

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

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**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 six clusters of eukaryotes that may represent the basic groupings similar to traditional “kingdoms.” The multicellular 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.

**S**INCE 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 Many traditional groups are no longer valid and have been abandoned (see Hausmann, Hülsmann, and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 Bütschli (1880–1889), which divided Protozoa into Sarcodina (amoeboid organisms), Sporozoa (a parasitic group), Mastigophora (flagellated species), and Infusoria (ciliates), was abandoned decades ago by protistologists. 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.

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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 six 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 oxymonads, parabasalids, 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 Chromalveolata, grouping the Alveolata (ciliates, dinoflagellates, Apicomplexa), the Stramenopiles (brown algae, diatoms, many zoosporic fungi, and the opalinids amongst others), with the Haptophyta and Cryptophyceae. It is argued that chromalveolates are derived from a single symbiosis of a phagotrophic heterotrophic eukaryote with a photosynthetic red alga eukaryote (Keeling 2003). The plastid was secondarily lost in several lineages (Delwiche et al. 2004). Whereas each of these lineages is monophyletic, the grouping of Alveolata and Stramenopiles with Haptophyta and Cryptophyceae may not be monophyletic. It remains contentious whether the Ciliophora had an ancestral Archaeplastida endosymbiont.

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), **zoosporic fungi** (an eclectic mix of heterotrophic and saprotrophic groups), and **protozoa** (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 loss of plastids, with partial retention of a plastid remnant, as for the Apicomplexa. We no longer formally recognize Haeckel's taxon Protista (Haeckel 1866) and Protoctista from Hogg's informal term protoktistae (Hogg 1860). The popular term **protist** is retained to describe eukaryotes with a unicellular level of organisation, without cell differentiation into tissues. Where vegetative cell differentiation occurs in protists, it is restricted to sexual reproduction, alternate vegetative morphology, and quiescent or resistant stages, such as cysts. In other words, task sharing by tissues, a property of multicellular species, does not occur in protists. Based on this new definition, we clearly recognize that some algae are multicellular. Protist morphology is varied and includes single independent cells that may or may not be motile, filamentous species, colonial (linked by a common stalk, or sheath, or cytoplasmic extensions), sheets of cells (phyllose), and parenchymatous or otherwise attached cells. Multinucleate forms (including coenocytic, plasmodial, hyphal, syncytial, or siphonous forms) occur in many taxa. We recognize **prokaryotes** to include the Archaea and the Eubacteria, with bacteria being a convenient common term for prokaryotes (Cavalier-Smith 2002; Walsh and Doolittle 2005). **Eukaryotes**, the Eukaryota Chatton, 1925, are distinguished from prokaryotes by the presence of a nucleus. The **nucleus** is defined as an organelle bounded by a double mem-

brane, the outer being derived from the endomembrane network, with the nuclear pore complex traversing both membranes, and with one or more linear chromosomes typically packaged by histones and usually with a centromere and telomeres. We recommend restricting the use of **cyst** to vegetative quiescent stages, while restricting the use of **spore** for reproductive stages. The eukaryote motility organelle is the **cilium**, or "eukaryotic flagellum," which consists of a cell membrane-bound extension supported by a microtubular-based axoneme and a basal body or kinetosome with associated cytoskeletal elements serving as anchors.

Overall, we have tried to be conservative with the classification by avoiding uncertain subdivision of lineages, and speculative clustering of the clades. Two groups warrant caution at this time. One is the grouping of the Cryptophyceae, Haptophyta, Stramenopiles, and Alveolata, together called the chromalveolates (Delwiche 1999; Fast et al. 2002; Harper and Keeling 2003; Harper, Waanders, and Keeling 2005; Yoon et al. 2002) and the other is the grouping of the Euglenozoa and Heterolobosea, together with other excavates (Simpson and Roger 2004). However, we show what these highest ranking clusters seem to be, based on current molecular phylogenies (Table 1). We have included in our descriptions in Table 2 the apomorphies for each group, where possible. Groups that are probably still paraphyletic are indicated with (P). For several groups, in particular within the Cercozoa, formal diagnosis did not exist and we provided descriptions based on characters that seemed to hold the group together. Groups that did not exist in the traditional taxonomy based on morphological characters but were established based on molecular phylogenetics, are indicated as ribogroups (R). Where a group is currently only known from one described species, it is indicated as being monotypic (M). We further understand that many described morphospecies are probably clusters of several biologically distinct entities.

We adopted a hierarchical system without formal rank designations, such as "class," "sub-class," "super-order," or "order" (Table 2). The decision to do so has been primarily motivated by utility, to avoid the common problem of a single change causing a cascade of changes to the system. The hierarchy is represented by indented paragraphs. We believe this to be more utilitarian, and less problematic than traditional conventions, as it is not constrained by formally attributing a limited number of rank names. This approach has the advantage of being more flexible and easier to modify. For this presentation, we limited our descriptions to the first four highest ranks for most groups. Several genera and groups remain with uncertain affiliations within the protists, and they have been listed separately (Table 3). It is comforting that this list is considerably shorter than the one provided by Patterson (2002). The most significant change has been the identification of several monophyletic lineages within the protists. The traditional "Kingdoms," such as Metazoa, Fungi, and Plantae, are now clearly recognized as being derived from within monophyletic protist lineages (Table 1, 2). It is now clear that the Animalia and Fungi arose within the Opisthokonta, and the plants from within Charophyta. Therefore, traditional classification schemes and modern cladistics were difficult to reconcile without having "Kingdoms" within "Kingdoms."

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,

Table 1. Highest ranks of the eukaryotes with the next two ranks as presented in Table 2.

Super-groups	First rank	Second rank, examples
Amoebozoa	Tubulinea	Leptomyxida, Testacealobosia, Tubulinida
	Flabellinea	<i>Cochliopodium</i> , Dactylopodia, Thecamoebida, Vanellida
	Stereomyxida	
	Acanthamoebidae	
	Entamoebida	
	Mastigamoebidae	
	<i>Pelomyxa</i> Eumycetozoa	Dictyostelia, Myxogastria, Protostelia
Opisthokonta	Fungi	Ascomycota, Basidiomycota, Chytridiomycetes, Glomeromycota, Microsporidia, Urediniomycetes, Ustilaginomycetes, Zygomycota
	Mesomycetozoa	Aphelidea, <i>Capsaspora</i> , <i>Corallochytrium</i> , Ichthyosporia, <i>Ministeria</i> , Nucleariida
	Choanomonada Metazoa <sup>*</sup>	Acanthoecidae, Monosigidae, Salpingoecidae Porifera, <i>Trichoplax</i> , Mesozoa, Animalia
Rhizaria	Cercozoa	Cercomonadida, Chlorarachniophyta, Nucleochelea, Phaeodarea, Phytomyxea, Silicofilosea
	Haplosporidia	
	Foraminifera	Subdivisions uncertain
	<i>Gromia</i> Radiolaria	Acantharia, Polycystinea, <i>Sticholonche</i>
Archaeplastida	Glaucophyta	
	Rhodophyceae	Subdivisions uncertain
	Chloroplastida	Charophyta <sup>*</sup> , Chlorodendrales, Chlorophyta, <i>Mesostigma</i> , Prasinophytae
Chromalveolata	Cryptophyceae	Cryptomonadales, Goniomonadales
	Haptophyta	Pavlovophyceae, Prymnesiophyceae
	Stramenopiles	Actinophryidae, Bacillariophyta, <i>Bolidomonas</i> , Bicosoecida, Chrysophyceae, Dictyochophyceae, Eustigmatales, Hypochytriales, Labyrinthulomycetes, Opalinata, Pelagophyceae, Peronosporomycetes, Phaeophyceae <sup>*</sup> , Phaeothamniophyceae, Pinguichrysidales, Raphidophyceae, <i>Schizocladia</i> , Synurales, Xanthophyceae
Excavata	Alveolata	Apicomplexa, Ciliophora, Dinozoa
	Fornicata	<i>Carpediemonas</i> , Eopharyngia
	<i>Malawimonas</i>	
	Parabasalia	Cristamonadida, Spirotrichonymphida, Trichomonadida, Trichonymphida
	Preaxostyla	Oxymonadida, <i>Trimastix</i>
	Jakobida	Histionidae, <i>Jakoba</i>
	Heterolobosea	Acrasidae, Gruberellidae, Vahlkampfiidae
Euglenozoa	Euglenida, Diplonemea, Kinetoplastea	

<sup>a</sup>Clades with multicellular groups.

in several instances, we have placed in brackets ranks of the 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: Peniculia].

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. (cont'd p. 446)

**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 names for the group that we did not accept and their taxonomic authority. References to the recent literature can be found in Appendix 1 under the major monophyletic clusters. Citations in the Notes to this table can be found in the LITERATURE CITED. 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 with only one described species; (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.

AMOEOBOZOA Lühe, 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 et al., 2005 (R)  
Naked or testate amoeboid organisms producing tubular sub-cylindrical pseudopodia or capable of altering shape from flattened and expanded to a sub-cylindrical one; mono-axial flow of the cytoplasm in entire cell or each pseudopodium; without centrosomes; locomotion based on actino-myosin cytoskeleton; cytoplasmic microtubules, if present, rare and never in bundles; without flagellate stages.
- Tubulinida Smirnov et al., 2005 (R)  
Without test; produce sub-cylindrical pseudopodia or are monopodial; without alteration of the locomotive morphology; non-adhesive uroid. *Amoeba*, *Cashia*, *Chaos*, *Deuteroamoeba*, *Glaeseria*, *Hartmannella*, *Hydramoeba*, *Nolandella*, *Parachaos*, *Polychaos*, *Saccamoeba*, *Trichamoeba*.
- Leptomyxida Pussard and Pons, 1976, emend. Page, 1987 (R)  
Locomotive form generally a flattened, reticulate or highly branched sheet; most active locomotive form sub-cylindrical; with adhesive uroid; uninucleate, sometimes multinucleate; glycocalyx thin and amorphous; cysts common, double-walled, without pores. *Flabellula*, *Gephyramoeba*, *Leptomyxa*, *Paraflabellula*, *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*, *Centro-pyxis*, *Diffflugia*.
- Incertae sedis Testacealobosia  
*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 overlain with mucin and embedded spicules in the other phase; multiple semi-permanent openings for pseudopodia (described as tactile dactylopods). *Trichosphaerium*.
- Incertae sedis Tubulinea: *Echinamoeba*.
- Flabellinea Smirnov et al., 2005 (P)  
Flattened locomotive amoebae, without tubular sub-cylindrical pseudopodia; the locomotive form is never altered; cytoplasmic flow poly-axial or without pronounced axis; locomotion based on actino-myosin cytoskeleton; without centrosome; without flagellate stages.

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1. AMOEOBOZOA: Testacealobosia: The testate amoebae 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.

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## AMOEBOZOA cont'd.

