserted in a flagellar pit; flagella beat in breast-stroke pattern; basal body rootlets structure in X2X2 configuration; with organic extracellular scales, outer layer of scales fused to form a theca; metacentric spindle collapses at telophase; nutrition by autotrophy and osmotrophy. Scherffelia, Tetraselms.

Prasinophytae Cavalier-Smith, 1998, emend. Lewis and McCourt, 2004 (P) Flagella, 1, 2, 4 or 8, inserted in a flagellar pit; basal body rootlet structure diverse; rhizoplast extends beyond nucleus; flagella forward and pulling, or undulating and pushing; flagella with lateral mastigonemes; cells with 1–7 distinct types of organic extracellular scales, sometimes elaborate, covering cell wall and flagella; some with extrusomes; cysts in some; mitosis variable, most with persistent telophase spindle; sexual reproduction at least in Nephroselms olivaceus; nutrition by autotrophy and osmotrophy. Cristomastix, Halosphaera, Nephroselms, Pedinomonas, Pyraimomomas.

Mesostigma Lauterborn, 1894, emend. McCourt in Adl et al., 2005 [Mesostigmata Turnel, Otis, and Lemieux, 2002] Asymmetrical cell with pair of lateral flagella emerging from a pit, without mastigonemes; basal body transition region with similarity to Streptophyta; multilayered structure anchor associated with basal body; with chlorophyll a and b; plastid with two membranes without periplastid endoplasmic reticulum; starch inside plastid; with glycolate oxidase; flagellar peroxisome present; cell wall of cellulose; organic scales cover cell wall and flagella. Mesostigma. Note 12.

Charophyta Karol et al., 2001, emend. Lewis and McCourt, 2004 [Charophytae Smith, 1938, emend. Mattox and Stewart, 1984] Asymmetric motile cells, when present, with pair of flagella without mastigonemes; basal bodies with distinctive multilayered structure of microtubular rootlet and cytokskeletal anchor; thylakoids stacked; plastid with two membranes without periplastid endoplasmic reticulum; starch inside plastid; open mitosis; usually with phycoplast, but some with phragmoplast and cell plate; with primary plasmodesmata between adjacent cells in filamentous forms; filaments branching or non-branching; with non-motile vegetative phase; some with multinucleate cells; with or without sexual reproduction; sexual species with haplobiontic life cycle; with desiccation-resistant cysts (zygospores); glycolate oxidase in peroxisomes; Cu/Zn super oxide dismutase; flagellar peroxisome. Sub-divisions not shown. Chaetosphaeridium, Chlorokybus, Coleochaete, Klebsormidium, Spirogyra.

Streptophyta Lewis and McCourt, 2004 Pair of basal bodies with two dissimilar rootlets, including a multilayered structure and a smaller rootlet; open mitosis with persistent mitotic spindle and phragmoplast at cell division; with cellulose-synthesizing rosettes; primary plasmodesmata between cells; multicellular with vegetative growth from apical cell at end of branches and main axis; sexual reproduction with oögamy and egg jacket, and sperm twisted; cell divisions patterned in three-dimensional space.

Charales Lindley, 1836 [Charophytae Engler, 1887] Thallus attached to substrate with rhizoids; thallus a central axis of multinucleate intermodal cells, with whorls of branchlets radiating from mono-nucleate cells at nodes; calcium carbonate accumulates in cell wall of many species; haplobiontic life cycle; sexual reproduction oögonous with sperm cells; differentiated sperm- and egg-producing organs. Chara, Nitella.

Plantae Haeckel, 1866 [Cormophyta Endlicher, 1836; Embryophyta Endlicher, 1836, emend. Lewis and McCourt, 2004] Flagella basal bodies, when present, with distinctive multilayered structure of microtubules and cytokskeletal anchor; open mitosis with phragmoplast at cytokinesis; plasmodesmata and other characteristic cell–cell junctions; pyrenoids absent in most members; diplobiontic life cycle, with vegetative propagation possible in many; alternation of generations, with fertilization of egg by sperm inside protective test; embryology with tissue differentiation coordinated by hormones; differentiated sperm and egg cells, may be on different sexual individuals, on different organs of the same individual, or in the same organ. Subdivisions not shown.

CHROMALVEOLATA Adl et al., 2005 Plastid from secondary endosymbiosis with an ancestral archaeplastid; plastid secondarily lost or reduced in some; with tertiary reacquisition of a plastid in others. Note 13.
- Cryptophyceae Pascher 1913, emend. Schoenichen, 1925
  [Cryptophyta Cavalier-Smith, 1986]
  Autotrophic, mixotrophic, and heterotrophic with ejectosomes (trichocysts); cisternae flat tubules; two flagella emerging sub-apically or dorsally; from right side of an anterior depression (vestibulum); longitudinal grooves (furrows) and/or tubular channels (gullets) or a combination of both, extending posteriorly from the vestibulum on the ventral side; gutter/furrow complexes lined with large ejectosomes; with or without plastid–nucleomorph complex; chloroplasts when present contain chlorophylls a and c, and phycobiliproteins, located in thylakoid lumen; chloroplast covering comprised of inner and superficial periplast components; (heterotrophic species formerly known as Chilomonas have been distributed to other genera); some genera diplomorphic (e.g. Cryptomonas, Proteomonas).

Note 14.

- Cryptomonadales Pascher, 1913
  Chloroplasts or leucoplasts present. Campylomonas, Chroomonas, Cryptomonas, Hemiselmis, Rhodomonas.

- Goniomonadales Novarino and Lucas, 1993
  Chloroplasts absent. Goniomonas.

  Autotrophic, mixotrophic or heterotrophic cells; solitary cells or in colonies or filaments; motile cells often possessing a haptonema (filiform appendage situated between flagella); characteristic cell covering of unmineralized and/or mineralized scales; motile cells with two flagella generally without appendages, inserted apically or subapically in a papilla or groove, or emerge from a papilla; 1–4 chloroplasts with thylakoids in groups of three; chloroplasts with immersed or bulging pyrenoid; nucleus usually posterior; outer membrane of nuclear envelope continuous with outer chloroplast membrane; major pigments chlorophylls a, c1, and c2 (c3 in prymnesiophyceans), β-carotene, diadinoxanthin, and diatoxanthin; chrysolaminarin often the main storage product; eyespots recorded in a few genera (e.g. Pavlova, Diacronema); life cycles include either single phases or alternating stages; in those with alternating stages, palmelloid (colonial) or filamentous stages alternate with motile stages; sexual reproduction may be common in prymnesiophyceans; some species ichthyotoxic. Note 15.

- Pavlovophyceae Cavalier-Smith, 1986, emend. Green and Medlin, 2000
  Biflagellate with unequal flagella inserted subapically or laterally; scales absent; shorter flagellum may have a swelling with densely staining projections on the side adjacent to the cell; haptonema short, tapered, and non-coiling; single chloroplast, sometimes with an eyespot beneath the short flagellum. Diacronema, Exanthemachrysis, Pavlova.

- Prymnesiophyceae Hibberd, 1976
  Unicellular or colonial flagellates with mineralized and/or unmineralized scales covering the cells; some species exhibit two stages in the life cycle, with either a colonial or filamentous stage alternating with a flagellate stage; haptonema may be long and coiling to short and non-coiling; flagella of equal or subequal lengths inserted apically or subapically.

- Prymnesiales Papenfuss, 1955
  Motile or non-motile cells, sometimes forming colonies; usually with two flagella and a coiling or flexible haptonema; covering of organic scales, sometimes absent; some alternate stages reported. Chrysochromulina, Phaeocystis, Prymnesium.

- Phaeocystales Medlin, 2000
  Motile cells with two flagella and short non-coiling haptonema; one to four chloroplasts per cell; the cell covered with scales of two sizes; life cycle consisting of non-motile and motile stages; non-motile cells colonial and embedded in gelatinous material. Phaeocystis.

- Isochrysidales Pascher, 1910
  Motile or non-motile cells; haptonema rudimentary or absent; motile cells covered with small organic scales; non-motile cells sometimes covered with coccoliths. Emiliania, Gephyrocapsa, Isochrysis.

- Coccolithales Schwarz, 1932
  Cells with calcified organic scales during some stage of the life cycle; single or alternating stages in the life cycle; haptonema short or highly reduced; some species lack chloroplasts. Balaniger, Calcosolenia, Coccolithus, Hymenomonas, Pleurochrysis, Reticulosphaera, Wigwamma.

- Stramenopiles Patterson, 1989, emend. Adl et al., 2005
  Motile cells typically biflagellate, typically with heterokont flagellation (i.e. anterior flagellum with tripartite mastigonemes in two opposite rows, and a posterior flagellum usually smooth); tubular cristae; typically four microtubular kinetosome roots. Note 16.

- Opalinata Wenyon, 1926, emend. Cavalier-Smith, 1997
  [Slopalinata Patterson, 1986]
  Pluriloculated with double-stranded transitional helix at the transitional region between kinetosome and flagellum; evenly spaced cortical ridges underlain by microtubules, ranging from singlet to ribbons; cyst forming.

- Proteromonadea Grassé, 1952
  One or two anterior pairs of anisokont flagella; uninucleate; endobionts in intestinal tract of amphibians, reptiles, and mammals. Karatomorpha, Proteromonas.

- Opalinina Wenyon, 1926
  Multiflagellated cells with flagella originating from an anterior morphogenetic centre, the falx, and forming oblique longitudinal rows or files; microtubular ribbons supporting longitudinal pellicular ridges between flagellar rows; two to many monomorphic nuclei; life cycle, complex, with sexual processes induced by hormones of host and linked to the host’s life cycle; endobionts in amphibians and some fish; Cepedeia, Opalina, Protopolanina, Protozelleriella, Zelleriella.

  Biflagellate with or without tripartite mastigonemes; without plastids; phagotrophic with cytostome supported by broad microtubular rootlet No.2 of anterior flagellum; predominantly sedentary, often attach to substrate with posterior flagellum; with or without lorica, solitary, and colonial. Adriasmonas, Bicosoeca, Cafeteria, Cyathobodo, Pseudobodo, Pseudodendromonas, Siluania.

- Labyrinthulomyctetes Dick, 2001
  Production of an ectoplasmic network of branched, anastomosing, wall-less filaments via a specialized organelle.
known as the bothosome; Golgi-derived scales; biflagellate zoospores with lateral insertion in many species.

