The Diversity of Eukaryotes

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ABSTRACT: The discipline of evolutionary protistology has emerged in the past 30 yr. There is as yet no agreed view of how protists are interrelated or how they should be classified. The foundations of a stable taxonomic superstructure for the protists and other eukaryotes lie in cataloging the diversity of the major monophyletic lineages of these organisms. The use of common patterns of cell organization (ultrastructural identity) seems to provide us with the most robust hypotheses of such lineages. These lineages are placed in 71 groups without identifiable sister taxa. These groups are here referred to as "major building blocks." For the first time, the compositions, ultrastructural identities, synapomorphies (where available), and subgroups of the major building blocks are summarized. More than 200 further lineages without clear identities are listed. This catalog includes all known major elements of the comprehensive evolutionary tree of protists and eukaryotes. Different approaches among protistologists to issues of nomenclature, ranking, and definitions of these groups are discussed, with particular reference to two groups—the stramenopiles and the Archezoa. The concept of "extended in-group" is introduced to refer to in-groups and the most proximate sister group and to assist in identifying the hierarchical location of taxa.

Keywords: protist diversity, protozoa, eukaryotes, evolutionary protistology, extended in-group.

The protists are a monophyletic (sensu Ashlock 1971) but paraphyletic group of eukaryotes. That is, the protists arose from a single source, the first eukaryotes, but some of the descendants of this ancestor are not (yet) considered to be protists. The eukaryotes that are excluded from the protists are the sister group of the choanoflagellates (the animals), the sister group of the charophytes (the plants), and the sister group of the chytrids (the fungi). The protists have been around for at least twice as long as any of the major multicellular groups. In terms of cytological diversity and abundance (if not species diversity), they dominate the world of eukaryotes. They include autotrophs, heterotrophs, and mixotrophs and can be found in any habitat in which there is a free aqueous phase, and cysts or other resistant forms may be found in other habitats. Most protists are small (5–20 μm), but they range in size from 1 μm to tens of meters long. Most protists are unicellular, but many are multicellular.

History

The discipline of evolutionary protistology is emerging from 30 yr of considerable upheaval (fig. 1). Much has yet to be done to create a comprehensive and coherent understanding of eukaryote evolution and to create a matching classification scheme. The transition period is distinguished by many new concepts and by progress along variously productive routes. A major, and possibly the most solid, development of this period has been the use of patterns of ultrastructural organization to distinguish monophyletic lineages of protists (Patterson 1994). It is for this reason that the discipline of evolutionary protistology could only develop solid foundations with the advent of reliable techniques of preservation of biological materials for electron microscopical examination. This happened in the 1960s. An older view of the diversity of protists developed from a light microscopical perspective has now given way to one in which the major groups of eukaryotes are regarded as those groups that share a common cytological organization (an "ultrastructural identity"; Patterson and Brugerolle 1988).

An ultrastructural identity refers to a variety of features made visible by electron microscopy. They include (but are not restricted to) the following: the shape of the cristae in the mitochondria (cristae may be tubular, long or bleb shaped, or branching; they may be discoidal, with or without a pedicel; or they may be flat plates—only very rarely does the form of cristae vary within a species or group of protists); the presence or absence of hairs, scales, or other excrescences on the flagella; the component parts of the transition region where the 9 + 2 organization of the axoneme transforms into the nine-triplet structure of the basal bodies; the length and orientation of the basal bodies and their associations with other organelles; the nature of the microtubular and

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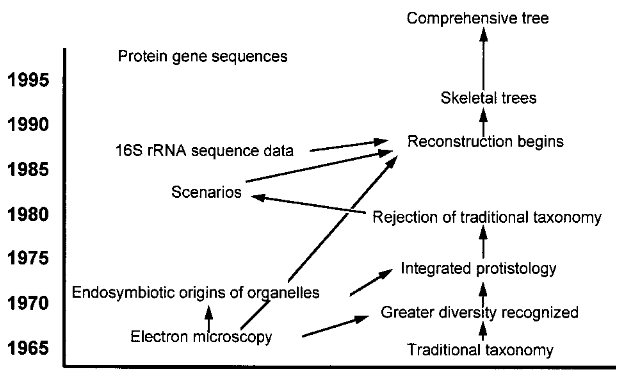

Figure 1: Summary of changes in evolutionary protistology in the past 30–35 yr.

other rootlet structures that arise from the basal bodies and the associations between these and other organelles; the source and deployment of other microtubular or other cytoskeletal arrays within the cell, especially under the cell surface; the nature, composition, origins, and appearance of any extracellular materials; the presence and nature of microtubule organizing centers; the number, nature, and heterogeneity of nuclei, structures within the nuclear envelope, intranuclear and paranuclear inclusions; the behavior of the nuclear envelope during mitosis (Is it retained, is it completely lost, or is it perforated in regions by the intruding spindle?); the behavior of the mitotic spindle (Where does it nucleate, is it located within the nucleus or external to the nucleus, or does it start in the cytoplasm and penetrate into the nucleus?); if there is a chloroplast, how many bounding membranes, how many thylakoids per lamella, the presence and nature of contained (e.g., stigma) or associated (e.g., nucleomorph) organelles; the identity and nature of other endomembranous organelles in the cell; and other idiosyncrasies.