- Dactylopodida Smirnov 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 nucleolus; parasomes in *Neoparamoeba* and *Paramoeba*; cell coat variable, consists of microscales, hexagonal or pentagonal glycostyles, or fibrous. *Korotnevella*, *Mayorella*, *Neoparamoeba*, *Paramoeba*, *Pseudoparamoeba*, *Vexillifera*. Other possible genera: *Boveella*, *Dactylosphaerium*, *Oscillodignum*, *Podostoma*, *Strioluatus*, *Subulamoeba*, *Trienamoeba*.
- 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*, *Lingulamoeba*) 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 (*Parvamoeba*, *Thecamoeba*) or smooth (other genera); cell coat amorphous, with glycostyles or fibrous. *Dermamoeba*, *Paradermamoeba*, *Parvamoeba*, *Sappinia*, *Thecamoeba*.
- *Cochliopodium* Hertwig and Lesser, 1874  
Dorsal surface covered with a tectum comprised of elaborate microscales; cysts in some. *Cochliopodium*.
- Incertae sedis Flabellinea: *Flamella*, *Ovalopodium*, *Paragocevia*, *Pellita*, *Pseudothecamoebea*, *Thecochaos*. Other possible genera: *Gibbodiscus*.
- Stereomyxida Grell, 1966 (P?)  
Branched or reticulate plasmodial organisms; trilaminar centrosome. *Corallomyxa*, *Stereomyxa*.
- Acanthamoebidae Sawyer and Griffin, 1975 (R)  
Glycocalyx 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; locomotion based on actino-myosin cytoskeleton; centriole-like body present. *Acanthamoeba* (syn. *Comandonia*), *Balamuthia*, *Protacanthamoeba*.
- 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 amoeboid 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 nucleoli 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 palustris*.

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## AMOEBOZOA cont'd.

- Eumycetozoa Zopf, 1884, emend. Olive, 1975 [Mycetozoa de Bary, 1873]  
 ‘‘Fruiting body’’ 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 as uninucleate obligate amoebae, multinucleate (2–10 nuclei) obligate amoebae, and multinucleate (up to  $> 10^7$  nuclei) obligate amoebae; some amoeboid states absent from some life cycles, other types of amoebae derived from modifications of amoeboid-flagellate or derived from the obligate amoebae that develop following the amoeboid-flagellate 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 (myxomycetes and protostelids), or a sorocarp, developing from an aggregate of amoeboid cells (dictyostelids).
- Protostelia Olive, 1975 (P)  
 Sporocarps from single amoeba or nucleated fragment of a multinucleate obligate amoeba; sporocarp a hollow acellular stalk (length from  $< 5$  to  $> 100 \mu\text{m}$ ) that supports 1–8 spores; spores monoclonal from cell division after the stalk has been secreted; trophic cells amoeboid-flagellates only, amoeboid-flagellates and obligate amoebae, or obligate amoebae only; filose pseudopodia; at least three separate origins of obligate amoebae likely, all morphologically and ultrastructurally distinct. *Cavostellium*, *Ceratiomyxa*, *Ceratiomyxella*, *Microglomus*, *Nematostelium*, *Protostelium*, *Tychosporium*.
- Myxogastria Macbride, 1899 [Myxomycetes Link, 1833, emend. Haeckel, 1866]  
 Trophic stages free-living, multinucleate amoeboid-flagellate and coenocytic, saprobic multinucleate obligate amoeba (plasmodium); under poor conditions plasmodium sometimes becomes a sclerotium; sporocarps ( $< 1 \text{ mm}$ –ca  $1 \text{ m}$ ) from multinucleate obligate amoeba, the plasmodium, or fragment of plasmodium; most with stalked sporangia but also sessile sporangia, plasmodiocarps, aethalia or pseudoaethalia; 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 capillitium; 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 amoeboid-flagellates twisted and obconic 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 amoeboid-flagellate in apomictic species; small and unveined with 8–100 nuclei (protoplasmodium) or large and veined network with  $10^2$ – $> 10^7$  nuclei with thick gel-like cortex shuttle in veins (phaneroplasmodium) or thin transparent veins (aphanoplasmodium); mitosis in plasmodium intra-nuclear with non-centric poles; dormancy as sclerotia of many macrocysts or as sporocarps. Traditional subdivisions may not represent monophyletic assemblages. *Arcyria*, *Badhamia*, *Barbyella*, *Brefeldia*, *Comatricha*, *Cribraria*, *Diachea*, *Diderma*, *Dydimium*, *Echinostelium*, *Fuligo*, *Lamproderma*, *Leocarpus*, *Lepidoderma*, *Licea*, *Lycogala*, *Macbrideola*, *Metatrichia*, *Perichaena*, *Physarella*, *Physarum*, *Stemonitis*, *Trichia*, *Tubulifera*, *Willkommlangea*.
- Dictyostelia Lister, 1909, emend. Olive, 1970  
 Cellular slime moulds, with stalked fruiting bodies from aggregation of amoebae; sorocarps of stalks with terminal sori of haploid spores; stalks (sorophores), acellular (*Acytostelium*), cellular, and unbranched to sparsely branched (*Dictyostelium*) or cellular with whorls of branches (*Polysphondylium*); stalk cells forming cell wall and dying; spores usually ellipsoid, occasionally reniform or spherical; trophic amoebae, non-flagellated, haploid, uninucleate; nucleus with reticulate peripheral

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## AMOEBOZOA cont'd.

- Dictyostelia cont'd.  
nucleolus; microtubular cytoskeleton of amoebae radiating from lamellar 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 at least the anterior end of the slug/sorogen; in taxa with cellular stalks an anterior population of prestalk cells becoming 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 macrocyst once all the haploid amoebae are ingested; meiosis occurring when dormancy of macrocyst is broken; haploid amoebae germinating from macrocyst. Classical ranks are not monophyletic. *Acytostelium*, *Dictyostelium*, *Polysphondylium*. Incertae sedis *Coenonia*.
  - Incertae sedis Eumycetozoa: *Copromyxa*, *Copromyxella*, *Fonticula*.
  - Incertae sedis AMOEBOZOA: *Filamoeba*, *Gocevia*, *Hartmannia*, *Janickia*, *Malamoeba*, *Malpigamoeba*, *Multicilia*, *Stygamoeba*.
  - Incertae sedis AMOEBOZOA: Spongomonadida Hibberd, 1983, emend. Karpov, 1990  
Sessile feeding cells, solitary or colonial, often embedded in mucoid matrix with endogenous globules; cells ovoid with one 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**.
  - *Phalansterium* Stein, 1878  
Single kinetosome and cilium; cilium surrounded by a collar of cytoplasm, used in feeding; often colonial in a gelatinous matrix. *Phalansterium*.
  - 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 mastigonemes, 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 multinucleate hyphae; walls, when present, with  $\beta$ -glucan and usually chitin, at least in spore walls; AAA lysine biosynthesis pathway; mitochondria and peroxisomes present, except in Microsporidia; flattened cristae; plastids and tubular mastigonemes absent.
  - Basidiomycota de Barry 1866, emend. Schaffer, 1975  
Mycelium present, but some with a yeast state primarily in the Tremellomycetidae; basidia produced in a fertile layer with or without fleshy sporocarp; basidia whole or divided longitudinally, typically with four spores per basidium but ranging from

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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 (Ekelund and Karpov, unpublished).

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## OPISTHOKONTA cont'd.

- Basidiomycota cont'd.  
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*, *Gautieria*, *Hyphodontia*, *Jaapia*, *Laccaria*, *Lycoperdon*, *Phlebia*, *Polyporus*, *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. *Agaricostilbum*, *Caeoma*, *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); asci 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 (mitospores) formed by fragmentation of vegetative hyphae (thallic), blastically from single cells, hyphae, or conidiophores; 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. **Note 3.**
- *Neoelecta* Spegazzini, 1881 [Neoelectomycetes Eriksson and Winka, 1997]  
Mycelium present, multinucleate; ascomata apothecial, stalked, fleshy; interascal tissue absent; cylindrical asci formed from binucleate cells that

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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.umu.se/myconet/Myconet.html>). For references on taxonomic treatments of specific groups see Kirk et al. (2001).



Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## OPISTHOKONTA cont'd.

- *Neolecta* cont'd.  
undergo karyogamy, meiosis and one mitotic division to produce eight cylindrical ascospores, thin-walled, walls blueing in iodine, ascus apex truncate, slightly thickened below ascus wall, with wide apical slit, persistent; ascospores ellipsoidal to globose, hyaline, aseptate; anamorph unknown; saprobic; found in wet mixed woodlands. *Neolecta*.
- Taphrinomycotina Eriksson and Winka, 1997  
Mycelium present or absent; asci produced from binucleate cells; do not form croziers or interascal tissue.
- *Pneumocystis* Delanoë and Delanoë, 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, delimited by enveloping membrane system (EMS), wall formed within bilayers of EMS, wall blueing 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; asci globose or ellipsoidal, eight-spored; ascospores hyaline, aseptate; biotrophic 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 or poorly developed; hyphae, when present, septate, with septa having numerous pores rather than a single septal pore; vegetative cells proliferating by budding or fission; walls usually lacking chitin except around bud scars; ascomata absent; sexual reproduction by fusion of two vegetative haploid cells or fusion of two haploid nuclei in a single cell or within diploid cells, followed by meiosis and, in some cases, one mitotic division to produce either four or eight nuclei; cells undergoing meiosis become asci, ascospores delimited by an enveloping membrane system (EMS), ascospore wall formed within bilayers of EMS; ascospores aseptate, colourless or pigmented, often with wall thickenings of various types; most osmotrophic, some species parasitic on animals. *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 discoid, perithecial, cleistothecial or occasionally lacking; antheridium (male sex organ) present or absent; ascogonium (female sex organ), ascogenous hyphae and croziers present; the penultimate

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## OPISTHOKONTA cont'd.

- Pezizomycotina cont'd.  
cell of the crozier, in which meiosis and usually one mitotic division occur, becomes the ascus; asci fissitunicate or not fissitunicate, cylindrical, clavate or saccate; asci 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 paraphysoids in a gel matrix; asci thick-walled, fissitunicate, blueing 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 lysigenously from stromatic tissue (ascolocular); interascal tissue present or absent, of branched paraphysoids or pseudoparaphyses; asci cylindrical to saccate, thick-walled, fissitunicate, rarely with apical structures; ascospores mostly septate or muriform, colorless to dark brown; anamorphs hyphomycetous or coelomycetous; saprobes, 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 periphysoids; hymenium usually blueing in iodine; asci fissitunicate, saccate; ascospores hyaline or brown, transversely septate or muriform; anamorphs hyphomycetous; epiphytic or biotrophic on leaves. *Chaetothyrium*.
- Eurotiomycetes Eriksson and Winka, 1997  
Ascomata cleistothecial, sometimes absent; peridium thin, membranous or hyphal; interascal tissue absent; asci 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); asci 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 ellipsoidal or globose, aseptate, hyaline to darkly pigmented, smooth or ornamented; anamorphs hyphomycetous, where known; saprobes on soil, dead wood or dung; some species hypogeous and mycorrhizal. *Ascobolus*, *Helvella*, *Morchella*, *Peziza*, *Sarcoscypha*.
- Laboulbeniomycetes Engler, 1898  
Mycelium absent except in Pyxidiophorales; cellular thallus hyaline to dark, with basal haustorium present; ascomata perithecial, frequently

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## OPISTHOKONTA cont'd.