**Labyrinthulaceae Haacke, 1868**
Spindle-shaped vegetative cells distributed in an extensive ectoplasmic net; zoospores with eyespots; sexual reproduction. *Labyrinthula.*

**Thraustochytriaeae Sparrow, 1943**
Small ectoplasmic net; presence of interphase centrioles in vegetative cells; no sexual reproduction; no eyespots. *Aithornia, Aplanochytrium, Elnia, Japonochytrium, Schizochytrium, Thraustochytrium, Ulkenia.*

**Hyphochytriales Sparrow, 1960**
Single anteriorly directed flagellum. *Hyphochytrium.*

Flagella, one anteriorly directed and one posteriorly directed; zoospores with lateral insertion in many species. *Allothecia, Aplanochytrium, Elnia, Japonochytrium, Schizochytrium, Thraustochytrium, Ulkenia.*

**Actinophryidae Claus, 1874, emend. Hartmann, 1926**
Axonemal pseudopodia emerging from amorphous centrosome near nuclei; axonemal microtubules in double interlocking coils; single central nucleus or several peripheral nuclei; tubular cristae; two types of extrusomes for prey-capture along axopodia; cysts covered with siliceous nuclei; tubular cristae; two types of extrusomes for prey-some near nuclei; axonemal microtubules in double interlocking coils; single central nucleus or several peripheral nuclei; tubular cristae; two types of extrusomes for prey-capture along axopodia; cysts covered with siliceous nuclei; tubular cristae; two types of extrusomes for prey.

**Peronosporomyctes Dick, 2001** [Oomycetes Winter, 1897, emend. Dick, 1976] Haplomitic-B nuclear cycle; lysine synthesized via the DAP pathway; lanosterol directly from squalene oxide; zoospores biflagellate and heterokont but rarely uniflagellate; flagella anteriorly inserted; anteriorly directed flagellum shorter; transitional plate of kinetosome sitting above the plasma membrane with a central bead; kinetid base structure with six parts, including four roots; oogamous reproduction that results in the formation of thick-walled sexual spores known as oospores, due to contact between male and female gametangia; thallus mainly aseptate; cell wall of glucan-cellulose, may have minor amount of chitin. *Achiyla, Leptomitus, Peronospora, Pythiogenot, Rhizidium, Saprolegia.* Incertae sedis: *Ciliomyces, Cryptocola, Ectrogella, Eurycusma, Haptoglossa, Lagenia, Lagenisma, Myzocytiopsis, Olpidiopsis, Pontisma, Pythiola, Sirolpidium, Rozellosia.*

**Actinophryidae Claus, 1874, emend. Hartmann, 1926**
Axonemal pseudopodia emerging from amorphous centrosome near nuclei; axonemal microtubules in double interlocking coils; single central nucleus or several peripheral nuclei; tubular cristae; two types of extrusomes for prey-capture along axopodia; cysts covered with siliceous elements; autogamy reported within spores. *Actinophrys, Actinosphaerium.*

**Bolidomonas Guillou and Chrétiennot-Dinet, 1999** [Bolidomyctes Guillou et al., 1999]
Single genus of naked, unicellular flagellates; chloroplast with girdle lamellae; outer chloroplast endoplasmic reticulum membrane with direct membrane connection to the outer nuclear envelope membrane; plastid DNA with ring-type genophore; no eyespot; plastid pigments include chlorophylls $a$ and $c_1$, fucoxanthin, 19-hydroxyfucoxanthin, diatoxanthin, and diadinoxanthin; swimming cells with two flagella, one anteriorly directed and one posteriorly directed; no microtubular or fibrillar kinetosome roots; flagellar transitional helix absent; no paraflagellar rod. *Bolidomonas.*

**Chrysophyceae Pascher, 1914**
Predominately flagellates but also capsoid, coccoid, filamentous, and parenchymatous forms; cell coverings, when present, include organic scales, silica scales, organic loria, and cellulose wall; chloroplast with girdle lamellae; outer chloroplast endoplasmic reticulum membrane with direct membrane connection to the outer nuclear envelope membrane; plastid DNA with ring-type genophore; eyespots present or absent; plastid pigments include chlorophylls $a$ and $c_1$, fucoxanthin, 19-hydroxyfucoxanthin, and neoxanthin; swimming cells with two flagella, one anteriorly directed, one laterally directed; tripartite mastigonemes with short and long lateral hairs on the shaft; kinetosome usually four microtubular kinetosome roots and one large striated root (rhizoplast); flagellar transitional helix with 4–6 gyres located above the major transitional plate; no paraflagellar rod.

**Chromulinales Pascher, 1910**
Swimming cells with only one flagellum visible by light microscopy; four microtubular kinetosome roots. *Chromulina, Chrysomonas.*

**Hibberdia Andersen, 1989 [Hibberdiiales Andersen, 1989]**
Swimming cells with only one flagellum visible by light microscopy; three microtubular kinetosome roots. *Hibberdia.*

**Ochomonadinales Pascher, 1910**
Swimming cells with two flagella visible by light microscopy. *Ochromonas.*

**Dictyochophyceae Silva, 1980**
Single cells, colonial flagellates or amoebae; cells naked, with organic scales or with siliceous skeleton; chloroplasts, when present, with girdle lamellae; plastid DNA with scattered granule-type genophore; no eyespot; plastid pigments include chlorophylls $a$ and $c_1$, fucoxanthin, diatoxanthin, and diadinoxanthin; swimming cells usually with one flagellum, anteriorly directed and bearing tripartite tubular hairs; kinetosomes adpressed to nucleus; no microtubular or fibrillar kinetosome roots; flagellar transitional helix present or absent; when present, with 0–2 gyres located below the major transitional plate; paraflagellar rod present.

**Dictyochales Haacke, 1894**
Silica skeleton present on at least one life stage; with chloroplasts. *Dictyocha.*

**Pedinellales Zimmermann, Moestrup, and Höllfors, 1984**
Naked, organically scaled or loricate flagellates; with or without chloroplasts. *Actinomonas, Apedinella, Ciliophrys, Mesopedinella, Palatinella, Pedinella, Pseudopedinella, Pteridomonas.*

**Rhizochromulinales O’Kelly and Wujek, 1994**
Vegetative cells amoeboid; zoospore flagellated; with chloroplasts. *Rhizochromulina.*

**Eustigmatinales Hibberd, 1981**
Coccolid organisms, single cells or colonies; cell walls present; chloroplast without girdle lamellae; outer chloro-
plast endoplasmic reticulum membrane with direct membrane connection to the outer nuclear envelope membrane; plastid DNA with ring-type genophore; eyespot present but located outside of the chloroplast; plastid pigments include chlorophylls $a$ and $c_1$, violaxanthin, and fucoxanthin; swimming cells with two flagella, one anteriorly directed and one posteriorly directed; four microtubular kinetosome roots and one large striated kinetosome root (rhizoplast); flagellar transitional helix with six gyres located above the major transitional plate; no paraflagellar rod. Botryochloropsis, Eustigmatos, Monadopsis, Nanochloropsis, Pseudocharaciopsis, Vischeria.

- Pelagophyceae Andersen and Saunders, 1993 Flagellate, capsoid, coccolid, sarcinoid or filamentous; cells naked or with organic thecae or cell walls; chloroplasts with girdle lamella; plastid DNA with scattered granule-type genophore; no eyespot; plastid pigments include chlorophylls $a$ and $c_1, 2$, fucoxanthin, $19'$-hexanoyloxyfucoxanthin, $19'$-butanoyloxyfucoxanthin, diatoxanthin, and diadinoxanthin; swimming cells with one or two flagella; anteriorly directed flagellum bearing bipartite or tripartite tubular hairs, second flagellum, when present, directed posteriorly; kinetosomes adpressed to nucleus; no microtubular or fibrillar kinetosome roots on uniflagellate cells; four microtubular roots on biflagellate cells; flagellar transitional helix present or absent; when present, with two gyres located below the major transitional plate; paraflagellar rod present or absent.

- Pelagomonadales Andersen and Saunders, 1993 Flagellate or coccolid organisms; when flagellate, a single flagellum without a second kinetosome; no kinetosome roots. Aureococcus, Aureoumbra, Pelaogococcus, Pelagomonas.

- Sarcinochrysidales Gayral and Billard, 1977 Sarcinoid, capsoid, flagellate or filamentous; cells typically with organic cell wall; flagellate cells with two flagella and four microtubular kinetosome roots. Ankylochrisis, Nematochrysis, Pulvinaria, Sarcinochrysis.

- Phaeothamniophyceae Andersen and Bailey in Bailey et al., 1998 Filamentous, capsoid, palmelloid, or coccolid; cells covered with an entire or two-pieced cell wall; chloroplast with girdle lamella; chloroplast endoplasmic reticulum membrane with direct membrane connection to the outer nuclear envelope membrane; plastid DNA with ring-type genophore; eyespots present; plastid pigments include chlorophylls $a$ and $c$, fucoxanthin, heteroxanthin, diatoxanthin, and diadinoxanthin; swimming cells with two flagella, anteriorly directed flagellum bearing bipartite tubular hairs, posteriorly directed flagellum without tripartite hairs; four microtubular kinetosome roots but no striated kinetosome root (rhizoplast); flagellar transitional helix with 4–6 gyres located above the major transitional plate; no paraflagellar rod.


- Pleurochloridales Ettl, 1956 (R) Distinguished from the Phaeothamnionales based on molecular phylogenetic analyses. Pleurochloridella.

- Pinguiochrysidales Kawachi, Inouye, Honda, O’Kelly, Bailey, Bidigare, and Andersen, 2003 Flagellate or coccolid organisms; cells naked or enclosed in mineralized lorica; chloroplast with girdle lamella; outer chloroplast endoplasmic reticulum membrane with direct membrane connection to the outer nuclear envelope membrane; plastid DNA with scattered granule-type genophore; eyespots absent; plastid pigments include chlorophylls $a$ and $c_1, 2$, fucoxanthin, and violaxanthin; swimming cells with one or two flagella; tripartite hairs present or absent on immature flagellum; 3–4 microtubular kinetosome roots and one large striated kinetosome root (rhizoplast); flagellar transitional helix with two gyres located below the major transitional plate; no paraflagellar rod. Glossomastix, Phaeomonas, Pinguiochrysis, Pinguiooccus, Polypodochrysis.

- Raphidophyceae Chadeauf, 1950, emend. Silva, 1980 Naked flagellates; chloroplast with or without girdle lamella; outer chloroplast endoplasmic reticulum membrane with no (or very weak) direct membrane connection to the outer nuclear envelope membrane; plastid DNA with scattered granule-type genophore; eyespots absent; plastid pigments include chlorophylls $a$ and $c_1, 2$; carotenoid composition distinct between marine (M) and freshwater (FW) species—fucoxanthin (M), violaxanthin (M), heteroxanthin (FW), vaucherioxanthin (FW); swimming cells with two flagella, one anteriorly directed and bearing tripartite tubular hairs, one posteriorly directed and lacking tripartite hairs; microtubular kinetosome roots present but poorly characterized; one large striated kinetosome root (rhizoplast) present; flagellar transitional helix absent; no paraflagellar rod. Chatonella, Fibrocapsa, Goniosomum, Haramonas, Heterosigma, Merotricha, Olisthodiscus, Vacuolaria.