The robustness of groupings (i.e., our hypotheses about what is related to what) defined by reference to ultrastructural identities to new data (i.e., to being tested) is virtually total (Patterson 1994). Through this process, descriptive protistology establishes major terminals or building blocks that phylogeneticists must then assemble into some form of evolutionary edifice as sister groups become evident. Several years ago, the vast majority of major taxa with a single ultrastructural identity were without sister groups. Now some of these have been brought together to form larger and also robust groupings. Examples include euglenids and kinetoplastids within the Euglenozoa; the chrysophytes sensu lato, opalines, oomycetes, diatoms, brown algae, inter alia to form the stramenopiles; and chytrids, choanoflagellates, fungi, and animals to form the opisthokonts.

A further body of data has been invaluable in seeking to explore evolutionary relationships. This is the one that incorporates the data on sequences of bases in genes. This approach has corroborated the groupings developed on the basis of ultrastructure and has suggested more extensive relationships. The first useful overall molecular trees were based on genes for the small subunit ribosomal RNA. As discussed elsewhere in this volume (Katz 1999; Roger 1999), the use of additional molecules has led to differing insights and now requires a reevaluation of the initial molecular insights.

Classificatory Philosophies in Protistology

Evolutionary edifices usually take the form of trees (dendrograms) or of classification schemes. Some protistologists (e.g., Lipscomb 1984; Patterson 1994; Simpson 1997) are convinced of the utility of creating monophyletic and holophyletic groups (i.e., organisms from a single source and all descendants therefrom). They are consequently committed to developing classification schemes that can easily be converted into evolutionary schemes (and vice versa) by sets of simple rules that have been developed within protistology (e.g., Patterson 1986) or have been reviewed more generally (Wiley 1981). The basic logic is that the hierarchical structure within a classification scheme should reflect the sister-group relationships of the lineages. The approach is that of the phylogenetic systematists and produces a logic that can be applied to all taxa, and the fidelity and consistency of the approach can be assessed (Wiley 1981). Ideally, this should lead discussion within evolutionary protistology into a mode of progression, rather than unresolvable dispute about details that arise from incompatible philosophies. To achieve the end of phylogenetic systematics, polyphyletic groups must be eliminated and paraphyletic groups must be minimized.

Among contemporary protistologists, only Cavalier-Smith (e.g., 1998) has developed a comprehensive classification using a logic that differs from the philosophy of phylogenetic systematics. Broadly speaking, this philosophy accepts evolutionary relationships as only one of several factors that will determine groupings of organisms. The ranking and compositions of taxa may (or may not) be determined by additional factors such as the "importance" of the group (e.g., Cavalier-Smith 1981, 1983, 1998).

Many of the other classification schemes of recent years (e.g., Krylov et al. 1980; Levine et al. 1980; Corliss 1984, 1994; Möhn 1984; Sleigh et al. 1984; Margulis et al. 1990; Leipe and Hausmann 1993; Hülsmann and Hausmann 1994; inter alia) have no explicit philosophy. Rather, they use a variety of criteria to create subsets of eukaryotic life. These criteria may include a desire to retain some but not all elements of historical classifications because of their familiarity (e.g., Corliss 1994). These later approaches foster subjectivism within classification. This in turn leads to the defense of paraphyletic taxa and the dispersal of the rigor that eliminates polyphyletic taxa. Speculation (here intended to refer to assertions that lack an evidential basis or are inconsistent with some evidence, or to situations where the relationship between the assertion and the evidence is ambiguous) becomes an admissible criterion by which taxa may be classified. The lack of agreed ground rules impedes the emergence of explicit arguments based on logic and data. The results are taxonomic schemes that, in their structure, fail to reveal the authors' understanding of relatedness in obvious and simple ways. A dispute arising from different approaches also directs efforts away from the fairly massive task of compiling and agreeing on all relevant and appropriate data since many schemes are flawed by not including all available information or by misinterpreting some of it (e.g., Lipscomb 1985).