- Laboulbeniomyces cont'd.  
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 epithecium; 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, multiseptate, rarely plurilocular, hyaline or pigmented; anamorphs pycnidial where known; mostly lichen forming with protococcoid algae, with thallus foliose, fruticose, crustose or occasionally absent; some lichenicolous, some saprobic. *Gyalecta*, *Lecanora*.
- Leotiomyces Eriksson and Winka, 1997 [Leotiomyces-1 sensu Lutzoni et al., 2004]  
Ascomata apothecial, discoid, cleistothecial, elongated or rarely absent; apothecia stalked or sessile, frequently fleshy, sometimes hairy or with appendages, occasionally stromatic or sclerotoid; interascal tissue of simple paraphyses or absent; peridium thin-walled; asci typically inoperculate, cylindrical, thin-walled, not fissitunicate, occasionally with apical pore; apical apparatus variable; ascospores aseptate or transversely septate, hyaline or pigmented and longitudinally slightly asymmetrical; anamorphs occasionally present, hyphomycetous or coelomycetous; saprobes or plant parasites, some lichenized or lichenicolous. *Crinula*, *Leotia*, *Rhytisma*, *Sclerotinia*, *Sphaerotheca*, *Uncinula*.
- Lichinomyces Reeb, Lutzoni, and Roux, 2004  
Ascomata apothecial, discoid, sometimes immersed, occasionally clavate, stalked, setose, and fleshy, peridium often not well-defined; interascal tissue varied; hymenium often stains blue with iodine; asci thin-walled or apically thickened, not fissitunicate, without well-defined apical structures, usually with an iodine-staining outer gelatinized layer; ascospores one-septate or occasionally multiseptate, ellipsoidal to fusiform, hyaline or pigmented; anamorphs pycnidial; lichenized with cyanobacteria forming crustose, fruticose or foliose often gelatinized thalli. *Lichina*, *Peltula*.
- Orbiliomyces Eriksson and Baral, 2003  
Ascomata apothecial, small, waxy, translucent or lightly pigmented; interascal tissue of simple paraphyses, usually with knob-like apices, united by a matrix; asci minute, not fissitunicate, apex truncate, with J apical rings, often forked at the base; ascospores minute, cylindrical, hyaline, often aseptate; anamorphs hyphomycetous where known; saprobic, often on wet wood. *Halorbilia*, *Orbilia*.
- Sordariomyces Eriksson and Winka, 1997, emend. Eriksson et al., 2004  
Ascomata perithecial or cleistothecial, sometimes translucent, coloured or darkly pigmented, often hairy; peridium thin- or thick-walled, membranous or carbonaceous; paraphyses septate, simple or branched or absent; asci not fissitunicate, with or without apical structures, cylindrical, clavate or globose, persistent or evanescent; ascospores with or without at least

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## OPISTHOKONTA cont'd.

- Sordariomycetes cont'd.  
one dark cell with germ pore, varied in shape and colour, with or without gelatinous sheaths or appendages; saprobic or parasitic on plants, coprophilous, fungicolous 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 uncertain at this time. *Amblyospora*, *Amphiacantha*, *Buxtehudia*, *Caudospora*, *Chytridiopsis*, *Desportesia*, *Encephalitozoon*, *Enterocytozoon*, *Glugea*, *Hessea*, *Metchnikovella*, *Nosema*, *Spraguea*, *Vairimorpha*.
- Glomeromycota Schüssler et al., 2001 [Glomales Morton and Benny, 1990; Glomomycetes Cavalier-Smith, 1998]  
Filamentous; primarily endomycorrhizal, arbuscular, sometimes with vesicles; without cilium; asexual spores outside host (chlamydospores, azygospores); without centrioles, conidia, and aerial spores. *Acaulospora*, *Archaeospora*, *Diversispora*, *Entrophospora*, *Geosiphon*, *Gigaspora*, *Glomus*, *Pacispora*, *Paraglomus*, *Scutellospora*.
- Zygomycota Fischer, 1892, emend. Benjamin, 1979, emend. Benny et al., 2001  
Primarily filamentous, without septa (coenocytic), or septa occurring irregularly to regularly; 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  
Hyphae 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*, *Dispira*, *Spinalia*, *Tieghemiomyces*.
- 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*, *Zygopolaris*.
- Kickxellales Benjamin, 1979  
Filamentous; hyphae possessing septa with a lenticular cavity; asexual reproduction by unispored sporangiola (merosporangia) produced on a sporocladium; saprobic or mycoparasitic, isolated from soil and dung. *Coemansia*, *Dipsacomyses*, *Kickxella*, *Linderina*, *Martensella*, *Martensiomycetes*, *Spirodactylon*, *Spiromycetes*.
- Zoopagales Benjamin, 1979  
Filamentous, hyphae coenocytic or septate; parasites of soil fungi, invertebrates and amoebae; asexual reproduction by conidia or merosporangia; sexual reproduction by globose zygospores with apposed suspensors. *Amoebophilus*, *Piptocephalis*, *Rhopalomycetes*, *Sigmoideomyces*, *Stylopage*.
- *Basidiobolus* Eidam, 1886  
Filamentous; without cilium; 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*.

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## OPISTHOKONTA cont'd.

- Mucorales Schröter, 1897 (P?)  
Filamentous fungi; generally saprotrophic, with exceptions; septa absent except in older hyphae; with plasmodesmata at septal pores; asexual reproduction with one to many spores in merosporangia, sporangiola, or sporangium; reproduction by zygospore, typically with opposed suspensors. Traditional subdivisions artificial. *Chaetocladium*, *Choanephora*, *Mortierella*, *Mucor*, *Phycomyces*, *Pilobolus*, *Syncephalestrum*, *Thamnidium*.
- 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*, *Sclerogone*, *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 secondary conidia. *Conidiobolus*, *Completozia*, *Entomophthora*, *Meristacrum*, *Neozygites*.
- 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  $\beta$ -1,3-1,6-glucan; AAA lysine biosynthesis pathway; glycogen storage product.
- Blastocladiales Petersen, 1909  
Uniciliated 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.
  - Blastocladiales Petersen, 1909  
Monocentric and/or polycentric with bipolar germination. *Allomyces*, *Blastocladia*, *Blastocladiella*, *Blastocladiopsis*, *Microallomyces*.
  - Catenariaceae Couch, 1945  
Filamentous and polycentric with monopolar germination. *Catenomyces*, *Catenophlyctis*, *Caternaria*.
  - Coelomomycetaceae Couch, 1945  
Obligate parasites of insect larvae with an alternate gametophyte generation on copepods. *Coelomomyces*.
  - Physodermataceae 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*, *Urophlyctis*.
  - *Sorochytrium* Dewel, 1985 [Sorochoytriaceae 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. *Sorochytrium milnesiophthora*.
- Monoblepharidales 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

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## OPISTHOKONTA cont'd.

- Monoblepharidales cont'd.  
parallel; with an electron-opaque plate in the kinetosome transition zone; a non-fenestrated rumposome present. **Note 4.**
  - Gonapodyaceae Sparrow, 1960  
Sex anisogamous. *Gonopodya*.
  - Monoblepharidaceae Fischer 1892, emend. Mollicone and Longcore, 1999  
Sex oogamous with a small male gamete fertilizing an oogonium. *Monoblepharella*, *Monoblepharis*.
  - Oedogoniomycetaceae Barr, 1990  
Asexual. *Oedogoniomyces*. Incertae sedis *Harpochytrium*.
- Spizellomycetales 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.**
  - Spizellomycetaceae Barr, 1980  
Monocentric with endogenous thallus development. *Gaertneriomyces*, *Karlingiomyces*, *Kochiomyces*, *Spizellomyces*, *Triparticular*.
  - Olpidiaceae Schroeter, 1889  
Monocentric with exogenous thallus development. *Caulochytrium*, *Entophlyctis* (P), *Olpidium*, *Rhizophlyctis*, *Rozella*.
- Neocallimastigaceae Li, Heath, and Packer, 1993  
Obligate anaerobes of the rumen and hindgut of herbivores; some 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, posterior-dome structure connected to the spur on the kinetosome by some of the root microtubules. *Anaeromyces*, *Caecomycetes*, *Cyllamyces*, *Neocallimastix*, *Orpinomyces*, *Piromycetes*.
- 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*, *Chytriumyces*, *Cladochytrium*, *Endochytrium*, *Entophlyctis* (P), *Lacustromyces*, *Nephrochytrium*, *Nowakowskiella*, *Obelidium*, *Phylctorhiza*,

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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 Chytridiales. 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: Spizellomycetales: Barr (2001) suggested that thallus development, which can vary greatly among and between genera and species, should be abandoned in favour of ultrastructure for classifying families. *Karlingiomyces* has been placed in a clade outside of the Spizellomycetales based on 18S rDNA sequence data by James et al. (2000).

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## OPISTHOKONTA cont'd.

## ●●● Chytridiales cont'd.

*Physocladia*, *Podochytrium*, *Polychytrium*, *Polyphagus*, *Rhizoclostridium*, *Rhizophyidium*, *Septochytrium*, *Synchytrium*. **Note 6.**

- Mesomycetozoa Mendoza et al., 2002, emend. Adl et al., 2005 [Choanozoa Cavalier-Smith, 1981] (R) (P)  
Usually flat cristae (exceptions e.g. Aphelidea, *Ichthyophonus*); 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 apophysis of spore, attached to host cell surface; characteristic central food vacuole with excretory body; cell division leads to flagellate or amoeboid dispersal cells released from host; tubular or lamellar cristae. *Amoebophilidium*, *Aphelidium*, *Pseudoaphelidium*.
- *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*.
- Ichthyosporae Cavalier-Smith, 1998 [Mesomycetozoa Mendoza et al., 2002]  
Single-celled trophic organisms (some with hyphal, multinucleated filaments, *Ichthyophonus*); 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.
- Rhinosporideae Mendoza et al., 2001 [Dermocystida Cavalier-Smith, 1998] (R)  
If present, posterior flagellum; flat cristae; when parasite 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. *Ambiociostidium ranae*, *Dermocystidium*, *Rhinosporidium seeberi*, *Sphaerothecum destruens*.
- Ichthyophonae Mendoza et al., 2001 [Ichthyophonida Cavalier-Smith, 1998; Amoebidiidae Reeves, 2003] (R)  
Parasites of fish, arthropods, and insects, or free-living and saprotrophic; usually with flat cristae but *Ichthyophonus* 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 richardsi*, *Ichthyophonus*, *Pseudoperkinsus tapetis*, *Psorospermium haeckeli*, *Sphaeroforma arctica*, Isolate LKM51, Isolate Ikaite un-c53.

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**6. FUNGI:** Chytridiales: Subdivisions in this group are considered artificial constructs and further work is needed to revise the current classification scheme. The numbers of families also differ between Sparrow's second edition of the Aquatic Phycomyces (1960) and Karling's Chytridiomycetorum Iconographia (1977). Although Karling did not intend his work to act as a monograph, 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).

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## OPISTHOKONTA cont'd.

- *Ministeria* Patterson et al., 1993, emend. Tong, 1997 [Ministeriida Cavalier-Smith, 1997]  
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*.
- Choanomonada 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**.
  - Monosigidae Zhukov and Karpov, 1985 [Codonosigidae Kent, 1880]  
Naked. *Codonosiga*, *Monosiga*, *Sphaeroeca*.
  - Salpingoecidae Kent, 1880  
Cellulose theca. *Salpingoeca*, *Stelaxomonas*.
  - Acanthoecidae Norris, 1965  
Lorica of siliceous strips. *Bicosta*, *Stephanoeca*.
- Metazoa Haeckel, 1874  
Multicellular; cells typically held together by intercellular junctions; extracellular matrix with fibrous proteins, typically collagens, 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 cristae; sexual species, mostly hermaphroditic, releasing monociliated 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 choanocytes, amoeboid cells, and digestive secretory 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*, *Lophocalyx*, *Monoraphis*, *Semperella*.
      - Demospongiae Sollas, 1885, emend. Borchellini 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 monociliated cells, except at posterior pole; one family (Cladorhizidae) with external digestion by amoeboid cell aggregation on captured crustacean prey. *Aplysina*, *Axinella*, *Ca-*

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



Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## OPISTHOKONTA cont'd.