- Schizocladiales Kawai, Maeba, Sasaki, Okuda, and Henry, 2003 (M) Branched filamentous growth; cell wall with alginates but lacking cellulose and plasmodesmata; anterior flagellum with tripartite mastigonemes, and posterior flagellum without mastigonemata and a striated root; flagellar transitional helix with 5–6 gyres located above the transitional plate; microtubular and striated roots undescribed; chloroplast with girdle lamella; outer chloroplast endoplasmic reticulum membrane with direct membrane connection to the outer nuclear envelope membrane; plastid-DNA with ring-type genophore; eyespot present; plastid pigments incude chlorophylls $a$ and $c$ and fucoxanthin (HPLC data absent); storage product unknown. Schizocladia.

- Synurales Andersen, 1987 Predominately flagellates, benthic palmelloid colonies known; cells covered with bilaterally symmetrical silica scales; chloroplast with girdle lamella; chloroplast endoplasmic reticulum membrane with no (or very weak) direct membrane connection to the outer nuclear envelope membrane; plastid DNA with ring-type genophore; eyespots absent; plastid pigments include chlorophylls $a$ and $c_1$, fucoxanthin, violaxanthin, anthaxanthin, and neoxanthin; swimming cells usually with two anteriorly directed flagella, one bearing tripartite tubular hairs; tripartite hairs with short and long lateral hairs on the shaft; two microtubular kinetosome roots and one large striated kinetosome root (rhizoplast); flagellar transitional helix with 6–9 gyres located above the major transitional plate; no paraflagellar rod. Chrysododymus, Mallomonas, Symura, Tesselaria.
Xanthophyceae Allorge, 1930, emend. Fritsch, 1935 [Heterokontae Luther, 1899; Heteromoneada Leedale, 1983; Xanthophyta Hibberd, 1990]
Predominately coccoid or filamentous, rarely amoeboid, flagellate or capsid; cell walls (probably cellulose) typical, either entire or H-shaped bifurcational walls; chloroplast with girdle lamella; outer chloroplast endoplasmic reticulum membrane with direct membrane connection to the outer nuclear envelope membrane; plastid DNA with ring-type genophore; eyespots present or absent; plastid pigments include chlorophylls a and b, violaxanthin, xanthophylls, and violaxanthin; swimming cells with two flagella, one anteriorly directed and bearing tripartite hairs; four microtubular kinetosome roots and one large striated kinetosome root (rhzoplast); flagellar transitional helix with six apparently double gyres located above the major transitional plate; no parflagellar rod. Note 17.

Tricornata Pascher, 1939
Filamentous, coccoid, and capsid forms, sometimes becoming parenchymatous or multinucleate with age; elaborate reproductive structures lacking; cell walls, when present, either with H-shaped overlapping cell wall pieces or with complete or entire cell walls. Botrydiunm, Bumilleriopsis, Characteropis, Chloromonon, Heterococcus, Ophiocystium, Sphaerosorus, Trichonyma, Xanthomona.

Vaucheriella Bohlin, 1901
Siphonous filaments, with elaborate sexual reproductive structures (antheridia, oögonia). Vaucheria.

Phaeophyceae Hansgirg, 1886
Filamentous, syntagmatic or parenchymatous; cell wall present, containing alginic compounds and cellulose; plasmodesmata or pores between cells in parenchymatous forms; chloroplasts with girdle lamella; outer chloroplast endoplasmic reticulum membrane with direct membrane connection to the outer nuclear envelope membrane; plastid DNA with ring-type genophore; eyespots present or absent; plastid pigments include chlorophylls a and b, fucoxanthin, and violaxanthin; swimming cells with two flagella usually inserted laterally, one anteriorly directed, one posteriorly directed; usually four microtubular kinetosome roots but no striated kinetosome root (rhzoplast); flagellar transitional helix typically with 6 gyres located above the major transitional plate; no parflagellar rod; little to substantial tissue differentiation occurring in parenchymatous forms. Several subdivisions, separated on the basis of life history and gene sequence information, but taxonomic classification still in flux.

Ascocideriales Petrov, 1964
Sporophyte parenchymatous, with intercalary growth; several scattered discard plastids with no pyrenoid; heteromorphic life cycle; gametophyte not free living; isogamous sexual reproduction. Ascociera.

Cutleriella Bessey, 1907
Gametophyte (larger) and sporophyte parenchymatous; several scattered discard plastids with no pyrenoid; gametophyte with trichothallic growth, sporophyte with apical growth; heteromorphic life cycle; isogamous sexual reproduction. Cutleriella (P), Microzonia, Zanardiina.

Desmarestiales Setchell and Gardner, 1925
Gametophyte small and filamentous, sporophyte larger and pseudo-parenchymatous; several scattered disciod plastids with no pyrenoid; trichothallic growth; heteromorphic life cycle, oögamous sexual reproduction. Arthrocladia, Desmarestia (P), Himantothallus, Phaeurus.

Dictyotales Bory de Saint-Vincent, 1828
Gametophyte and sporophyte parenchymatous, with apical or marginal growth; several scattered disciod plastids and no pyrenoid; isomorphic life cycle; oögamous sexual reproduction. Dictyota, Dilophus, Lobophora, Padina, Stypopodium, Taonia, Zonaria.

Ectocarpales Bessey, 1907, emend. Silva and Reviers, 2000
Gametophyte and sporophyte uniseriate filaments (branched or unbranched), with diffuse growth; one or more ribbon-shaped plastids with pyrenoid; isomorphic life cycle; isogamous, anisogamous or oögamous sexual reproduction. Adencystis, Acinetospora, Chordaria, Ectocarpus, Cystoseirales Petrov, 1964
Siphonous filaments, with elaborate sexual reproduction. Vaucheria.

Ishige Yendo, 1907 [Ishigeeacea Okamura, 1935; Ishigeeales Cho, Lee, and Boo, 2004]
Isomorphic alternation of generations, with apical cell growth; scattered discard plastids and no pyrenoid; diploid life stage only, meiosis produces gametes; (mostly) oögamous sexual reproduction. Ascophyllum, Bifurcaria, Cystoseira, Dravilaea, Fucus, Hormosira, Sargassum, Turbinaria.

Ishige Yendo, 1907 [Ishigeeacea Okamura, 1935; Ishigeeales Cho, Lee, and Boo, 2004]
Isomorphic alternation of generations, with apical cell growth; scattered discard plastids and no pyrenoid; terminal unicellular sporangia, or uniseriate plurilocular sporangia; cortex pseudoparenchymatous with assimilatory filamentsphaeophycean hairs in cryptostigmata. Ishige.

Laminariales Migula, 1908
Gametophyte small and filamentous with apical growth; sporophyte large and parenchymatous, with intercalary growth; several scattered discard plastids with no pyrenoid; heteromorphic life cycle; oögamous sexual reproduction. (eggs sometimes flagellate). Akkessophyccus, Alaria, Chorda, Costaria, Laminaria, Lessonia, Pseudodocha.
single anterior flagellum with a 9+0 axoneme and mastigones; òøagous sexual reproduction. Bellota, Carpowithara, Nereia, Sporochonous, Tomaculopsis.

Syringodermatales Henry, 1984
Gametophyte 2–4 cells, sporophyte parenchymatous with apical and marginal growth; several scattered discoid plastids with no pyrenoid; heteromorphic alternation of generations; òøagous sexual reproduction. Syringodermatales Henry, 1984 [Diatomea Dumortier, 1821]

Tilopteridales Bessey, 1907
Isomorphic alternation of generations with polystichous construction of the thallus, which grows by a trichothallic meristem; several scattered plastids, without pyrenoids; òøagous sexual reproduction. Halosipon, Haplosopora, Phaeosiphoniella, Phyllaria Tilopteris.

Bacillariophyta Haeckel, 1878 [Diatomea Dumortier, 1821]
Vegetative cells cylindrical with a circular, elongate or multipolar cross section; lacking any trace of flagella, surrounded by a cell wall composed of tightly integrated silicified elements; cell wall comprised of two valves (at each end of the cell) and several girdle bands (hoops or segments covering the cylindrical “girdle” lying between the valves); chloroplasts usually present, bounded by four covering the cylindrical “girdle” lying between the valves); chloroplasts usually present, bounded by four membranes, and with lamellae of three thylakoids and a ring nucleoid (rarely multiple nucleoids); flagellate cells not free living; isogamous sexual reproduction. Syringoderma.

Coscinodiscophyta Medlin and Kaczmarska, 2004
Valve outline circular (rarely elliptical); valve pattern radiating from a central or subcentral circular annulus; rimoportulae usually present; girdle bands loop like or segmental; sexual reproduction òøagous, with non-motile eggs and unflagellate sperm; auxospore with scales but no rimoportulae present or absent; girdle bands usually hoop like; sexual reproduction òøagamous (with non-motile eggs and unflagellate sperm) or isogamous (gametes without flagella, amoeboïd); auxospore usually with band-like elements (perizonium or properizonium); chloroplasts many, few or one.

Mediophyceae Jousse and Proshkina-Lavenko in Medlin and Kaczmarska, 2004 (P)
Valve outline bipolar or multipolar, sometimes circular; valve pattern radiating from a central circular or elongate annulus or from a sternum; areas of special pores or slits often present, involved in mucilage secretion; rimoportulae present or absent; girdle bands usually hoop like; sexual reproduction òøagamous; auxospore with band-like elements (properizonium) or scales; chloroplasts usually many, small. Chaetoceros, Cymatodes, Ditylum, Odontella, Skeletonema, Thalassiosira.

Bacillariophyceae Haeckel, 1878
Valve outline almost always bipolar; valve pattern organized bilaterally about an elongate axial rib (sternum), as in a feather; rimoportulae generally only one or two per valve or none, sometimes accompanied or (?) replaced by special slits (the “raphe”) involved in motility; sexual reproduction morphologically isogamous (although sometimes with behavioural differentiation), involving gametangiogamy; auxospores usually with band-like elements in two series (transverse and longitudinal), forming a ’perizonium’; chloroplasts usually only 1, 2 or a few and large, but sometimes many and small. Asterotheca, Eunotia, Navicula, Nitzschia, Raphoneis.

Alveoluta Cavalier-Smith, 1991
Cortical alveolae; alveolae sometimes secondarily lost; with ciliary pit or micro pore; cristae tubular or ampulliform.

Dinozoa Cavalier-Smith, 1981, emend. Cavalier-Smith and Chao, 2004
Usually with extranuclear spindle within cytoplasmic channels through nucleus; cortical alveoli typically discrete and
inflated; often with bipartite trichocysts with a dense square-sectioned basal rod and twisted hollow trichocyst filaments.

  Cells with two flagella in the motile stage, one transverse and one longitudinal; typically, transverse flagellum ribbon like, with multiple waves beating to the cell’s left, and longitudinal flagellum beating posteriorly, with only one or few waves; typically with dinokaryotic nucleus that lacks histones, and chromosomes remain condensed during interphase.