The current situation, in which there are a number of different and apparently incompatible classification schemes, is confusing for observers and participants alike. This confusion can be reduced if the discussion on philosophy can be separated from the debate on the taxa that emerge as the result of the application of the philosophy. Constructive debate on taxa only takes place within the context of its relevant philosophy and not between philosophies.

The general discussion that follows is divided into a discussion on options that seem to apply within protistology. The longer part of this article elaborates an earlier effort (Patterson 1994) to list all major lineages for which no sister taxon can be identified or for which there is no agreement. The list is set in the context of phylogenetic systematics. It contributes to the assembly of a scheme of classification for the major evolutionary lines of eukaryotes in which the hierarchical structure is determined by insights into ancestor/descendent relationships. This list does not refer to schemes arising from other philosophies or taxa derived from them except where those approaches have intentionally or accidentally produced monophyletic and holophyletic groups. In a sense, the resulting list may be thought of as a boundary between understanding evolutionary relationships and ignorance.

Naming of Taxa and the Exemplar Groups, Stramenopiles and Archezoa

The following discussion of how protistologists have tended to address nomenclature, ranks, and definitions refers to two particular groups—the stramenopiles (Patterson 1989) and the Archezoa (Cavalier-Smith 1983). The groups were conceived in different ways, and reference to them helps to clarify the benefits and disadvantages of different approaches.

Names are labels that refer to a collection of organisms. The naming of a taxon is an exercise that follows from the identification of a group of organisms. The way in which a name is applied is often independent of the process of defining a taxon. Although it would be ideal for there to be universal agreement on how names should be determined and used, there are few or no nomenclatural codes or guidelines as to spelling, priority, or other factors that operate above the level of family to protect stability and clarity.

The quality of a name can be judged in reference to several criteria that will protect clarity and stability. First, the link between the name and the group should be unambiguous. Each label should either refer to a definition or to a particular composition of a taxon. Second, the same name should not refer to different collectives or organisms (i.e., there should be no homonyms). Third, the meanings of names should not change with time. Finally, names should have a long life.

"The stramenopiles" was a concept introduced to allow reference to a collection of protists many of which had previously been referred to as "heterokont algae," "chromophytes," "chrysophytes," or "chromists" (Patterson 1989). During their long history, earlier concepts accreted and shed various subtaxa (Green et al. 1989). This was because it was evident that algal "heterokonts" (defined by having different kinds of flagella) were related to algae that were not heterokonts (such as diatoms or kelps) and to various organisms that were "fungi" (the Oomycetes) or protozoa (opalines). The traditional groupings that relied on composition or circumscription or on key characters were proving to be ambiguous and incapable of responding to the accelerating insights of evolutionary protistology except by considerable changes in meaning of the term "heterokont." The term "stramenopiles" was introduced to refer to a similar but monophyletic and holophyletic group defined by a character innovation, that is, that group of organisms having tripartite hairs or derived from such organisms.

The stability of this label is dependent on the homology of the defining synapomorphic trait (in this case, the tripartite tubular hairs). Although there is some uncertainty about whether the hairs of cryptomonads or the body hairs of proteromonads are homologous with the tripartite hairs (Green et al. 1989), the concept does appear to be robust. Although the composition of the taxon has changed, the way the name was introduced makes its meaning independent of composition. The most destabilizing factor has been the translation of the term into "traditional" taxonomy (i.e., with a rank and a diagnosis) that has led to various changed spellings (e.g., the straminipiles of Ragan and Gutell [1995]) or its treatment as a synonym of alternative concepts (e.g., Lipscomb et al. 1998).

The Archezoa was introduced by Cavalier-Smith (1983), which, from subsequent usage, appears to have been intended to refer to the most primitive ("basal paraphyletic") eukaryotes (Cavalier-Smith 1998). The word "Archezoa" had been introduced into the literature independently and with different meanings by Haeckel (see Copeland 1956) and by Perty (1852). The existence of homonyms is unfortunate, but Haeckel's and Perty's uses are now obsolete. Any ambiguity in respect to the homonyms can be resolved by relying on the context to clarify the meaning of the word (i.e., by stating Archezoa, sensu Cavalier-Smith 1991*a*).

Ranks and Hierarchy

The past 30 yr have seen a proliferation of phyla and kingdoms largely among the protists. In 1964, the Society of Protozoologists created a scheme of classification with a single phylum of protozoa (Honigberg et al. 1964). More recent classification schemes that use ranks contain dozens of phyla (e.g., Corliss 1984; Cavalier-Smith 1998) within a variable number of kingdoms. This taxonomic inflation and the use of different ranks in a short space of time is disquieting.