- Demospongiae cont'd.  
*cospongia*, *Chondrosia*, *Cliona*, *Euspongia*, *Halisarca*, *Hippospongia*, *Oscarella*, *Plakina*, *Spongilla*, *Suberites*. Excludes Homoscleromorpha.
- Homoscleromorpha Lévi, 1973, emend. Borchiellini et al., 2004 (R)  
No unambiguous characters congruent with molecular phylogenies.  
Node: includes *Oscarella lobularis*, excludes *Beroe ovata*, *Geodia cydonium*, *Hydra viridis*, *Leucosolenia variabilis*, *Oopsacas minuta*.
- Calcispongia Johnston, 1842 [Calcarea Bowerbank, 1864]  
Calcium carbonate spicules; larva with outer monociliated cells, larger at posterior; invagination of anterior cells at attachment of posterior to substrate.
- Calcinea Hartman, 1958, emend. Borchiellini et al., 2004 (R)  
Unambiguous characters congruent with molecular phylogenies unclear.  
*Clathrinida*, *Murrayona*.
- Calcaronea Hartman, 1958, emend. Borchiellini et al., 2004 (R)  
Unambiguous characters congruent with molecular phylogenies unclear.  
*Grantiopsis-Paralurilla*, *Vosmacropsis-Sycettusa*, includes Heteropiidae, Staurorrhaphidae, Minchinellidae.
- *Trichoplax* von Schultze, 1883 [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 adhaerens*.
- 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 ciliary necklace; kinetosome pair with rootlet horizontal, pointing anterior; without digestive tissues; only osmotrophic endoparasites known; sexual with testis and egg cells; without gastrulation; without basal membrane or extracellular matrix; tubular cristae.
- Orthonectida Giard, 1880  
Epithelial cells in rings of alternating pluriciliated and non-ciliated cells; contractile cells, with differentiated testis and egg cells. *Ciliocincta*, *Rhopalura*, *Stoecharthrum*.
- 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*, *Dicyemenea*.
- Animalia Linnaeus, 1758, emend. Adl et al., 2005 [Eumetazoa Bütschli, 1910]  
Reproduction through an egg cell, usually fertilized by a monociliated 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 Grassé, 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 net-

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## OPISTHOKONTA cont'd.

- Animalia cont'd.  
work; epithelial contractile cells between endoderm–ectoderm use actin-myosin. 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.
- Cercomonadida Poche, 1913, emend. Vickerman, 1983, emend. Mylnikov, 1986  
Amoeboflagellates without cell wall; two heterodynamic flagella without mastigonemes; pseudopodia used for feeding; some species have complex life cycle including multinuclear and multflagellar plasmodium stage; cysts occur; kinetosomes connected to the nucleus; tubular cristae; with microbodies and extrusomes.
- Cercomonadidae Kent, 1880, emend. Mylnikov and Karpov, 2004 [Cercobodonidae Hollande, 1942] (P?)  
Gliding cells with two flagella; posterior flagellum adhering to the cell; with transient pseudopodia. *Cercomonas*, *Helkesimastix*, *Neocercomonas*. **Note 8.**
- Heteromitidae Kent, 1880, emend. Mylnikov, 1990, emend. Mylnikov and Karpov, 2004 [Bodomorphidae Hollande, 1952]  
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* Hollande, 1952 = *Sciviamonas* Ekelund and Patterson, 1997); kinetosome microtubular cone absent. *Allantion*, *Cholamonas*, *Heteromita*, *Katabia*, *Protaspis*, *Sainouron*.
- Silicoflosea Adl et al., 2005 [Imbricatea Cavalier-Smith and Chao, 2003]  
Secreted surface silica scales; tubular cristae.
- Thaumatomonadida Shirkina, 1987 [Thaumatomastigidae Patterson and Zöllf, 1991]  
Heterotrophic 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 multflagellate stages known. Subdivisions unknown. *Allas*, *Gyromitus*, *Thaumatomonas*, *Thaumatomastix*.
- Euglyphida Copeland, 1956, emend. Cavalier-Smith, 1997  
Secreted silica plates bound by an organic cement into a test. Subdivisions based on morphology.
- Euglyphidae Wallich, 1864  
Thin, round to elliptical scales. *Assulina*, *Euglypha*, *Placosista*, *Pareuglypha*, *Sphenoderia*, *Tracheleuglypha*, *Trachelocorythion*.
- Trinemmatidae Hoogenraad and De Groot, 1940  
Test with bilateral symmetry; opening invaginated in some. *Corythion*, *Deharvengia*, *Pileolus*, *Playfairina*, *Trinema*.

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**8. RHIZARIA: Cercomonadidae:** The contemporary concept of *Cercomonas* Dujardin, 1841 was recently revised along molecular phylogenetic lines: the new taxon *Neocercomonas* is distinguishable from *Cercomonas* (= *Dimastigamoeba* Blochmann, 1894 = *Prismatomonas* Massart, 1920 = *Reptomonas* Kent, 1880 = *Cercomastix* Lemmermann, 1913 = *Cercobodo* Krassiltschik, 1886 = *Dimorpha* Klebs, 1892) by sequence data and other criteria (Ekelund et al. 2004).

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## RHIZARIA cont'd.

- Cyphoderiidae de Saedeleer, 1934  
Scales circular to oval; test aperture angled, some with collar. *Campascus*, *Corythionella*, *Cyphoderia*, *Messemvriella*, *Pseudocorythion*, *Schaudinmulla*.
- Paulinellidae de Saedeller, 1934  
Scales long, with length perpendicular to opening; with cyanelle. *Paulinella*.
- Incertae sedis Euglyphida: *Ampullataria*, *Euglyphidion*, *Heteroglypha*, *Matsakision*.
- Chlorarachniophyta Hibberd and Norris, 1984  
Amoeboid with plastids 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*, *Cryptochlora*.
- 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*, *Phagomyxa*, *Pongomyxa*, *Sorosphaera*, *Spongospora*.
- Phaeodarea Haeckel, 1879 [Triplylea 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 "parapylae", 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; tubular cristae.
- 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. *Coelodendrum*, *Coelographis*, *Conchellium*, *Conchopsis*.
- Phaeocystina Haeckel, 1879  
Central capsule suspended in the centre of the extra-capsular cytoplasmic network; skeleton absent or incomplete, composed of numerous solitary, scattered pieces or spicules without organic connections. *Aulacantha*, *Aulographis*, *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*, *Sagosphaera*.

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## RHIZARIA cont'd.

- Nucleohelea Cavalier-Smith, 1993  
Amorphous centrosome adjacent to nuclear envelope (axoplast); axopodial pseudopods supported by microtubules; tubular cristae.
- Clathrulinidae Claus, 1874 [Desmothoracida 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*, *Clathrulina*, *Hedriocystis*. Incertae sedis *Servetia*.
- Gymnosphaerida Poche, 1913, emend. Mikrjukov, 2000  
Axopodial 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*, *Hedraiophrys*. Incertae sedis *Actinolophus*, *Wagnerella*.
- Incertae sedis Cercozoa: *Cryothecomonas*, *Gymnophrys*, *Lecythium*, *Massisteria*, *Metopion*, *Proleptomonas*, *Pseudodiffugia*.
- Haplosporidia Caullery and Mesnil, 1899  
Plasmodial endoparasites of marine and sometimes freshwater animals; distinctive lid-ded 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; intra-nuclear spindle, a rudiment of which persists in interphase nuclei (“kernstab”); tubular cristae. *Haplosporidium*, *Minchinia*, *Urosporidium*.
- Foraminifera d’Orbigny, 1826  
Filopodia with granular cytoplasm, forming branching and anastomosing network (reticulopodia); bidirectional rapid ( $\sim 10 \mu\text{m/s}$ ) 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 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 agamont 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. rotaliids and miliolids) are monophyletic. *Allogromia*, *Ammonia*, *Biomyxa*, *Carpenteria*, *Cycloclypeus*, *Globigerinella*, *Komokiacea*, *Lana*, *Lenticula*, *Nodogenerina*, *Textularia*. **Note 9.**

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**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 miliolids, characterized by microgranular, low-Mg calcitic walls (Pawlowski et al. 2003b).

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## RHIZARIA cont'd.

- *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; multi-nucleate; tubular cristae; 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 intracapsulum, which contains the nucleus or nuclei and cytoplasmic organelles; tubular cristae; 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  
Skeleton either absent or when present, composed of scattered spicules within the extra-capsulum; solitary or colonial forms. *Collosphaera*, *Collozoum*, *Lampoxanthium*, *Physematium*, *Siphonsphaera*, *Sphaerouzoum*, *Thalassicolla*.
- Sphaerellaria Haeckel, 1887  
Skeleton a porous or latticed shell; skeleton single or multiple, and of various shapes: spherical, discoidal, quadrangular, trigonal, or bilocular. *Actinomma*, *Didymocyrtis*, *Euchitonia*, *Hexacantium*, *Hexalonche*, *Hexastylus*, *Octodendron*, *Plegmosphaera*, *Saturnalis*, *Spongaster*, *Spongospaera*.
- 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.
- Plectellaria Haeckel, 1887  
Skeleton absent or when present, simple tripod or sagittal ring. *Lophospyris*, *Plagonium*, *Tetraplecta*, *Zygocircus*.
- Cyrtellaria Haeckel, 1887  
Skeleton, a helmet-shaped “cephalis”, bilocular with sagittal constriction, or multilocular and segmented with two or more constrictions, or simple without constriction and lobes. *Botryostrobos*, *Callimitra*, *Cornutella*, *Eucyrtidium*, *Lamprocyclas*, *Pterocanium*, *Spirocyrtis*, *Theopilium*.

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**10.** Radiolaria: We have retained the name 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.

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## RHIZARIA cont'd.

- *Sticholonche* Hertwig, 1877 [Taxopoda Fol, 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; tubular cristae. *Sticholonche*.
- 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-type 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 unknown; sexual reproduction involving consecutive mitotic and meiotic divisions that ultimately release  $10^2$ – $10^3$  biciliated 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*, *Stauracantha*.
- 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; litholophus stage prior to reproduction; hexagonal microtubular arrays in axopodia; contractile matrix at base of spicules. *Amphiacon*, *Conacon*, *Gigartacon*, *Heteracon*, *Stauracon*.
- 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. *Acanthochiasma*, *Acanthocolla*, *Acanthoplegma*.
- 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. *Amphilithium*, *Astrolonche*, *Pseudolithium*.

## ARCHAEPLASTIDA Adl et al., 2005

Photosynthetic plastid with chlorophyll *a* from an ancestral primary endosymbiosis with a cyanobacterium; plastid secondarily lost or reduced in some; usually with cellulose cell wall; flat cristae; starch storage product.

- Glaucophyta Skuja, 1954 [Glaucocystophyta Kies and Kremer, 1986]  
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 *a* only, with phycobiliproteins and other pigments; flagellate and non-flagellate species or life cycle stages. *Cyanophora*, *Glaucocystis*, *Gloeochaete*.
- Rhodophyceae Thuret, 1855, emend. Rabenhorst, 1863, emend. Adl et al., 2005 [Rhodophyta Wettstein, 1901; Rhodoplantae Saunders and Hommersand, 2004]

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## ARCHAEPLASTIDA cont'd.