- Dinophyceae Pascher, 1914
  With a dinokaryon through the entire life cycle; cell cortex (amphiesma) containing alveolae (amphiesmal vesicles) that may or may not contain cellulosic thecal plates, the pattern thus formed (i.e., tabulation) being a crucial morphological criterion in recognizing affinities among dinophyceans.

- Gymnodiniphycidae Fensome et al., 1993
  With numerous amphiesmal vesicles, arranged non-serially or in more than six latitudinal series or with the pellicle as the principal amphiesmal element or the amphiesmal structure uncertain but not comprising a theca divisible into six or fewer latitudinal plates. Amphidinium, Gymnodinium, Ptychodiscus, Symbiodinium, Woloszynskia

- Peridiniphycidae Fensome et al., 1993
  With a tabulation that accord with, or derives from, a pattern in which there are five or six latitudinal plate series; sagittal suture lacking. Alexandrium, Amphidinopsis, Amphidinium, Blepharocysta, Ceratium, Crypthecodinium, Gonyaulax, Heterocapsa, Peridinella, Peridinium, Pfiesteria, Pyrocystis

- Dinophysiphyceidae Möhn, 1984, emend. Fensome et al., 1993
  With a cingulum, sulcus, and sagittal suture. Fossil taxa. Dinophysis, Triposolenia

- Prorocentrales Lemmermann, 1910 [Prorocentrophyceidae Fensome et al., 1993]
  Without cingulum or sulcus; flagella apical, one wavy and one not; wavy flagellum clearly homologous with transverse flagellum of other dinoflagellates; thecal plates. Fossils unknown. Proprorocentrum

- Phytodiniales Christensen, 1962, emend. Loeblich, 1970
  Principal life cycle stage a non-calcareous coccoid stage (vegetative cyst) or continuous-walled multicellular stage or an amoeboid stage present in a life cycle that also includes a coccoid stage. Fossils unknown. Dinothrix, Hemedinium.

- Blastodiniales Chatton, 1906 [Blastodiniphyceae Fensome et al., 1993]
  Parasitic with dinokaryon during part of life cycle only; not highly vacuolated. Fossils unknown. Crepidodinium, Dissodinium.

- Noctilucales Haacke, 1894 [Noctiluciphycaceae Fensome et al., 1993]
  Dinokaryon during part of life cycle only; principal life cycle stage comprising a large free-living motile cell inflated by vacuoles. Fossils unknown. Kofoedium, Noctiluca.

- Syndiniiales Loeblich III, 1976
  With motile cells (i.e., dinospores or gametes) with a dinokont arrangement of flagella, and in which the nucleus possesses histones. Amoebophrya, Duboscquellea, Merodinium, Syndinium.

- Oxyrrhineaceae Sournia, 1984
  Without true cingulum and sulcus; intranuclear mitotic spindle; with amphiesmal vesicles and trichocysts; flagella inserted laterally. Oxyrrhis.

- Perkinsiidae Levine, 1978, emend. Adl et al., 2005
  Trophozoites parasitic, dividing by successive binary fissions; released trophozoites (termed hypnospores) developing outside host to form zoospores via the formation of zoosporangia or morphologically undifferentiated mononucleate cells via a hypha-like tube; zoospores with two flagella; apical organelles including an incomplete conoid (open along one side), rhoptries, micronemes, and micropropores, and a microtubular cytoskeleton with both an anterior and posterior polar ring. Parvilucifera, Perkinsus.

- Apicomplexa Levine, 1980, emend. Adl et al., 2005
  At least one stage of the life cycle with flattened subpellicular vesicles and an apical complex consisting of one or more polar rings, rhoptries, micronemes, conoid, and subpellicular microtubules; sexuality, where known, by synogamy followed by immediate meiosis to produce haploid progeny; asexual reproduction of haploid stages occurring by binary fission, endodyogeny, endopolyogeny, and/or schizogony; locomotion by gliding, body flexion, longitudinal ridges, and/or flagella. All parasitic except Colpodellida.

- Colpodellida Cavalier-Smith, 1993, emend. Adl et al., 2005
  Predatory flagellates on other protists; apical complex and rostrum; two flagella in known species; tubular cristae; microtubules beneath alveolae; micropore; cysts at least in some species. Alphanomonas, Colpodella, Voromonas.

- Aconoidasida Mehlhorn, Peters, and Haberkorn, 1980 (P)
  Incomplete apical complex (conoid not present) in asexual motile stages; some diploid motile zygotes (ōokinete) with conoid; macrogametes and microgametes forming independently; heteroxenous.

- Haemopspororida Danilewsky, 1885
  Zygote motile (ōokinese) with conoid; flagellated microgametes produced by schizogonous process; ōocyst formed in which sporozoites develop. Mesnilium, Plasmodium.

- Pirolaspororida Wenyon, 1926
  Piriform, round, rod shaped or amoeboid; conoid and flagella absent in all stages; without ōocyst; probably sexuality associated with the formation of large axopodium-like “Strahlen”. Babesia, Theileria.
Conoidasida Levine, 1988 (P)
Complete apical complex, including a conoid in all or most asexual motile stages; flagella, where present, found exclusively in microgametes (male gametes); with the exception of microgametes, motility generally via gliding with possibility of body flexion and undulation of longitudinal pellicular ridges; heteroxenous or homoxenous. This group is not monophyletic. Subdivisions are artificial and unclear at this time.

Cocciadinia Leuckart, 1879 (P)
Mature gametes develop intracellularly; microgamont typically produces numerous microgametes; syzygy absent; zygote rarely motile; sporocysts usually formed within oöcysts. Cryptosporidium, Cyclospora, Eimeria, Hepatozoon.

Gregarinina Dufour, 1828 (P)
Mature gamonts usually develop extracellularly; syzygy of gamonts generally occurring with production of gametocyst; similar numbers of microgametes and microgamonts maturing from paired gamonts in syzygy within the gametocyst; synangy of mature gametes leading to gametocyst that contains few to many oöcysts, each which contains sporozoites; sporocysts absent; asexual replication (merogony) absent in some species. Acuta, Cephalolobus, Gregarina, Levinea, Menospora, Nematocystis, Nematothrix, Steinina, Trichorhynchus.

Ciliophora Doflein, 1901 [Ciliata Perty, 1852, Infusoria Bütschli, 1887]
Cells with nuclear dimorphism, including a typically poly- genomic macronucleus and at least one diploid micronucleus; somatic kinetids having a postciliary microtubular ribbon arising from triplet 9, a kinetodesmal fibril or striated rootlet homologue arising near triplets 5–8, and a transverse ribbon arising from triplet 9, a kinetodesmal fibril or striated nucleus; somatic kineties having a postciliary microtubular genombic macronucleus and at least one diploid micrornuclei with paradiploid macronuclei surrounding one or more micronuclei; each macronucleus possibly organized as a single composite chromosome. Protocruzia.

Postciliodesmatophora Gerassimova and Seravin, 1976
Somatic dikinetids with postciliodesmata, an arrangement of laterally overlapping postciliary microtubular ribbons associated with somatic dikinetids.

Karyorelictea Corliss, 1974
Two to many macronuclei containing approximately, sometimes slightly more than, the diploid amount of DNA; macronuclei not dividing but replaced at cell division by division of micronuclei; major postciliary ribbons separated by two groups of microtubules. Kentrophoros, Losodes, Trachelocerca.

Heterotrichia Stein, 1859
Polygenomic macronucleus dividing by extra-macronuclear microtubules; major postciliary ribbons separated by one microtubule. Blepharisma, Clima- costomum, Folliculina, Stentor.

Intramacronucleata Lynn, 1996
Polygenomic macronucleus dividing by intramacronuclear microtubules.

Spirotrichea Bütschli, 1889 (R)
Conspicuous right and left oral and/or pre-oral cilia- ture; left serial oral polykinetids leading, usually clock- wise into the oral cavity, either around a broad anterior end or along anterior and left margins of the body; DNA replication in the macronucleus accomplished by a complicated migrating structure called a replication band in all but Protocruzia and Phacodinium.

Protocruzia Faria da Cunha and Pinto, 1922
[Protocruzia de Puytorac et al., 1987] (M) Nuclear apparatus a cluster of similar-sized nuclei with paradiploid macronuclei surrounding one or more micronuclei; each macronucleus possibly organized as a single composite chromosome. Protocruzia.

Phacodinium Prowazek, 1900 [Phacodiniidida Small and Lynn, 1985] (M) Somatic kinetics of linear polykinetids; each kinetosome bearing a kinetodesmal fibril, and sometimes accompanied by a partner kinetosome in some regions of the body, thus resembling a cirrus. Phacodinium.

Licnophora Claparède, 1867 [Licnophoria Cor- liss, 1957] (M) Body hour-glass shaped, both ends discoid; posterior disc adhesive, with peripheral rings of cilia; an anterior disc with serial oral polykinetids around oral region; ectosymbionts, temporarily attached to substrate or host by ciliated, mobile, posterior adhesive disc. Licnophora.

Hypotrichia Stein, 1859
Ventral ciliature as cirri and dorsal ciliature as somatic dikinetids with a kinetodesmal fibril; during morphogenetic processes, only the ventral somatic infraciliature either turned over or replaced. Aspidiscus, Discoccephalus, Euplotes.

Oligotrichia Bütschli, 1887
Oral polykinetids forming an open circle, typically with an anterior "collar" and a more ventral "lapel"; somatic kinetics reduced in number and variable in pattern, forming bristles, girdles, and spirals. Cryostrombidium, Laboea, Strombidium.

Choreotrichia Small and Lynn, 1985
Oral polykinetids forming a closed circle around the anterior end of the body, several often extending into the oral cavity; planktonic tint- innids are all loricate. Codonella, Favella, Strombidinopsis, Strobilidium, Tintinopsis.

Stichotrichia Small and Lynn, 1985
Ventral ciliature as cirri and dorsal ciliature as somatic dikinetids without a kinetodesmal fibril; during morphogenetic processes, entire ventral and dorsal somatic infraciliature turned over or replaced. Halleria, Oxytricha, Stylonychia.

Armophorea Jankowski, 1964 (R)
Typically dependent upon methanogenic endosymbionts, suggesting that hydrogenases within
this group may be monophyletic; at present, only established on similarities in nuclear and hydrogenosomal gene sequences for several included genera.

Armophorida Jankowksi, 1964
Body usually twisted to left, often much so; oral region spiralled, with series of 3–5 perialoral or perizonal somatic kineties along its edge. *Caenomorpha*, *Metopus*.

Clevelandellida de Puytorac and Grain, 1976
Oral polykinetids with a fourth row of kinetosomes directly opposite those of the third, leading to their designation as hetero-membranelles. *Clevelandella*, *Nyctotherus*, *Paracichlidotherus*.