- Rhodophyceae cont'd.  
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-zonal 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 may be of cellulose; cells in filamentous forms linked by pit plugs, formed between cells after incomplete cell division; sexual reproduction typically oogamous; triphasic life history common. Subdivisions of this group unknown at this time. Traditional subgroups are artificial constructs, and no longer valid. *Bonne-maisonia*, *Ceramium*, *Dasya*, *Dasyphloea*, *Eucheuma*, *Gracilaria*, *Nemalion*, *Nizymania*, *Porphyra*, *Rhodophysema*, *Rhodymenia*, *Sphaerococcus*.
- Chloroplastida Adl et al., 2005 [Viridiplantae Cavalier-Smith, 1981; Chlorobionta Jeffrey, 1982, emend. Bremer, 1985, emend. Lewis and McCourt, 2004; Chlorobiota Kendrick and Crane, 1997]  
Plastid with chlorophylls *a* and *b*; pyrenoid often present inside plastid; cell wall with cellulose usually present; with centrioles. **Note 11.**
- Chlorophyta Pascher, 1914, emend. Lewis and Mc Court, 2004  
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 mastigonemes; basal bodies with four 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 distromatic sheet (phyllose), or cushiony forms of compacted tubes; thallus often multinucleate and siphonous; free-living diplobiontic life cycle, iso- or heteromorphic. *Acetabularia*, *Caulerpa*, *Chladophora*, *Codium*, *Pithophora*, *Pseudonochloris*, *Rhizoclonium*.
- Trebouxiophyceae Friedl, 1995 [Pleurostrophyceae Mattox 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 free-living forms; osmotrophy and autotrophy. *Botryococcus*, *Chlorella*, *Choricystis*, *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

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**11.** ARCHAEPLASTIDA: Chloroplastida: 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.

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## ARCHAEPLASTIDA cont'd.

- Chlorophyceae cont'd.  
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 oogamy; asexual reproduction by aplanospores, akinetes, or autospores; osmotrophy and autotrophy. *Bracteacoccus*, *Chlamydomonas* (P), *Desmodesmus*, *Floydiella*, *Hydrodictyon*, *Oedogonium*, *Pediastrum*, *Scenedesmus*, *Volvox*. Incertae sedis: *Carteria*, *Cylindrocapsa*, *Hafniomonas*, *Mychanastes*, *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*, *Tetraselmis*.
- 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 *Nephroselmis olivacea*; nutrition by autotrophy and osmotrophy. *Crustomastix*, *Halosphaera*, *Nephroselmis*, *Pedinomonas*, *Pyramimonas*.
- *Mesostigma* Lauterborn, 1894, emend. McCourt in Adl et al., 2005 [Mesostigmata Turmel, Otis, and Lemieux, 2002]  
Asymmetrical cell with pair of lateral flagella emerging from a pit, without mastigonemes; basal body transition region with similarity to Streptophytina; multilayered structure anchor associated with basal body; with chlorophylls *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 [Charophyceae 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 cytoskeletal 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 superoxide dismutase; flagellar peroxisome. Sub-divisions other than Streptophytina not shown. *Chaetosphaeridium*, *Chlorokybus*, *Coleochaete*, *Klebsormidium*, *Spirogyra*.
- Streptophytina 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 api-

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**12.** ARCHAEPALSTIDA: *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 is basal in the Charophyta.



Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## ARCHAEPLASTIDA cont'd.

- Streptophytina cont'd.  
cal cell at end of branches and main axis; sexual reproduction with öogamy 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 internodal 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 öogamous 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]  
Flagellar basal bodies, when present, with distinctive multilayered structure of microtubules and cytoskeletal 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 (P?)

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 ejectisomes (trichocysts); cristae flat tubules; two flagella emerging subapically 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; gullet/furrow complexes lined with large ejectisomes; with or without plastid–nucleomorph complex; chloroplasts when present contain chlorophylls *a* and *c*<sub>2</sub> and phycobiliproteins, located in thylakoid lumen; chloroplast covering comprised of inner and superficial periplast components; (heterotrophic species formerly known as *Chlomonas* have been distributed to other genera); some genera diplomorphic (e.g. *Cryptomonas*, *Proteomonas*). **Note 14.**

**13. CHROMALVEOLATA:** This proposed union of Alveolata Cavalier-Smith, 1991 with the Cryptophyceae, Haptophyta, and Stramenopiles (the Chromista *sensu* Cavalier-Smith, 1998) is tentative, based on arguments by Keeling (2003), Harper et al. (2005), 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 (periplastidial space), which is formed by an extension of the nuclear envelope (chloroplast or periplastidial endoplasmic reticulum). Periplastidial 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.

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## CHROMALVEOLATA cont'd.

- Cryptomonadales Pascher, 1913  
Chloroplasts or leucoplasts present. *Campylomonas*, *Chroomonas*, *Cryptomonas*, *Hemiselmis*, *Rhodomonas*.
- Goniomonadales Novarino and Lucas, 1993  
Chloroplasts absent. *Goniomonas*.
- Haptophyta Hibberd, 1976, emend. Edvardsen and Eikrem, 2000  
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*, *c*<sub>1</sub>, and *c*<sub>2</sub> (*c*<sub>3</sub> 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; autotrophic, mixotrophic or heterotrophic cells with 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*, *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*.

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**15. CHROMALVEOLATA: Haptophyta.** Ultrastructural features: The haptonema 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 microfibrils or calcified (coccoliths), the latter often occurring over unmineralized 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.

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## CHROMALVEOLATA cont'd.

- 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*, *Calciosolenia*, *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, emend. Adl et al., 2005 [Slopalinata Patterson, 1986]  
Pluriciliated with double-stranded transitional helix at the transitional region between kinetosome and cilium; 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. *Karotomorpha*, *Proteromonas*.
- Opaline 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. *Cepedea*, *Opalina*, *Protoopalina*, *Protozelleriella*, *Zelleriella*.
- *Blastocystis* Alexieff, 1911, emend. Brumpt, 1912  
Without flagella; anaerobic; mitochondria without typical enzyme activities and cytochromes; 2 or more nuclei; can be pathogenic. *Blastocystis*.
- Bicosoecida Grassé, 1926, emend. Karpov, 1998  
Biflagellate with or without tripartite mastigonemes; without plastids; phagotrophic with cytostome supported by broad microtubular rootlet; predominantly sedentary, often attach to substrate with posterior flagellum; with or without lorica, solitary, and colonial. *Adriamonas*, *Bicosoeca*, *Cafeteria*, *Cyathobodo*, *Pseudobodo*, *Pseudodendromonas*, *Siluania*.

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**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—*stra mi'ne'us*, a, um, adj. [stramen], *made of straw*—thus, it should have been spelled straminopile. However, Patterson (1989) clearly stated 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, 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.

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## CHROMALVEOLATA cont'd.

- Labyrinthulomycetes Dick, 2001  
Production of an ectoplasmic network of branched, anastomosing, wall-less filaments via a specialized organelle known as the bothrosome; Golgi-derived scales; biflagellate zoospores with lateral insertion in many species.
- Labyrinthulaceae Haeckel, 1868  
Spindle-shaped vegetative cells distributed in an extensive ectoplasmic net; zoospores with eyespots; sexual reproduction. *Labyrinthula*.
- Thraustochytriaceae Sparrow, 1943  
Small ectoplasmic net; presence of interphase centrioles in vegetative cells; no sexual reproduction; no eyespots. *Althornia*, *Aplanochytrium*, *Elnia*, *Japonochytrium*, *Schizochytrium*, *Thraustochytrium*, *Ulkenia*.
- Hyphochytriales Sparrow 1960  
Single anteriorly directed flagellum with mastigonemes.
- Anisolpidiaceae Karling, 1943, emend. Dick, 2001  
Thallus holocarpic. *Anisolpidium*, *Canteriomyces*.
- Hyphochytridiomycetaceae Fischer, 1892, emend. Karling, 1939  
Thallus eucarpic and polycentric. *Hyphochytrium*.
- Rhizidiomycetaceae Karling, 1943  
Thallus eucarpic and monocentric. *Latrostium*, *Rhizidiomyces*, *Rhizidiomycopsis*.
- Peronosporomycetes Dick, 2001 [Öomycetes Winter, 1897, emend. Dick, 1976]  
Haplontic-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; öogamous reproduction that results in the formation of thick-walled sexual spores known as öospores, due to contact between male and female gametangia; thallus mainly aseptate; cell wall of glucan-cellulose, may have minor amount of chitin. *Achyla*, *Leptomitus*, *Peronospora*, *Pythiogeton*, *Rhipidium*, *Saprolegnia*. Incertae sedis: *Ciliomyces*, *Crypticola*, *Ectrogella*, *Eurychasma*, *Haptoglossa*, *Lagena*, *Lagenisma*, *Myzocytiopsis*, *Olpidiopsis*, *Pontisma*, *Pythiella*, *Rozellopsis*, *Sirolopidium*.
- 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 [Bolidophyceae Guillou et al., 1999]  
Naked, unicellular flagellates; 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; no eyespot; plastid pigments include chlorophylls *a* and *c*<sub>1-3</sub>, fucoxanthin, 19'-butanoyloxyfucoxanthin, 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 lorica, and cellulose cell wall; chloroplast with girdle lamella; outer

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## CHROMALVEOLATA cont'd.

- Chrysophyceae cont'd.  
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*<sub>1,2</sub>, fucoxanthin, violaxanthin, anthaxanthin, 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 with 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 [Hibberdiales Andersen, 1989] (M)  
Swimming cells with only one flagellum visible by light microscopy; three microtubular kinetosome roots. *Hibberdia magna*.
- Ochromonadales 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 lamella; plastid DNA with scattered granule-type genophore; no eyespot; plastid pigments include chlorophylls *a* and *c*<sub>1,2</sub>, 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 Haeckel, 1894  
Silica skeleton present on at least one life stage; with chloroplasts. *Dictyocha*.
- Pedinellales Zimmermann, Møestrup, and Hällfors, 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*.
- Eustigmatales Hibberd, 1981  
Coccoid organisms, single cells or colonies; cell walls present; chloroplast without 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 but located outside of the chloroplast; plastid pigments include chlorophyll *a*, violaxanthin, and vaucherioxanthin; 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*, *Monodopsis*, *Nannochloropsis*, *Pseudocharaciopsis*, *Vischeria*.
- Pelagophyceae Andersen and Saunders, 1993  
Flagellate, capsoid, coccoid, 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*<sub>1,2</sub>, fucoxanthin, 19'-hexanoyloxyfucoxanthin, 19'-butanoyloxyfucoxanthin,

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## CHROMALVEOLATA cont'd.