Odontostomatida Sawaya, 1940
Small body usually laterally compressed, often bearing spines; somatic kineties typically of dikinetids, sometimes separated into anterior and posterior segments; oral cilia inconspicuous, usually <10 oral polykinetids. *Discomorphella*, *Epalsella*.

Litostomatea Small and Lynn, 1981
Somatic monokinetics with two transverse ribbons, a slightly convergent postciliary ribbon, and a laterally directed kinetodesmal fibril that does not overlap those of adjacent kineties; one transverse ribbon tangential to the kinetosome perimeter and extending anteriorly into the somatic ridge to the left of the kinetid while the other transverse ribbon is radial to the kinetosome perimeter and extending transversely into the adjacent somatic ridge.

Haptoria Corliss, 1974
Toxicysts typically between transverse microtubules of oral dikinetids; oral region on body surface bordered by oral dikinetids; typically free-living predators of other protists, both ciliates and flagellates. *Didinium*, *Dileptus*, *Lacrymaria*, *Lagynophrya*.

Trichostomatia Bütschli, 1889
Toxicysts absent; oral region or oral cavity densely ciliated, sometimes organized as “polylekintids”; typically endosymbionts in vertebrates. *Balantidium*, *Entodinium*, *Isotricha*, *Macropodinium*, *Ophryoscolex*.

Phyllopharyngia de Puytorac et al., 1974
The ciliated stage with somatic kineties mostly as monokinetics that each have a lateral kinetodesmal fibril, a reduced (or absent) transverse microtubular ribbon (usually accompanied by a left-directed transverse fibre), and a somewhat convergent postciliary ribbon extending posteriorly to accompany ribbons of more anterior monokinetics; ribbon-like subkinetal nematodesmata arising from somatic monokinetics and extending, either anteriorly or posteriorly, beneath kineties as subkinetal ribbons; oral region with radially arranged microtubular ribbons, called phyllae.

Phyllopharyngia de Puytorac et al., 1974
Oral ciliature typically composed of one preoral kinety and two circumoral kineties; true cytosome and cytopharynx surrounded by phyllae and rod-shaped nematodesmata; macronucleus heteromeroerous. *Brooklynella*, *Chidonella*.

Chonotrichia Wallengren, 1895
Sedentary and sessile forms with somatic cilia only on walls of perioral funnel or cone-shaped region, which may be flared or compressed; oral cilia absent or only as several inverted kineties next to cytosome; cytopharyngeal apparatus with phyllae, but no nematodesmata; macronucleus, heteromeroerous; unequal cell division typical, producing “bud” for dispersal; most species are ecytosymbionts on crustacean appendages. *Chilodocha, Spirochina*, *Vasichona*.

Rhynchodia Chatton and Lwoff, 1939
Oral apparatus a suctorial tube supported by radially arranged microtubular ribbons (= phyllae) enclosing toxic (?) extrusomes as haptotrichocysts; predators of other ciliates or endosymbiotic parasites of bivalve molluscs and other marine invertebrates. *Ignotocoma*, *Sphenophrya*.

Suctoria Claparède and Lachmann, 1858
Mature sessile trophonts, usually non-ciliated, with one to many tentacles that ingest prey; extrusomes at tentacle tips as haptocysts; tentacles supported by an outer ring of microtubules and an inner set of microtubular ribbons (= phyllae); unequal cell division typical with ciliated, migratory dispersal “larvae” or swarmers typically bearing neither tentacles nor stalk. *Actineta*, *Discophrya*, *Ephelota*, *Tokophrya*.

Nassophorea Small and Lynn, 1981
Somatic cilia as monokinetics and dikinetids; monokinetid with an anterior, tangential transverse ribbon, a divergent postciliary ribbon, and anteriorly directed kinetodesmal fibril; somatic alveoli well developed with paired alveolocysts sometimes present; oral nematodesmata are well developed as the cytos in several groups. *Microthorax*, *Nassula*, *Pseudomicrothorax*.

Colpodea Small and Lynn, 1981
Ciliated somatic dikinetids with one transverse ribbon and at least one postciliary microtubule associated with the anterior kinetosome and one transverse ribbon, one postciliary ribbon, and one kinetodesmal fibril associated with the posterior kinetosome; posterior transverse ribbons extending posteriorly and overlapping one another, the so-called transversodesmata. *Barsaria*, *Colpoda*, *Pseudoplatyophrya*, *Woodruffia*.

Prostomatea Schewiakoff, 1896
Oral dikinetids, radial to tangential to perimeter of oral area with postciliary microtubular ribbons that extend laterally from each dikinetid, overlapping one another, and, in some species, forming a circular microtubular band that supports the wall of a shallow pre-cytosomal cavity; associated oral ciliature as two or more assemblages of dikinetids, often called a “brush”. *Coleps*, *Cryptocaryon*, *Holophrya*, *Prorodon*, *Urotricha*.
Plagiopylea Small and Lynn, 1985 (R)
Somatic monokinetid with divergent postciliary microtubular ribbon, well-developed anterior-directed kinetodesmal fibril and a transverse ribbon extending laterally or anteriorly; cytoplasm typically containing conspicuous “sandwich” assemblages of methanogens and ciliate hydrogenosomes. Lechtiopyla, Plagiopyla, Sonderia, Trimyema.

Oligohymenophorea de Puytorac et al., 1974
Oral apparatus with a distinct right paroral dikinetid and typically three left oral polykinetids, residing in a ventral oral cavity or deeper infundibulum (secondarily lost (?) in Astomatia and some astomatous Hymenostomatia); somatic monokinetids with anteriorly directed overlapping kinetodesmal fibrils, divergent postciliary ribbons, and radial transverse ribbons (except in Penicilia).

Peniculia Fauré-Fremiet in Corliss, 1956
Somatic kinetids with tangential transverse ribbons; cortical alveoli lie between kinetosomal rows of oral polykinetids; extrusome as typical fibrous trichocyst. Frontonia, Paramecium, Stokesia.

Scuticciatula Small, 1967
Paroral dikinetid with a, b, and c segments; stomatogenesis by proliferation of kinetosomes from the c segment or a “scutico”-vestige posterior to a and b segments, with varying involvement of kinetosomes in the a and b segments. Anophryoides, Cyclidium, Philasterides, Pleuronema.

Hymenostomatia Delage and Hérouard, 1896
Stomatogenesis by proliferation of kinetosomes typically in the mid-ventral region of the cell body, posterior to and some distance from the parental oral apparatus. Colpidium, Glaucoma, Ichthyophthirius, Stokesia.

Apostomatia Chatton and Lwoff, 1928
Ciliates with a polymorphic life cycle; usually as epibionts of marine Crustacea; novel cortical structures including a “rosette” organelle and the x, y, and z kineties. Foettingeria, Gymnodinioides, Hyalophyxa.

Peritrichia Stein, 1859
Body divided into three major areas: (1) oral, with a prominent peristome bordered by a dikinetid file (haplokinety) and an oral polykinetid that both originate in an oral cavity (infundibulum) at the base of which is the cytosome; (2) aboral, including kinetosomes as part of the scopula, which secretes the stalk of sessile species; and (3) telotroch band, permanently ciliated on mobile species. Carchesium, Epistyliis, Vorticella, Zoothamnium.

Astomatia Schewiakoff, 1896
Without cytostome; symbionts typically found in the digestive tract of annelids, especially oligochaetes; cortical cytoskeleton in the anterior region may be conspicuously developed as an attachment structure(s). Anoplophrya, Haplophrya.

Incercatae sedis Alveolata: Colponema, Ellobiopsidae.

EXCAVATA Cavalier-Smith, 2002, emend. Simpson, 2003 (P?)
Typically with suspension-feeding groove (cytopharynx) of the “excavate” type (i.e. homologous to that in Jakoba libera); presumed to be secondarily lost in many taxa; feeding groove used for capture and ingestion of small particles from feeding current generated by a posteriorly directed flagellum (F1), right margin and floor of groove are supported by parts of the R1 microtubular root, usually also supported by non-microtubular fibres (B fibre, composite fibre), and the left margin by the R2 microtubular root and C fibre. Note 19.

Fornicata Simpson, 2003
Lacking typical mitochondria; with single kinetid and nucleus, or one pair each of kinetids and nuclei; two to four kinetosomes per kinetid; usually with a feeding groove or cytopharyngeal tube associated with each kinetid. Apomorphy: “B fibre” origin against R2 microtubular root.

Eohaplophryia Cavalier-Smith, 1993
Single kinetid and nucleus, or one pair each of kinetids and nuclei; usually with four kinetosomes and flagella per kinetid (occasionally three or two); usually with feeding grooves or cytopharyngeal tubes; mitochondrial homologues and dyctyosomes inconspicuous/transition.

Diplomonadida Wenyon, 1926, emend. Brugerolle et al., 1975
With a pair of kinetids and two nuclei, each kinetid usually with four kinetosomes and flagella (sometimes three or two), uncommonly, one kinetid and nucleus; at least one flagellum per kinetid directed posteriorly, associated with a cytopharyngeal tube or groove, or lying axially within the cell; various non-microtubular fibres supporting the nucleus and cytopharyngeal apparatus; free-living or endobiotic, often parasitic. Apomorphy: diplomonad cell organisation.

Hexamitinae Kent, 1880, emend. Brugerolle et al., 1975
With functional feeding apparatuses; with an alternate genetic code (TAR codon for Glutamine). Hexamita, Spirotrichida, Trepomonas.

Giardiinae Kulda and Nohynkova, 1978
Without functional feeding apparatuses; one posteriorly directed flagellum from each kinetid (F1?) running through the length of the cell axially and intra-cytoplasmic; all endobiotic. Giardia, Octonitus.

Incercatae sedis Diplomonadida: Enteromonadida Brugerolle, 1975
Traditionally considered ancestral to or a sister group of other diplomonads, now suspected to fall within Hexamitinae, but probably polyphyletic. Caviomonas, Enteromonas, Trimitus.