- Pelagophyceae cont'd.  
diatoxanthin, and diadinoxanthin; swimming cells with 1–2 flagella; anteriorly directed flagellum bearing bipartite or tripartite tubular hairs, second flagellum, when present, directed posteriorly; kinetosome(s) 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 coccoid organisms; when flagellate, a single flagellum without a second kinetosome; no kinetosome roots. *Aureococcus*, *Aureoumbra*, *Pelagococcus*, *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. *Ankylochrysis*, *Nematochryopsis*, *Pulvinaria*, *Sarcinochrysis*.
- Phaeothamniophyceae Andersen and Bailey in Bailey et al., 1998  
Filamentous, capsoid, palmelloid, or coccoid; 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 tripartite 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.
- Phaeothamniales Burrelly, 1954, emend. Andersen and Bailey in Bailey et al., 1998 (R)  
Distinguished from the Pleurochloridales based on molecular phylogenetic analyses. *Phaeothamnion*.
- Pleurochloridales Ettl, 1956 (R)  
Distinguished from the Phaeothamniales based on molecular phylogenetic analyses. *Pleurochloridella*.
- Pinguochrysidales Kawachi, Inouye, Honda, O'Kelly, Bailey, Bidigare, and Andersen, 2003  
Flagellate or coccoid 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*<sub>1,2</sub>, 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*, *Pinguochrysis*, *Pinguicoccus*, *Polypodochrysis*.
- Raphidophyceae Chadeaud, 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*<sub>1,2</sub>; carotenoid composition distinctly different between marine (M) and freshwater (FW) species—fucoxanthin (M), violaxanthin (M), heteroxanthin (FW),

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## CHROMALVEOLATA cont'd.

- Raphidophyceae cont'd.  
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. *Chattonella*, *Fibrocapsa*, *Goniostomum*, *Haramonas*, *Heterosigma*, *Merotricha*, *Olisthodiscus*, *Vacuolaria*.
- *Schizocladia* 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 mastigonemes; kinetosome 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 include chlorophylls *a* and *c* and fucoxanthin (HPLC data absent); storage product unknown. *Schizocladia ischiensis*.
- 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*<sub>1</sub>, 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. *Chrysodidymus*, *Mallomonas*, *Synura*, *Tesselaria*.
- Xanthophyceae Allorge, 1930, emend. Fritsch, 1935 [Heterokontae Luther 1899; Heteromonadea Leedale, 1983; Xanthophyta Hibberd, 1990]  
Predominately coccoid or filamentous, rarely amoeboid, flagellate or capsoid; cell walls (probably cellulose) typical, either entire or H-shaped bisectoidal 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 *c*<sub>1,2</sub>, violaxanthin, heteroxanthin, and vaucherioxanthin; swimming cells with two flagella, one anteriorly directed and bearing tripartite tubular hairs, one posteriorly directed and lacking tripartite hairs; four microtubular kinetosome roots and one large striated kinetosome root (rhizoplast); flagellar transitional helix with six apparently double gyres located above the major transitional plate; no paraflagellar rod. **Note 17.**
- Tribonematales Pascher, 1939  
Filamentous, coccoid, and capsoid 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. *Botrydium*, *Bumilleriopsis*, *Characiopsis*, *Chloromeson*, *Heterococcus*, *Ophiocytium*, *Sphaerosorus*, *Tribonema*, *Xanthonema*.

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**17. CHROMALVEOLATA: Xanthophyceae:** Traditionally, subdivisions were based upon gross morphology and life stage (e.g. amoeboid = Rhizochloridales, coccoid = 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.

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## CHROMALVEOLATA cont'd.

- Vaucheriales Bohlin, 1901  
Siphonous filaments, with elaborate sexual reproductive structures (antheridia, öogonia). *Vaucheria*.
- Phaeophyceae Hansgirg, 1886  
Filamentous, syntagmatic or parenchymatous; cell wall present, containing alginate 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 *c*<sub>1,2</sub>, 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 (rhizoplast); flagellar transitional helix typically with 6 gyres located above the major transitional plate; no paraflagellar 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.
- Ascoseirales Petrov, 1964  
Sporophyte parenchymatous, with intercalary growth; several scattered discoid plastids with no pyrenoid; heteromorphic life cycle, gametophyte not free-living; isogamous sexual reproduction. *Ascoseira*.
- Cutleriales Bessey, 1907  
Gametophyte (larger) and sporophyte parenchymatous; several scattered discoid plastids with no pyrenoid; gametophyte with trichothallic growth, sporophyte with apical growth; heteromorphic life cycle; anisogamous sexual reproduction. *Cutleria* (P), *Microzonia*, *Zanardinia*.
- Desmarestiales Setchell and Gardner, 1925  
Gametophyte small and filamentous, sporophyte larger and pseudo-parenchymatous; several scattered discoid plastids with no pyrenoid; trichothallic growth; heteromorphic life cycle; öogamous sexual reproduction. *Arthrocladia*, *Desmarestia* (P), *Himantothallus*, *Phaeurus*.
- Dictyotales Bory de Saint-Vincent, 1828  
Gametophyte and sporophyte parenchymatous, with apical or marginal growth; several scattered discoid plastids and no pyrenoid; isomorphic life cycle; öogamous sexual reproduction. *Dictyota*, *Dilophus*, *Lobophora*, *Padina*, *Styopodium*, *Taonia*, *Zonaria*.
- Ectocarpales Bessey, 1907, emend. Silva and Reviere, 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 öogamous sexual reproduction. *Acinetospora*, *Adenocystis*, *Chordaria*, *Ectocarpus*, *Scytosiphon*. Incertae sedis: *Asterocladon*, *Asteronema*.
- Fucales Bory de Saint-Vincent, 1927  
Sporophyte parenchymatous, with apical cell growth; several scattered discoid plastids and no pyrenoid; diploid life stage only, meiosis produces gametes; (mostly) öogamous sexual reproduction. *Ascophyllum*, *Bifurcaria*, *Cystoseira*, *Druvillaea*, *Fucus*, *Hormosira*, *Sargassum*, *Turbinaria*.
- *Ishige* Yendo, 1907 [Ishigeacea Okamura, 1935; Ishigeales Cho, Lee, and Boo, 2004]  
Isomorphic alternation of generations, with apical cell growth; scattered discoid plastids with no pyrenoids; terminal unilocular sporangia, or uniseriate plurilocular sporangia; cortex pseudoparenchymatous with assimilatory filaments phaeophycean hairs in cryptostigmata. *Ishige*.



Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## CHROMALVEOLATA cont'd.

- Laminariales Migula, 1908  
Gametophyte small and filamentous with apical growth; sporophyte large and parenchymatous, with intercalary growth; several scattered discoid plastids with no pyrenoid; heteromorphic life cycle; öogamous sexual reproduction (eggs sometimes flagellate). *Akkesiophycus*, *Alaria*, *Chorda*, *Costaria*, *Laminaria*, *Lessonia*, *Pseudochoda*.
- Scytothamnales Peters and Clayton, 1998  
Gametophyte large and parenchymatous, with intercalary growth; sporophyte small and filamentous, with apical growth; 1 or more stellate or axial plastids with pyrenoid; heteromorphic alternation of generations; anisogamous sexual reproduction. *Scytothamnus*, *Splachnidium*, *Stereocladon*.
- Sphacelariales Migula, 1908  
Gametophyte and sporophyte branched multiseriate filaments, with apical growth; several scattered discoid plastids and no pyrenoid; (usually) isomorphic alternation of generations; isogamous, anisogamous or öogamous sexual reproduction. *Chaetopteris*, *Halopteris*, *Onslowia*, *Sphacelaria*, *Stypocaulon*, *Verosphacella*.
- Sporochnales Sauvageau, 1926  
Gametophyte and larger sporophyte pseudoparenchymatous, with trichothallic growth; several scattered discoid plastids with no pyrenoid; heteromorphic alternation of generations; öogamous sexual reproduction. *Bellotia*, *Carpomitra*, *Nereia*, *Sporochonus*, *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; gametophyte not free-living; isogamous sexual reproduction. *Syringoderma*.
- Tilopteridales Bessey, 1907  
Isomorphic alternation of generations with polystichous construction of the thallus, which grows by a trichothallic meristem; several scattered plastids, without pyrenoids; öogamous sexual reproduction. *Halosipon*, *Haplospora*, *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 membranes, and with lamellae of three thylakoids and a ring nucleoid (rarely multiple nucleoids); flagellate cells (only present as the sperm of centric lineages) bearing a single anterior flagellum with a 9+0 axoneme and mastigonemes; life cycle diplontic and of unique pattern: slow size reduction (~ years) during the vegetative phase, caused by an unusual internal wall morphogenesis, alternating with rapid (~ days) size restitution via a growth phase (auxospore). **Note 18.**

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**18. CHROMALVEOLATA: Bacillariophyta:** Traditionally, diatoms ( $\gg 10^5$  species) are classified into “centric” and “pennate” on the basis of pattern (radial organization versus bilateral organization), pattern centre (ring-like annulus versus elongate sternum), and sexual reproduction (öogamous 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 no or few morphological or life history traits that can be convincingly argued to be synapomorphies.

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## CHROMALVEOLATA cont'd.

- Coscinodiscophytina Medlin and Kaczmarska, 2004 (P)  
Valve outline circular (rarely elliptical); valve pattern radiating from a central or subcentral circular annulus; rimoportulae usually present; girdle bands hoop-like or segmental; sexual reproduction oogamous, with non-motile eggs and uniflagellate sperm; auxospore with scales but no band-like elements; many small chloroplasts.
- Paralids Mann in Adl et al., 2005 (R)  
Chain-forming, heavily silicified; valves circular, radially symmetrical; rimoportulae or tube processes small, restricted to the mantle; girdle bands hoop-like. *Paralia*.
- Melosirids Mann in Adl et al., 2005 (R)  
Usually chain forming; valves circular, radially symmetrical; rimoportulae small, scattered on the valve face or marginal; girdle bands hoop-like or segmental. *Aulacoseira*, *Melosira*, *Stephanopyxis*.
- Coscinodiscids Mann in Adl et al., 2005 (R)  
Solitary; valves generally circular, radiating from a central, subcentral or submarginal circular annulus; rimoportulae central, scattered on the valve face or marginal; girdle bands hoop-like. *Actinoptychus*, *Coscinodiscus*.
- Arachnoidiscids Mann in Adl et al., 2005 (R)  
Solitary, heterovalvar; valves circular, radially symmetrical; valve centre with radial slits (apparently modified rimoportulae); girdle bands hoop-like. *Arachnoidiscus*.
- Rhizosolenids Mann in Adl et al., 2005 (R)  
Chain-forming, rarely solitary; valves circular, radially symmetrical or with the pattern centre displaced towards one side; rimoportula single, associated closely with the annulus, sometimes developed into a spine; girdle bands segmental. *Guinardia*, *Leptocylindrus*, *Rhizosolenia*.
- Corethrids Mann in Adl et al., 2005 (R)  
Solitary; valves circular; radially symmetrical; articulating spines secreted from around the valve margin; rimoportulae absent; girdle bands segmental. *Corethron*.
- Bacillariophytina Medlin and Kaczmarska, 2004  
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 oogamous (with non-motile eggs and uniflagellate sperm) or isogamous (gametes without flagella, amoeboid); auxospore usually with band-like elements (perizonium or properizonium); chloroplasts many, few or one.
- Mediophyceae Jousé and Proshkina-Lavrenko in Medlin and Kaczmarska, 2004 (P)  
Valve outline bipolar or multipolar, sometimes (secondarily?) circular; valve pattern radiating from a central circular or elongate annulus; rimoportulae central or marginal; sexual reproduction oogamous; auxospore with band-like elements (properizonium) or scales; chloroplasts usually many, small. *Chaetoceros*, *Cymatosira*, *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 gen-

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## CHROMALVEOLATA cont'd.

- Bacillariophyceae cont'd.  
erally 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. *Asterionella*, *Eunotia*, *Navicula*, *Nitzschia*, *Rhaphoneis*.
- Alveolata Cavalier-Smith, 1991  
Cortical alveolae; alveolae sometimes secondarily lost; with ciliary pit or micropore; cristae tubular or ampulliform.
- Dinozoa Cavalier-Smith, 1981, emend. Cavalier-Smith and Chao, 2004, emend. Adl et al., 2005  
Usually with extranuclear spindle within cytoplasmic channels through the nucleus; cortical alveoli typically discrete and inflated; often with bipartite trichocysts with a dense square-sectioned basal rod and twisted hollow trichocyst filaments.
- Dinoflagellata Bütschli, 1885, emend. Fensome, Taylor, Sarjeant, Norris, Wharton, and Williams, 1993  
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 that 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 accords with, or derives from, a pattern in which there are five or six latitudinal plate series; sagittal suture lacking. *Alexandrium*, *Amphidinopsis*, *Amphidoma*, *Blepharocysta*, *Ceratium*, *Crypthecodinium*, *Gonyaulax*, *Heterocapsa*, *Peridinella*, *Peridinium*, *Pfiesteria*, *Pyrocystis*.
- Dinophysiphycidae Möhn, 1984, emend. Fensome et al., 1993  
With a cingulum, sulcus, and sagittal suture. Fossil taxa. *Dinophysis*, *Triposolenia*.
- Prorocentrales Lemmermann, 1910 [Prorocentrophycidae 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. *Prorocentrum*.

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## CHROMALVEOLATA cont'd.

- 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*, *Hemidinium*.
- 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 Haeckel, 1894 [Noctiluciphyceae 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. *Kofoidinium*, *Noctiluca*.
- Syndiniales 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*, *Duboscquella*, *Merodinium*, *Syndinium*.
- *Oxyrrhis* Dujardin, 1841 [Oxyrrhinaceae Sournia, 1984] (M)  
Without true cingulum and sulcus; intranuclear mitotic spindle; with amphiesmal vesicles and trichocysts; flagella inserted laterally. *Oxyrrhis marina*.
- Perkinsidae 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 micropores, 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 syngamy followed by immediate meiosis to produce haploid progeny; asexual reproduction of haploid stages occurring by binary fission, endodyogony, endopolyogony, and/or schizogony; locomotion by gliding, body flexion, longitudinal ridges, and/or flagella. All parasitic except Colpodellida.
- Colpodellida Cavalier-Smith, 1993  
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. *Alphamonas*, *Colpodella*, *Voromonas*.
- Aconoidasida Mehlhorn, Peters, and Haberkorn, 1980 (P)  
Incomplete apical complex (conoid not present) in asexual motile stages; some diploid motile zygotes (öokinetes) with conoid; macrogametes and microgametes forming independently; heteroxenous.
- Haemospororida Danilewsky, 1885  
Zygote motile (öokinete) with conoid; flagellated microgametes produced by schizogonous process; öocyst formed in which sporozoites develop. *Mesnilium*, *Plasmodium*.
- Piroplasmorida Wenyon, 1926  
Piriform, round, rod-shaped or amoeboid; conoid and flagella absent in all stages; without öocyst; probably sexuality associated with the formation of large axopodium-like "Strahlen". *Babesia*, *Theileria*.

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## CHROMALVEOLATA cont'd.

- 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.
- Coccidiasina Leuckart, 1879 (P)  
Mature gametes develop intracellularly; microgamont typically produces numerous microgametes; syzygy absent; zygote rarely motile; sporocysts usually formed within oocysts. *Cryptosporidium*, *Cyclospora*, *Eimeria*, *Hepatozoon*.
- Gregarinasina Dufour, 1828 (P)  
Mature gamonts usually develop extracellularly; syzygy of gamonts generally occurring with production of gametocyst; similar numbers of macrogametes and microgametes maturing from paired gamonts in syzygy within the gametocyst; syngamy of mature gametes leading to gametocyst that contains few to many oocysts, each of which contain sporozoites; sporocysts absent; asexual replication (merogony) absent in some species. *Acuta*, *Cephalolobus*, *Gregarina*, *Levinea*, *Menospora*, *Nematocystis*, *Nematopsis*, *Steinina*, *Trichorhynchus*.
- Ciliophora Doflein, 1901 [Ciliata Perty, 1852; Infusoria Bütschli, 1887]  
Cells with nuclear dimorphism, including a typically polygenomic 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 microtubular ribbon arising in the region of triplets 4–6; sexual reproduction, when present, by conjugation typically with mutual exchange of haploid gametic nuclei that fuse to form the synkaryon or zygotic nucleus.
- 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*, *Loxodes*, *Trachelocerca*.
- Heterotrichea Stein, 1859  
Polygenomic macronucleus dividing by extra-macronuclear microtubules; major postciliary ribbons separated by one microtubule. *Blepharisma*, *Climacostomum*, *Folliculina*, *Stentor*.
- Intramacronucleata Lynn, 1996  
Polygenomic macronucleus dividing by intramacronuclear microtubules.
- Spirotrichea Bütschli, 1889 (R)  
Conspicuous right and left oral and/or pre-oral ciliature; left serial oral polykinetids leading, usually clockwise 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 *Protocruziidia* and *Phacodiniidia*.

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## CHROMALVEOLATA cont'd.

- *Protocruzia* Faria da Cunha and Pinto, 1922 [Protocruziidia de Puytorac et al., 1987]  
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 [Phacodiniidia Small and Lynn, 1985]  
Somatic kineties 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 Corliss, 1957]  
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. *Aspidisca*, *Discocephalus*, *Euplotes*.
- Oligotrichia Bütschli, 1887  
Oral polykinetids forming an open circle, typically with an anterior “collar” and a more ventral “lapel”; somatic kineties reduced in number and variable in pattern, forming bristles, girdles, and spirals. *Cyrtostrombidium*, *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 tintinnids are all loricate. *Codonella*, *Favella*, *Strombidinopsis*, *Strobilidium*, *Tintinnopsis*.
- 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. *Halteria*, *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 Jankowski, 1964  
Body usually twisted to left, often much so; oral region spiralled, with series of 3–5 perioral 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 heteromembranelles. *Clevelandella*, *Nyctotherus*, *Paracichlidotherus*.

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## CHROMALVEOLATA cont'd.

- 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*, *Epalxella*.
- Litostomatea Small and Lynn, 1981  
Somatic monokinetids 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 ‘polykinetids’; typically endosymbionts in vertebrates. *Balantidium*, *Entodinium*, *Isotricha*, *Macropodinium*, *Ophryoscolex*.
- Phyllopharyngea de Puytorac et al., 1974  
The ciliated stage with somatic kineties mostly as monokinetids 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 monokinetids; ribbon-like subkinetal nematodesmata arising from somatic monokinetids and extending, either anteriorly or posteriorly, beneath kineties as subkinetal ribbons; oral region with radially arranged microtubular ribbons, called phyllae.
- Cyrtophoria Fauré-Fremiet in Corliss, 1956  
Oral ciliature typically composed of one preoral kinety and two circumoral kineties; true cytostome and cytopharynx surrounded by phyllae and rod-shaped nematodesmata; macronucleus heteromorous. *Brooklynella*, *Chilodonella*.
- 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 cytostome; cytopharyngeal apparatus with phyllae, but no nematodesmata; macronucleus, heteromorous; unequal cell division typical, producing ‘bud’ for dispersal; most species are ectosymbionts on crustacean appendages. *Chilodochona*, *Spirochona*, *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*.

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## CHROMALVEOLATA cont'd.

- 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 swimmers typically bearing neither tentacles nor stalk. *Acineta*, *Discophrya*, *Ephelota*, *Tokophrya*.
- Nassophorea Small and Lynn, 1981  
Somatic cilia as monokinetids 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 cyrtos 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. *Bursaria*, *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-cytostomal 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. *Lechriopyla*, *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 Peniculia).
- 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*.
- Scuticociliatia 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



Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## CHROMALVEOLATA cont'd.

- Scuticociliatia cont'd.  
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*, *Tetrahymena*.
  - 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*, *Hyalophysa*.
  - 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 cytostome; (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*, *Epistylis*, *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*, *Haptophrya*.
- Incertae sedis Alveolata: *Colponema*, Ellobiopsidae.

## EXCAVATA Cavalier-Smith, 2002, emend. Simpson, 2003 (P?)

Typically with suspension-feeding groove (cytostome) 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.
- Eopharyngia Cavalier-Smith, 1993  
Single kinetid and nucleus, or one pair each of kinetids and nuclei; usually four kinetosomes and flagella per kinetid (occasionally three or two); usually with feeding grooves or cytopharyngeal tubes; mitochondrial homologues and dictyosomes inconspicuous/transient.
- 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), or uncommonly, one kinetid and

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

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## EXCAVATA cont'd.

- Diplomonadida cont'd.  
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*, *Spironucleus*, *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*, *Octomitus*.
- Incertae 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 (*Chilomastix*) emergent flagella; one flagellum has 2–3 vanes and runs posteriorly, associated with a conspicuous ventral feeding groove with discrete posterior cytostome; cell surface underlain by a corset of microtubules; internal mitotic spindle partially described; all endobiotic, except one free-living species. Apomorphy: ‘lapel’ structure as an electron-dense sheet supporting the anterior origin of the peripheral microtubules. *Chilomastix*, *Retortamonas*.
- *Carpediemonas* Ekeboom, 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 homologue. *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 including a conspicuous microtubular paradesm; hydrogenosomes in place of mitochondria. Apomorphy: parabasal apparatus.
- 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*, *Trichomitopsis*, *Trichomonas*, *Tritrichomonas*.
- Cristamonadida Brugerolle and Patterson, 2001  
Parabasalids with a ‘crista’ (crest) consisting of four privileged kinetosomes/flagella, and often hundreds or thousands of additional flagella; all kinetosomes except

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## EXCAVATA cont'd.

- Cristamonadida cont'd.  
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*, *Coronympha*, *Deltotrichonympha*, *Devescovina*, *Foaina*, *Joenia*, *Kofoidia*, *Lophomonas*, *Rhizonympha*.
- Spirotrichonymphida Light, 1927  
Parabasalids 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; from hindgut of lower termites. *Holomastigotes*, *Holomastigotoides*, *Microjoenia*, *Spironympha*, *Spirotrichonympha*.
- Trichonymphida Poche, 1913  
Parabasalids with a rostrum composed of two juxtaposed hemi-rostra associated in bilateral symmetry or with a superimposed tetra-axostyle symmetry; each hemi-rostrum with a privileged kinetosome bearing sigmoid fibres and a flagellar area with hundreds to thousands of 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*. *Barbulanympha*, *Eucomonympha*, *Hoplonympha*, *Spirotrichosoma*, *Staurojoenina*, *Teronympha*, *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*).
- Oxymonadida 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). *Dinenympha*, *Monocercomonoides*, *Oxymonas*, *Polymastix*, *Pyrsonympha*, *Saccinobaculus*, *Streblomastix*.
- *Trimastix* Kent 1880  
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  
Feeding cells sessile and loricate; tubular cristae. Apomorphy: lorica. *Histiona*, *Reclinomonas*. Incertae sedis *Stenocodon*, *Stomatochone*.

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## EXCAVATA cont'd.