Retortamonadida Grassé, 1952
Single flagellar apparatus with four kinetosomes and either two (Retortamonas) or four (Chilomonas) emergent flagella; one flagellum has 2–3 vanes and runs posteriorly,
associated with a conspicuous ventral feeding groove with discrete posterior cytosome; cell surface underlain by a corset of microtubules; internal mitotic spindle partially described; all endobiotic, except one free-living species. Apomorphy: “lapel” structure—an electron dense sheet supporting the anterior origin of the peripheral microtubules. *Chilomastix, Retortamonas.*

- **Carpediemonas** Ekebom, Patterson, and Vors, 1996 (M)
  Biflagellated free-living cells with broad ventral suspension-feeding groove, in which beats the longer posterior flagellum; in *Carpediemonas membranifera* the posterior flagellum bears three vanes; kinetid with three kinetosomes; a dictyosome; conspicuous acristate presumptive mitochondrial homologence. *Carpediemonas.*

- **Malawimonas** O’Kelly and Nerad, 1999 (M)
  Similar to *Carpediemonas* but not specifically related in molecular phylogenies; the one studied isolate (*Malawimonas jakobiformis*), with mitochondrion, two kinetosomes, a single ventral flagellar vane. *Malawimonas.*

- **Parabasalia** Honigberg, 1973
  Cells with a parabasal apparatus; two or more striated parabasal fibres connecting the Golgi-dictyosomes to the flagellar apparatus; kinetid generally with four flagella/kinetosomes, but frequently with additional flagella (one to thousands); one kinetosome bears sigmoid fibres that connect to a pelta–axostyle complex; reduction or loss of the flagellar apparatus in some taxa, or multiplication of all, or parts, of the flagellar apparatus in several taxa; closed mitosis with an external spindle; mitochondrial division. *Parabasalia.*

- **Trichomonadida** Kirby, 1947, emend. Brugerolle and Patterson, 2001 (P)
  Kinetid of 3–5 anterior kinetosomes and one posterior kinetosome, almost always bearing flagella, and with a conspicuous pelta–axostyle complex (exceptions *Dientamoeba, Histomonas*); recurrent flagellum often associated with a lamellar undulating membrane underlain by a striated costal fibre; almost certainly paraphyletic. *Cochlosoma, Dientamoeba, Monocercomonas, Pentatrichomonoides, Pseudotrichomonas, Trichomitus, Trichomonas, Tririchomonas.*

- **Cristomonadida** Brugerolle and Patterson, 2001
  Parasaladis with a “crista” (crest) consisting of four privileged kinetosomes/flagella, and, often hundreds or thousands of additional flagella; all kinetosomes except the privileged are discarded at division; neither undulating membrane nor elongate costa, but one flagellum sometimes associated with a shorter “cresta” (Devescovinidae); pelta–axostyle system with one or several spiralled rows of microtubules in the axostylar trunk; parabasal apparatus with at least two main branches that may further subdivide; occasionally with multiple tetraflagellated karyomastigonts. *Calonympha, Corononympha, Deltotrichonympha, Devescovina, Foaina, Joenia, Kofoidia, Lophomonas, Rhizonympha.*

- **Spirotrichonymphida** Light, 1927
  Parasaladis with two or more spiralled rows of linked flagellated kinetosomes; each row associated with a parabasal fibre, and beginning with a privileged kinetosome bearing sigmoid fibres connected to the anterior pelta–axostyle complex; axostyle simple or multiple, absent in some; at mitosis spindle paradesmosis arising between two kinetosome rows, with half the rows going to each daughter cell. Known from hindgut of lower termites. *Holomastigotes, Holomastigotoides, Microjoenia, Spiromonas, Spirotrichonympha.*

- **Trichonymphida** Poche, 1913
  Parasaladis with a rostrum composed of two juxtaposed hemi-rostra associated in bilateral symmetry or with a superimposed tetraradiate symmetry; each hemi-rostrum with a privileged kinetosome bearing sigmoid fibres and a flagellar area with hundreds to thousands kinetosomes associated with multibranched parabasal apparatuses; pelta–axostyle complex originating at the top of the rostrum; at division, one parent hemi-rostrum going to each daughter cell; all living in the hindguts of lower termites or *Cryptocercus.* *Barbulanymphe, Eucomonympha, Hoplonympha, Spirotrichosoma, Staurojoenia, Teranympha, Trichonympha.*

- **Preaxostyla** Simpson, 2003
  Heterotrophic unicells with four flagella and kinetosomes per kinetid; lacking mitochondria. Apomorphy: “I fibre” with “preaxostylar” substructure (the oxymonad preaxostyle is homologous to the R1 root and I fibre of *Trimastix*).

- **Oxyonadida** Grassé, 1952
  Single kinetid (occasionally multiple kinetids) consisting of two pairs of flagellated kinetosomes distantly separated by a pre-axostyle (microtubular root, R1, with paracrystalline lamina), from which arises a microtubular axostyle, which is contractile or motile in some taxa; microtubular pelta usually present; many taxa attach to host using an anterior holdfast; closed mitosis with internal spindle; gut endosymbionts, mostly in lower termites and *Cryptocercus.* Apomorphy: axostyle (non-homologous with that of Parabasalia). *Dienonympha, Monocercomonoides, Oxyononas, Polytaenella, Pyrsonympha, Saccinobaculus, Sirebliomastix.*

- **Trimastix** Kent 1880 (M)
  Free-living quadriflagellate bearing a broad ventral feeding groove, in which beats the posteriorly directed flagellum; posterior flagellum with two broad vanes; small dense organelles in place of mitochondria. *Trimastix.*

- **Jakobida** Cavalier-Smith, 1993, emend. Adl et al., 2005
  Two flagella at the head of a broad ventral feeding groove, in which beats the posterior flagellum; posterior flagellum with a single dorsal vane (distinctive among excavates but possibly plesiomorphic).

- **Jakoba** Patterson, 1990
  Free-swimming cells, attaching temporarily to surfaces by the distal portion of the anterior flagellum; flat cristae. *Jakoba.*

- **Histionidae** Flavin and Nerad, 1993

- **Incertae sedis** Jacobida: “*Seculamonas*” (not formally described).
- Heterolobosea Page and Blanton, 1985
  Heterotrophic amoebae with eruptive pseudopodia; amoeboid morphology usually dominant; some with flagellate form, usually with two or four parallel flagella, one genus, an obligate flagellate; flagellate form rarely capable of feeding or using a groove-like cytostome; closed mitosis with internal spindle; cristae flattened, often discoidal; discrete dictyosomes not observed. Apomorphy: eruptive pseudopodia, not homologous to that in Amoebozoa.

- Vahlkampfiidae Jollos, 1917 (P)
  Nucleolus persists through mitosis; single nucleus; one genus an obligate amoeba, another genus, an obligate flagellate; cysts common. Heteramoeba. Naegeieria, Percolomonas, Psalteriomonas, Tetramitus, Vahlkampfia.

- Gruberellidae Page and Blanton, 1985
  Nucleolus fragments during mitosis; uninucleate or multinucleate; flagellate form observed in unidentified species of Stachyamoeba. Gruberella, Stachyamoeba.

- Acraсидae Poche, 1913
  Amoebae aggregate to form fruiting bodies; nucleus may or may not fragment. Apomorphy: formation of fruiting bodies. Acrasis, Pocheina.


  Cells with two (occasionally one, rarely more) flagella, inserted into an apical/subapical flagellar pocket; with rare exceptions, emergent flagella with paraxonemal rods; usually with tubular feeding apparatus associated with flagellar apparatus; basic flagellar apparatus pattern consisting of two functional kinetosomes and three asymmetrically arranged microtubular roots; mostly with discoidal cristae. Apomorphy: Heteromorphic paraxonemal rods (tubular/whorled in anterior flagellum F2, parallel lattice in posterior flagellum F1).

- Euglenida Bütschli, 1884, emend. Simpson 1997
  With a pellicle of proteinaceous strips, fused in some taxa; with unfused strips capable of active distortion (metaboly); where known, paramylon is the carbohydrate store. Apomorphy: Pellicle of protein strips. Note 20.

- Heteronematina Leedale, 1967 (P)
  With ingestion apparatus capable of phagotrophy; lacking plastids; most glide on surfaces; a paraphyletic assemblage from which Euglena and Aphaeaea are independently descended. Dinema, Entostiphon, Peranema, Petalomonas, Plocoeia.

- Euglenaceae Bütschli, 1884, emend. Busse and Preisfeld, 2002
  Phototrophic with plastids of secondary origin; some taxa secondarily osmotrophic; most swim. Apomorphy: plastid. Euglena, Eutreptia, Phacus, Trachelomonas.

- Aphaeaea Cavalier-Smith, 1993, emend. Busse and Preisfeld, 2002
  Osmotrophic euglenids lacking photosensory apparatus and plastids; one or two emergent flagella; no ingestion apparatus. Distigma, Rhabdomonas.

  Heterotrophic cells exhibiting pronounced metaboly; in trophic phase flagella are short and lack paraxonemal rods; sometimes with dispersal phase with longer paraxonemal rod-bearing flagella; apical papilla, feeding apparatus with "pseudovanes"; giant, flattened cristae. Apomorphy: Paraxonemal rods absent in trophic phase, homologous to that in Diplonema ambulator Larsen and Patterson 1990. Diplonema, Rhynchospora.

- Kinetoplastida Honigberg, 1963
  Euglenozoa with a kinetoplast, which is a large mass (or masses) of fibrillar DNA (kDNA) in the mitochondrion, often in close association with the flagellar bases. Apomorphy: kinetoplast.

- Prokinetoplastina Vickerman in Moreira, Lopez-Garcia, and Vickerman, 2004 (R)
  Ichthyobodo are ectoparasites of fish. Perkinisella is an endosymbiont ("parasome") of certain amoebae. Ichthyobodo, Perkinisella.

- Metakinetoplastina Vickerman in Moreira, Lopez-Garcia, and Vickerman, 2004 (R)
  Group identified by SSU rRNA phylogenies. With a node-based definition: The clade stemming from the most recent common ancestor of Bodo, Cryptobia, Crithidia, Dimastigella, Leishmania, Procryptobia, Rhynchobodo, Trypanoplasma, Trypanosoma.

- Neobodonida Vickerman in Moreira, Lopez-Garcia, and Vickerman 2004 (R)
  Eu- or polykinetoplastic kDNA not in network; biflagellate, without conspicuous mastigonemes; posterior flagellum attached or free; phagotrophic or osmotrophic; prefagellar rostrum containing apical cytosome. Node: Cruzella, Dimastigella, Neobodo, Rhynchobodo, Rhynchosomas.

- Parabodoniida Vickerman in Moreira, Lopez-Garcia, and Vickerman 2004 (R)
  Eu- or pankinetoplastic kDNA not in network; biflagellate, without mastigonemes; posterior flagellum attached or free; phagotrophic or osmotrophic; cytosome, when present, anterolateral; free-living or commensal/parasitic. Node: Cryptobia, Parabodo, Procryptobia, Trypanoplasma.

- Eubodonida Vickerman in Moreira, Lopez-Garcia, and Vickerman, 2004 (R)
  Eukinetoplast with kDNA not in network; biflagellate, without mastigonemes; anterior flagellum attached or free; phagotrophic or osmotrophic; anterolateral cytosome surrounded by lappets; free living. Bodo.

- Trypanosomatida Kent, 1880, emend. Vickerman in Moreira, Lopez-Garcia, and Vickerman, 2004
  Eukinetoplastic with kDNA network; uniflagellate with flagellum lacking mastigonemes and emerging from anterior pocket, or emerging laterally and attached to body; phagotrophic or osmotrophic; cytosome, when present, simple and close to flagellar pocket; exclusively parasitic. Node: Blastocrithidia, Crithidia, Endotrypanum, Herpetomonas, Leishmania, Leptomonas, Phytomonas, Rhyynchodinoma, Sauroleishmania, Trypanosoma, Wallaceina.
Ancyromonas Kent, 1880
Centrohelida Kühn, 1926
Apusomonadidae Karpov and Mylnikov, 1989

Ancyromonas

Benthic gliding cells with two unequal flagella; apical anterior flagellum may be very thin or absent; posterior flagellum inserted ventrally/laterally; anterior region forms lateral “snout” containing extrusomes; food particles ingested below snout; cell membrane supported by a thin theca reminiscent of that of Apusomonadidae; affinity with Apusomonadidae suggested by some SSU rRNA phylogenies. Ancyromonas.

Centrohelida Kühn, 1926

Axopodia supported by microtubules in hexagonal or triangular arrays; retractable axopodia by microtubule depolymerization; kinetocyst extrusomes along axopodia; centrosome as trilaminar disc with fibrous electron dense cortex, called centraoplast; flat cristae.

Acanthocystidae Claus, 1874

Periplast of siliceous elements arranged in internal and external layers; internal layer of scales; external layer of scales possessing central sternum and additional structures or radial spicules with developed shaft. Acanthocystis, Choanocystis, Echinocystis, Pseudoraphidiophrya, Pseudoraphidiocystis, Pterocystis.

Heterophryidae Poche, 1913

Periplasmic mucous coat, with or without organic spicules. Chlamydoaster, Heterophrya, Oxnerella, Sphaerastrum.

Raphidiophryidae Mikjukov, 1996

Periplast of siliceous scales or spicules arranged in one or more layers. Paraphaerastrum, Polyplacocystis, Raphidiocystis, Raphidiophrya.

Collodictyonidae Brugerolle, Bricheux, Philippe, and Coffe, 2002

Free-swimming cells with two or four equal apical flagella perpendicualr to each other; phagocytosis of eukaryotic cells in a conspicuous cytostome; cytostome a gutter that extends to posterior end giving a double-horned appearance; flagellar transition zone long with a two-part axosome. Collodictyon, Diphylliea.

Ehriaceae Lemmermann, 1901 [Ehriaceae Poche, 1913]

Cells with two subapically inserting flagella; open internal skeleton of silica; phagotrophic, without plastids. Ehria, Hermesium.

Spironemidae Doflein, 1916 [Hemimastigophora Foissner, Blatterer, and Foissner, 1988]

Flagella laterally arranged in two more or less complete rows, with up to about a dozen per row; sub-membranous thecal plates separate the flagella; thecal plates rotationally symmetrical, supported by microtubules; anterior differentiated into a capitulum for phagocytosis; cristae tubular and saccular; with bottle-shaped extrusomes. Hemimastix, Spironema, Stereonema.

Kathablepharidae Vers, 1992

Free-swimming cells with two heterodynamic flagella inserting subapically/medially; cell membrane thickened by lamellar sheath; ingest eukaryotic prey through an apical cytostome supported by bands of longitudinal microtubules; extrusomes are large coiled-ribbon arrayed near kinetosomes, somewhat similar to those of Cryptophyceae; tubular cristae; plastids not observed. Kathablepharis, Leucocryptos.

Stephanopogon Entz, 1884 [Pseudociliata Cavalier-Smith, 1993; Pseudociliatae Cavalier-Smith, 1981; Pseudociliata Corliss and Lipscomb, 1982; Stephanopogonidae Corliss, 1961]

Cells with many similar flagella arranged as unininkets in rows; cytostome for phagocytosis at anterior; single nucleus; discoidal cristae. Stephanopogon.

1. AMOEBOZOA: Testaceaobiosia: The testate amoeboidea in this group are poorly studied, with very little taxonomic sampling in molecular phylogenies. Although some genera clearly belong to the Arcellinida, for many genera, we simply do not know. The rank is retained because without doubt, there are undescribed subdivisions in this clade besides the Arcellinida.

2. AMOEBOZOA: Spongomonadidae: Initially in Rhizaria, placement follows small subunit rRNA phylogenies; Spongomonas sp. 7A and Spongomonas minima UT1 (Cavalier-Smith and Chao, 2003) were not correctly identified.

3. FUNGI: Information on the Ascomycota was compiled from the following references: Alexopoulos et al. (1996); Eriksson and Winka (1997, 1998); Eriksson et al. (2004); Kirk et al. (2001); Liu and Hall (2004); and Lutzoni et al. (2004). The Ascomycota is the largest group of fungal species. Many species remain to be discovered and relationships among most existing species are not well understood. For many groups, classification is currently unsettled with several different taxonomic systems in use. For periodic updates on the classification the reader is referred to Myconet (http://www.unu.se/myconet/Myconet.html). For references on taxonomic treatments of specific groups see Kirk et al. (2001).

4. FUNGI: Monoblepharidales: Emerson and Whisler (1968) placed Harpochytrium in the order Harpochytriales along with Oedogoniomyces. The order was later abandoned by Barr (1990) and the two genera were moved to separate orders. Barr (1990) erected a family, Harpochytriaceae, for Harpochytrium in the order Chytridiidales. Since then cell ultrastructure and sequence data (18S rDNA and mitochondrial genes) have supported the inclusion of the genus in the Monoblepharidales. No decision has been made as to which family the genus should be placed.

5. FUNGI: Spizellomyxidales: Barr (2001) suggested that thallus developmental should be abandoned in favour of ultrastructure for classifying families as it can vary greatly among and between genera and species. Karlingiomyces has been placed in a clade outside of the order based on 18S rDNA sequence data by James et al. (2000).

6. FUNGI: Chytridiidales: Families in this order are considered artificial constructs and further work is needed to revise the current classification scheme. The number of families also differ between Sparrow’s second edition of the Aquatic Phycmycetes (1960) and Karling’s Chytridiomycetaceae Iconographia (1977). Although Karling did not intend his work to be a complete family list, taxonomic changes were made that need to be considered in any update of the group. Since neither Sparrow nor Karling’s family-level organization schemes are considered phylogenetically valid it is not worthwhile to suggest one over the other at the present time. In addition, Parsimony and Maximum Likelihood analysis of 18S rDNA suggest that the order itself is not monophyletic and could possibly be broken up into several different orders (James et al. 2000).

7. OPISTHOKONTA: Choanomonada: Cavalier-Smith and Chao (1997) argued for two groups based on absence/presence of lorica (Craspedia, without lorica; Acanthocida, with lorica).

8. RHIZARIA: Cercomonomadidae: The contemporary concept of Cercomonas Dujardin, 1841 was recently revised along molecular phylogenetic line: the new taxon Neocercomonas is distinguishable from Cercomonas (= Dimastigamoeba) Blochmann, 1894 = Prismanomonas Massart,
9. Foraminifera: The division of the Foraminifera into subgroups is problematic; existing morphology-based schemes (e.g. Loeblich and Tappan 1988) are not fully consistent with molecular phylogenetic data. SSU rRNA possesses unique inserts (Pawlowski 2000); one that maps to the 3′ major domain (Region II) represents a molecular synapomorphy for the group (Habura et al. 2004). SSU rRNA phylogenetic analyses (Pawlowski et al. 2002) reveal an early radiation of naked (athalamid) and single-chambered (monothalamous) forms. Such studies also show that at least one member of the Xenophyophorea, previously incertae sedis, branches within this early radiation (Pawlowski et al. 2003a). Molecular analyses reveal that polythalamous tests evolved at least twice: in the lineage leading to a large radiation of agglutinated textulariids and calcareous rotaliids, and in the lineage leading to milliolidis, characterized by microgranular, low-Mg calcitic walls (Pawlowski et al. 2003b).

10. Radiolaria: We have retained the rank of “Radiolaria” as a practical decision since it is widely recognized as a placeholder for this group. Until recently the Radiolaria were considered to be polyphyletic. Since Radiolaria are of particular interest to biologists and micropaleontologists, the higher order taxonomic scheme presented here is one that hopefully will be of value to both groups.

11. ARCHAEPLASTIDA: We did not accept the terms Chlorobiota and Chlorobionta because there are many green species outside of the Archaeplastida. We did not accept the term Viridiplantae (green plant) because most of these species are not plants, traditionally or as defined here.

12. ARCHAEPLASTIDA: Mesostigma: this genus belongs at the base of the Chlorophyta and Charophyta. It is unclear at this time whether it is a sister lineage to both, or whether it belongs at the base of the Charophyta.

13. CHROMALVEOLATA: This proposed union of Alveolata Cava- lier-Smith, 1991 with the Cryptophyceae, Haptophyta, and Stramenopiles, the Chromista sensu Cavalier-Smith, 1998, is tentative, based on arguments by Keeling (2003) and references therein. It remains unclear whether Ciliophora had an ancestral Archaeplastida endosymbiont.

14. CHROMALVEOLATA—Cryptophyceae: Ultrastructural features (see Kugrens et al. 2002): Associations formed from secondary endosymbioses with eukaryotes, the symbiont located in a membrane-bound compartment (periplastidal space), which is formed by an extension of the nuclear envelope (chloroplast or periplastidial endoplasmic reticulum). Periplastidal space contains one or two plastids, one or two nucleomorph(s) (reduced red algal nucleus), and starch grains. Single mitochondrion often extensive and reticulate in shape; cristae flattened. Two sizes of extrusive organelles (ejectisomes) coiled into ribbons and consist of a large and small component. Large and small ejectisomes associated with cell surface beneath the plasma membrane. Geometrically positioned plates or a continuous sheet of protein material always underlies the membrane; in some genera also occurring outside the plasma membrane. Small scales and/or fibrillar material may be attached to cell body and sometimes the flagella. Both flagella with stiff bipartite hairs. Basal body apparatus usually with striated or multi-lamellate root structure (rhizostyle) and several microtubular roots. Thylakoids usually in pairs, sometimes in threes, with phycobiliproteins in thylakoid lumen. For references, see Kugrens and Lee (1987), Kugrens, Clay, and Lee (1999), and Novarino (2003).

15. CHROMALVEOLATA—Haptophyta: Ultrastructural features: The haptomonad typically consists of 6–7 microtubules surrounded by a sheath of endoplasmic reticulum and linked to basal body bases by fibrous structures. It may be long and coiling, short and flexible, or occasionally absent. One to four chloroplasts per cell, an encircling girdle lamella is absent. A peripheral endoplasmic reticulum (PER) is situated underneath the plasma membrane, absent in the region of flagellar insertion, but extends into the haptonema. The cell covering has 1–4 types of scales in layers, composed of organic microfilbrils or calcified (coccoliths), the latter often occurring over mineralized scales. The Golgi apparatus situated in the anterior end of the cell near the basal bodies has a fan like arrangement of cisternae that are perpendicular to the long axis of the cell, and are involved in scale biosynthesis. For references, see Fresnel and Probert (2005) and Sym and Kawachi (2000).