- Incertae sedis Jakobida: *Seculamonas* nomen nudum.
- 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 pseudopodia 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*, *Naegleria*, *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*.
- Acrasidae Poche, 1913  
Amoebae aggregate to form fruiting bodies; nucleus may or may not fragment. Apomorphy: formation of fruiting bodies. *Acrasis*, *Pocheina*.
- Incertae sedis Heterolobosea: *Macropharyngimonas halophila* nomen nudum (= *Percolomonas salina* (Ruinen, 1938) Larsen and Patterson, 1990), *Pernina*, *Rosculus*.
- Euglenozoa Cavalier-Smith, 1981, emend. Simpson, 1997  
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 Euglenea and Aphagea are independently descended. *Dinema*, *Entosiphon*, *Peranema*, *Petalomonas*, *Ploetia*.
- Euglenea 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*.
- Aphagea 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*.
- Diplonemea Cavalier-Smith, 1993, emend. Simpson, 1997  
Heterotrophic cells exhibiting pronounced metaboly; in trophic phase, flagella are short and lack paraxonemal rods; sometimes with dispersal phase with longer par-

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**20.** Euglenida: Relationships among phagotrophic euglenids are poorly understood. Most higher taxa proposed within the group are probably not monophyletic and/or are ill defined. No names of higher taxa are in wide use.

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## EXCAVATA cont'd.

- Diplonemea cont'd.  
axonemal rod-bearing flagella; apical papilla, feeding apparatus with “pseudovaness”; giant, flattened cristae. Apomorphy: paraxonemal rods absent in trophic phase, homologous to that in *Diplonema ambulator* Larsen and Patterson, 1990. *Diplonema*, *Rhynchopus*.
- Kinetoplastea 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. *Perkinsiella* is an endosymbiont (“parasome”) of certain amoebae. *Ichthyobodo*, *Perkinsiella*.
- 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*, *Crithidia*, *Cryptobia*, *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; preflagellar rostrum containing apical cytosome. Node: *Cruzella*, *Dimastigella*, *Neobodo*, *Rhynchobodo*, *Rhynchomonas*.
- Parabodonida 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; cytostome, 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, anterior flagellum with non-tubular mastigonemes; phagotrophic; anterolateral cytostome 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; cytostome, when present, simple and close to flagellar pocket; exclusively parasitic. Node: *Blastocrithidia*, *Crithidia*, *Endotrypanum*, *Herpetomonas*, *Leishmania*, *Leptomonas*, *Phytomonas*, *Rhynchoidomonas*, *Sauroleishmania*, *Trypanosoma*, *Wallaceina*.
- Incertae sedis Kinetoplastea: *Bordnamonas*, *Cephalothamnium*, *Hemistasia*.
- Incertae sedis Euglenozoa: *Calkinsia*, *Postgaardi*.

## Incertae sedis EUKARYOTA

- *Ancyromonas* Kent, 1880  
Benthic gliding cells with two unequal flagella; apical anterior flagellum may be very thin or absent; posterior flagellum inserted ventrally/laterally; anterior region forms

Table 2. Classification of the higher ranks of the protists and multicellular groups. cont'd.

## EUKARYOTA cont'd.

- *Ancyromonas* cont'd.  
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*.
  - Apusomonadidae Karpov and Mylnikov, 1989  
Gliding cells with two heterodynamic flagella, one inside a proboscis; flexible organic coverings (perhaps composed of two membranes); vesicular-tubular cristae; ventral groove with lateral folds for feeding, which may extend as pseudopodia; multinuclear plasmodia known; without known cyst stage. *Amastigomonas*, *Apusomonas* (= *Thecamonas* Larsen and Patterson, 1990 = *Rostromonas* Karpov and Zhukov, 1980).
  - 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 centroplast; 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*, *Pseudoraphidiophrys*, *Pseudoraphidocystis*, *Pterocystis*.
    - Heterophryidae Poche, 1913  
Periplasmic mucous coat, with or without organic spicules. *Chlamydaster*, *Heterophrys*, *Oxnerella*, *Sphaerastrum*.
    - Raphidiophryidae Mikrjukov, 1996  
Periplast of siliceous scales or spicules arranged in one or more layers. *Parasphaerastrum*, *Polyplacocystis*, *Raphidiocystis*, *Raphidiophrys*.
  - Collodictyonidae Brugerolle, Bricheux, Philippe, and Coffe, 2002  
Free-swimming cells with two or four equal apical flagella perpendicular 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*, *Diphylleia*.
  - Ebriacea Lemmermann, 1901 [Ebriidae Poche, 1913]  
Cells with two subapically inserting flagella; open internal skeleton of silica; phagotrophic, without plastids. *Ebria*, *Hermesinum*.
  - Spironemidae Doflein, 1916 [Hemimastigophora Foissner, Blatterer, and Foissner, 1988]  
Flagella lateral 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 Vørs, 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; Pseudociliatea Cavalier-Smith, 1981; Pseudociliatida Corliss and Lipscomb, 1982; Stephanopogonidae Corliss, 1961]  
Cells with many similar flagella arranged as unikinets in rows; cytostome for phagocytosis at anterior; single nucleus; discoidal cristae. *Stephanopogon*.
-

Table 3. Genera with uncertain affiliation within protists. Based on Patterson (2002), and modified from that presented on Tree of Life website <http://tolweb.org> (accessed December 16, 2004).

<i>Acinetactis</i>	<i>Embryocola</i>	<i>Parastasiella</i>
<i>Actinastrum</i>	<i>Endemosarca</i>	<i>Peliainia</i>
<i>Actinellius</i>	<i>Endobiella</i>	<i>Peltomonas</i>
<i>Actinocoma</i>	<i>Endomonas</i>	<i>Penardia</i>
<i>Actinolophus</i>	<i>Endospora</i>	<i>Petasaria</i>
<i>Adinomonas</i>	<i>Endostelium</i>	<i>Phagodinium</i>
<i>Aletium</i>	<i>Enteromyxa</i>	<i>Phanerobia</i>
<i>Alphamonas</i>	<i>Eperythrocytozoon</i>	<i>Phialonema</i>
<i>Amphimonas</i>	<i>Errera</i>	<i>Phloxamoeba</i>
<i>Amphitrema</i>	<i>Euchitonia</i>	<i>Phyllomonas</i>
<i>Amylophagus</i>	<i>Euglenocapsa</i>	<i>Physcosporidium</i>
<i>Aphelidiopsis</i>	<i>Fromentella</i>	<i>Piridium</i>
<i>Apogromia</i>	<i>Glaucocystopsis</i>	<i>Platytheca</i>
<i>Archaeosphaerodiniopsis</i>	<i>Globidiellum</i>	<i>Pleuophrys</i>
<i>Artodiscus</i>	<i>Goniodinium</i>	<i>Pleuromastix</i>
<i>Asterocaelum</i>	<i>Gymnococcus</i>	<i>Pleurostomum</i>
<i>Asthmatos</i>	<i>Gymnophrydium</i>	<i>Podactinellus</i>
<i>Astrolophus</i>	<i>Haematotractidium</i>	<i>Podostoma</i>
<i>Aulomonas</i>	<i>Hartmannina</i>	<i>Polysporella</i>
<i>Aurospora</i>	<i>Heliobodo</i>	<i>Pontomyxa</i>
<i>Barbetia</i>	<i>Heliomonas</i>	<i>Protenterospora</i>
<i>Belaria</i>	<i>Hermisenella</i>	<i>Protogenes</i>
<i>Belonocystis</i>	<i>Heterogromia</i>	<i>Protomonas</i>
<i>Berghiella</i>	<i>Heteromastix</i>	<i>Protomyxa</i>
<i>Bertarellia</i>	<i>Hillea</i>	<i>Pseudoactiniscus</i>
<i>Bertramia</i>	<i>Histiophysis</i>	<i>Pseudosporopsis</i>
<i>Bjornbergiella</i>	<i>Hyalochlorella</i>	<i>Quadrifilia</i>
<i>Bodopsis</i>	<i>Hyalodaktylethra</i>	<i>Raphidiophryopsis</i>
<i>Boekelovia</i>	<i>Imnoplasma</i>	<i>Reticulamoeba</i>
<i>Branchipocola</i>	<i>Isoselmis</i>	<i>Rhabdospora</i>
<i>Campanoeca</i>	<i>Kamera</i>	<i>Rhizomonas</i>
<i>Camptoptycha</i>	<i>Kibisidytes</i>	<i>Rhizoplasma</i>
<i>Chalarodora</i>	<i>Kiitoksia</i>	<i>Rhynchodinium</i>
<i>Chlamydomyxa</i>	<i>Labyrinthomyxa</i>	<i>Rigidomastix</i>
<i>Cibdelia</i>	<i>Lagenidiopsids</i>	<i>Salpingorhiza</i>
<i>Cichkovia</i>	<i>Leptophrys</i>	<i>Schewiakoffia</i>
<i>Cinetidomyxa</i>	<i>Leukarachnion</i>	<i>Sergentella</i>
<i>Cingula</i>	<i>Liegeosia</i>	<i>Serpentoplasma</i>
<i>Cladomonas</i>	<i>Ligniera</i>	<i>Servetia</i>
<i>Clathrella</i>	<i>Lithocola</i>	<i>Spermatobium</i>
<i>Clautriavia</i>	<i>Luffisphaera</i>	<i>Sphaerasuctans</i>
<i>Codonoeca</i>	<i>Lymphocytozoon</i>	<i>Spiriopsis</i>
<i>Coelosporidium</i>	<i>Lymphosporidium</i>	<i>Spirogregarian</i>
<i>Copromonas</i>	<i>Macappella</i>	<i>Spongastericus</i>
<i>Cristalloidophora</i>	<i>Magosphaera</i>	<i>Spongocyclia</i>
<i>Cyanomastix</i>	<i>Malpighiella</i>	<i>Stephanomonas</i>
<i>Cyclomonas</i>	<i>Martineziella</i>	<i>Strobilomonas</i>
<i>Cytamoeba</i>	<i>Megamoebomyxa</i>	<i>Syncrypta</i>
<i>Dallingeria</i>	<i>Melanodinium</i>	<i>Telonema</i>
<i>Dictyomyxa</i>	<i>Meringosphaera</i>	<i>Tetragonidium</i>
<i>Dimastigamoeba</i>	<i>Microcometes</i>	<i>Thalssomyxa</i>
<i>Dinamoeba</i>	<i>Microgromia</i>	<i>Thaulirens</i>
<i>Dinemula</i>	<i>Monodus</i>	<i>Thaumatodinium</i>
<i>Dingensia</i>	<i>Mononema</i>	<i>Theratromyxa</i>
<i>Dinoasteromonas</i>	<i>Myrmicisporidium</i>	<i>Thylakomonas</i>
<i>Dinoceras</i>	<i>Myxodictyum</i>	<i>Topsentella</i>
<i>Dinomonas</i>	<i>Naupliicola</i>	<i>Toshiba</i>
<i>Diplocalium</i>	<i>Nephrodinium</i>	<i>Toxocystis</i>
<i>Diplomita</i>	<i>Neurosporidium</i>	<i>Triangulomonas</i>
<i>Diplophysalis</i>	<i>Ovicola</i>	<i>Trichonema</i>
<i>Diploselmis</i>	<i>Pachydinium</i>	<i>Trizona</i>
<i>Dobellina</i>	<i>Palisporomonas</i>	<i>Trophosphaera</i>
<i>Ducellera</i>	<i>Pansporella</i>	<i>Urbanella</i>
<i>Echinococcidium</i>	<i>Paradinemula</i>	<i>Wagnerella</i>
<i>Ectobiella</i>	<i>Paramastix</i>	<i>X-cells</i>
<i>Elaeorhanis</i>	<i>Paramonas</i>	
<i>Elleipsisoma</i>	<i>Paraplasma</i>	

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## APPENDIX 1.

## SELECTED REFERENCES TO PROTIST GROUPS

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