16. CHROMALVEOLATA—Chromista/Stramenopile: The terms Heterokonta, Chromista, and Stramenopile have been used by different authors to include different groups. They have also been used both as formal and informal terms to refer to various clusters of lineages. Regarding the spelling of stramenopile, it was originally spelled stramenopile. The Latin word for “straw” is strūmincēnus, a, um, adj. [stramen], made of straw—thus, it should have been spelled straminopile. However, Patterson (1989) clearly states that this is a common name (hence, lower case, not capitalized) and as a common name, it can be spelled as Patterson chooses. If he had stipulated that the name was a formal name, governed by rules of nomenclature, then his spelling would have been an orthogonal mutation and one would simply correct the spelling in subsequent publications (e.g. Straminopiles). But, it was not Patterson’s desire to use the term in a formal sense. Thus, if we use it in a formal sense, it must be formally described (and in addition, in Latin, if it is to be used botanically). However, and here is the strange part of this thing, many people liked the name, but wanted it to be used formally. So they capitalized the first letter, and made it Stramenopiles; others corrected the Latin spelling to Straminopiles.

17. CHROMALVEOLATA—Xanthophyceae: Traditionally, subdivisions were based upon gross morphology and life stage (e.g. amoeboid = Rhizochloridales, cocoid = Mischococcales). However, molecular studies show that for all those examined to date, the traditional orders do not form monophyletic groups. Therefore, the classification herein is reduced to two groups until the matter is resolved. There is some evidence that the algae with H-shaped cell walls constitute one lineage of the Tribonematales and those with entire cell walls constitute a second lineage, but this observation has not yet been put forward in a classification.

18. CHROMALVEOLATA—Bacillariophyta: Traditionally, diatoms (~10 species) are classified into “centric” and “penate” on the basis of pattern (radial organization versus bilateral organization), pattern centre (ring-like annulus versus elongate sternum), and sexual reproduction (isogamous versus morphologically isogamous) (Round, Crawford, and Mann 1990). Molecular data (Kooistra et al. 2003; Medlin and Kaczmarska 2004) show the centrics as a whole to be paraphyletic, but relationships between the principal groups, and whether particular groups are monophyletic or paraphyletic, is currently unclear. Several major molecular clades are cryptic, with or few morphological or life history traits that can be convincingly argued to be synapomorphies.

19. EXCAVATA: There is strong evidence that Heterolobosea and Euglenozoa are closely related, and they often united as a taxon “Disci- crisata”. However, some molecular evidence suggests a specific relationship between Heterolobosea and Jakobida. The relationships amongst these three groups are unresolved at this time.

20. Euglenida: Relationships among phagotrophic euglenids are poorly understood. Most higher taxa proposed within the group are probably monophyletic and/or are ill defined. No names of higher taxa are in wide use.
Table 3. Groups or genera with uncertain affiliation within protists.

| Acinetactis      | Elleipsisoma      | Paramonas        |
| Actinastrum      | Embryocola        | Paraplasma       |
| Actinella        | Endemosarca       | Parastasiella    |
| Actinocoma       | Endobiella        | Pelaiania        |
| Actinolophus     | Endomonas         | Peltomonas       |
| Adinomonas       | Endospora         | Penardia         |
| Aletium          | Endostelium       | Petasaria        |
| Alphononas       | Enteronymyx       | Phagodinium      |
| Amphimonas       | Eperythrocytozoon | Phanerobia       |
| Amphitrema       | Ererra            | Phialomena       |
| Amylophagus      | Euchitonia        | Phloxamoeba      |
| Aphelidiopsis    | Euglenocapsa      | Phyllomonas      |
| Apogromia        | Fromentella       | Physcosporidium  |
| Archaeosphaerodiniopsis | Glauocystopisis | Piritium         |
| Artococcus       | Globidiellum      | Platyheca        |
| Asteroacelaum    | Goniodynamium     | Pleuophrys       |
| Asthamatos       | Gymnococcus       | Pleurostomum     |
| Astrolophus      | Gymnophrydium     | Podactinellus    |
| Autonomas        | Haematotraetacidium | Podostoma    |
| Aurospera        | Hartmannima       | Polyspora        |
| Barbeta          | Helibodo          | Pontomyxa        |
| Belatina         | Heliomonas        | Protertospora    |
| Belmaricystis    | Hermisenella      | Protogones       |
| Berghiera        | Heterogromia      | Protomonas       |
| Berterellia      | Heteromastix      | Protomysa        |
| Bertramia        | Hillea            | Pseudactinaxis   |
| Biomyxa          | Histiophysis      | Pseudosporoprisis|
| Bjornbergiella   | Hyalochorella     | Quadricillia     |
| Bodopsis         | Hyaloladakylehra  | Raphidiophyrsis  |
| Boekelovia       | Immnoiplasma      | Raphidophrys     |
| Branchiopoda     | Ioselmis          | Recitulamoeba    |
| Campanoeca       | Kamena            | Rhadospora       |
| Camptotyche      | Kibisidyes        | Rhizomonas       |
| Chalarodora      | Kiitoksa          | Rhizoplasma      |
| Chemomyxia       | Komokicae         | Rhynchodinium    |
| Cibdelia         | Labyrinthomyxa    | Rigidomastix     |
| Cichlovia        | Lagenidiopsids    | Salpingorhica    |
| Cintidoniomyxa   | Leptophrys        | Schewiakoffa     |
| Cingula          | Leukarachnin      | Sergentella      |
| Cladomonas       | Ligeosia          | Serpentoplasmia  |
| Clathrella       | Ligniera          | Servetia         |
| Clauatria        | Lithocolla        | Spermatothium    |
| Codonoea         | Luffispheara      | Sphaer Dasductans|
| Coelosporidium   | Lympnoctocytozoon | Spirosis         |
| Copromonas       | Lymphosporidium   | Spriogregarian   |
| Cristalldophora  | Macappella        | Spongastericus   |
| Cyanomastix      | Magosphaera       | Spongocylia      |
| Cyclmonas        | Malpighiella      | Stephanomonas    |
| Cytramoeba       | Martineziella     | Strobilomonas    |
| Dallingeria      | Meganoebomyxa     | Syncrypta        |
| Dictomyxua       | Melanocodinium    | Synrumons        |
| Dinastigamoeba   | Meringoephaera    | Telonema         |
| Dinamoeba        | Microcometes      | Thalssomyxa      |
| Dinemula         | Microgromia       | Thalulires       |
| Dingensia        | Monodus           | Thiaumatodinium  |
| Dinoasteromonas  | Mononema          | Theratromysa     |
| Dinocerae        | Myrmicosporidium  | Theratryzma      |
| Dinomonas        | Myxodictyam       | Thyakomyxa       |
| Diplolocalium    | Nauplicola        | Topsentella      |
| Diplomatia       | Nephrodominum     | Toshiba          |
| Diplophysalis    | Neurosporidium    | Toxocystis       |
| Diploselmis      | Ovorea            | Triangulomonas   |
| Dobellina        | Pachydanium       | Trichomena       |
| Ducelleria       | Palisporonoma     | Trophosphera     |
| Echinococcidium  | Pansporella       | Urbanella        |
| Ectobia          | Paradinemula      | Wagnerrela       |
| Elaeorhanis      | Paramastix        | X-cells          |

Based on Patterson (2002), and modified from that presented on Tree of Life website http://tolweb.org (accessed December 16, 2004).
ACKNOWLEDGMENTS

We acknowledge the critical evaluations of Andrew Roger (Dalhousie University) for the overall structure of this classification. This is a Geological Survey of Canada contribution 2004375.

LITERATURE CITED


APUSOMONADS


ARCHAEOPLASTIDA


CHROMALVEOLATA/CHROMISTA/CRYPTOPHYCEAE/HAPTOPHYTA


**EXACAVATA**

**FORAMINIFERA**

**FUNGI**


RADIOLARIA


Karpov, S. A., Ekelund, F. & Moestrup, Ø. 2003. Katabia gromovi nov. gen. sp.—a new soil flagellate with affinities to Heteromita (Cerco-


Received: 05/20/05; accepted: 05/28/05
Dear Author,

During the copy-editing of your paper, the following queries arose. Please respond to these by marking up your proofs with the necessary changes/additions. Please write your answers clearly on the query sheet if there is insufficient space on the page proofs. If returning the proof by fax do not write too close to the paper’s edge. Please remember that illegible mark-ups may delay publication.

<table>
<thead>
<tr>
<th>Query No.</th>
<th>Description</th>
<th>Author Response</th>
</tr>
</thead>
<tbody>
<tr>
<td>Q1</td>
<td>1889 or 1880-1889; please check the year in reference Bötschli (1889).</td>
<td>-</td>
</tr>
<tr>
<td>Q2</td>
<td>Please cite reference Nikolaev et al., 2004 in text or delete from the list.</td>
<td>-</td>
</tr>
<tr>
<td>Q3</td>
<td>Please check the initials of the first author (A. or A. V. Smirnov) and update the reference A. Smirnov et al., in press (Appendix).</td>
<td>-</td>
</tr>
<tr>
<td>Q4</td>
<td>Please check the page range in reference O Kelly and et al., 2003 (section EXACAVATA).</td>
<td>-</td>
</tr>
<tr>
<td>Q5</td>
<td>Please check the page range in reference Bauer et al., (1997) (Section Fungi).</td>
<td>-</td>
</tr>
<tr>
<td>Q6</td>
<td>Please check the initials of the editors in reference Bauer et al., 2001 (followed reference Barr, 2001) (Appendix).</td>
<td>-</td>
</tr>
<tr>
<td>Q7</td>
<td>Please check the book title in reference Cavalier-Smith, 2001 (Appendix).</td>
<td>-</td>
</tr>
<tr>
<td>Q8</td>
<td>Please check the year in reference Lumbscha et al (200 changed to 2000) (Appendix).</td>
<td>-</td>
</tr>
<tr>
<td>Q9</td>
<td>Please provide complete details for reference Zhukov and Karpov, 1985 (Appendix).</td>
<td>-</td>
</tr>
<tr>
<td>Q10</td>
<td>Please update reference Moreira et al., in press (Appendix).</td>
<td>-</td>
</tr>
<tr>
<td>Q11</td>
<td>Mylnikov or Myl'nikov (inclusion of apostrophe); please check the spelling in reference Mylnikov, 1990.</td>
<td>-</td>
</tr>
<tr>
<td>Q12</td>
<td>In Table 2 please check if the quotes should come after the punctuation as followed in the text (as per journal style requirements). Followed cover sheet instructions not to change any punctuation in the table.</td>
<td>-</td>
</tr>
</tbody>
</table>