It is not unusual to encounter statements along the lines of "the morphological and chemical uniformity of (the group) is so marked that they should be ranked only as phylum" (Cavalier-Smith 1998); there is rarely any discussion, let alone agreement, as to what criteria underpin such a statement. Ranking is consequently subjective. The same group can simultaneously or sequentially have different ranks without the acquisition of new knowledge (Patterson 1986). The rank of a given taxon may be determined by an arbitrary mixture of factors such as distinctiveness, numbers of subordinate taxa, age, sister group relationships, and ego of author. The rank of a taxon may be driven by a hierarchical structure starting from genus and going up or starting from kingdom and working down. The latter seems to be the most widespread approach but is not applied in any rigid fashion.

The most reasonable approach consistent with phylogenetic systematics is to assign sister taxa the same rank. On the downside, this approach would be incomplete because we do not know all relationships and it would destabilize the existing hierarchical structure and would require a change in rank with every new insight.

The term "stramenopiles" (table 1) was introduced as a rankless informal name (i.e., spelled "stramenopiles," not "Stramenopiles"). The group has been included within a rankless hierarchy with subtaxa (Patterson 1994). This has not impaired its use. Some authors have sought to formalize the name and apply a rank (the Kingdom Stramenopila; Beakes 1998).

Table 1: Current composition of the stramenopiles

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

The Archezoa was introduced with the rank of subkingdom and currently has this rank, although it, in the interval, has been ranked as a kingdom and as a superkingdom (Cavalier-Smith 1983, 1990, 1993, 1998). The instability of the rank suggests that it does not reflect ancestor-descendent relationships, distinctiveness of the organisms in the group, or even composition of the group because the same rank is applied to "Archezoa" with differing compositions (table 2). This particular case indicates that ranks do not need to be determined by objective criteria but are (usually?) determined by a subjective assessment of equivalency with other evolutionary concepts.

Ranks are potentially and actually unstable and so communicate little or no unambiguous information. The case of the stramenopiles illustrates that ranks are not needed. I conclude that ranks are superfluous and are not applied here.

Defining Taxa

Taxa may be defined in a variety of different ways. Unless some effort is made to reflect on this, multiple types of definition may be used simultaneously. As these may be in conflict or may come into conflict after the acquisition of new data or insights, the result can be ambiguity or confusion. Some of the approaches that protistologists seem to have taken to defining taxa are listed below. Most groups are defined by an unspecified amalgam of these definitions.

Typified Definitions. Typified definitions are those definitions in which the concept of a group (and its name) is tied to the type genus. The name of the genus is driven by considerations of priority. This is a rather botanical tradition, an example is Prymnesiophyta (a synonym of Haptophyta). The Prymnesiophyta is then the division within which the genus *Prymnesium* finds itself. This approach stabilizes the name. However, changes in composition of the group may emerge from changed perceptions of relatedness or by arbitrary shifts in rank. In such cases, the defining concept survives even in the event of considerable change in composition, circumscription, or phylogenetic location. As phylogeny is appropriately becoming the dominating ethos in taxonomy, "typified definitions" tend not to be able to reflect phylogenetic insights and such definitions are here regarded as undesirable.

Circumscriptive Definitions. Circumscriptive definitions seek to describe the appearance of all included taxa. Frequently they can include contrasting characters (e.g., "possessing mitochondria and peroxisomes" and "when mitochondria and peroxisomes are both secondarily absent"), nondefining characters (e.g., "predominantly unicellular, plasmodial, or colonial"), or even to negative characters such as "haptonema absent" (examples from the diagnosis of Protozoa; Cavalier-Smith 1993). This is probably the most widespread approach to defining groups. These definitions may emphasize one or a few characters. This approach may describe taxa but can fail to distinguish taxa. It is reactive in the sense that the definition does not determine membership, membership determines the definition. There is often no clear link between the name, definition, and composition. This approach allows more than one concept of the taxon to exist at the same time. Although circumscriptive definitions could easily be regarded as "bad," these less appetizing traits seem not to be an impediment to their continued use.

Definitions by Composition. These seek to define a group by the subordinate taxa included within it. Such an approach is precise at any one time, but any changes in composition will cause a change in the concept. One name will have many meanings with the passage of time. The resulting ambiguity can only be dispelled by a detailed reference to the context in which the term is used. An alternative to allowing the meaning of the name to drift is to introduce a new name with every change in composition. This would be highly destabilizing and confusing. Compositional definitions foster ambiguity and are therefore not desirable.

Phylogenetic Definitions. Phylogenetic definitions were mentioned by Cavalier-Smith (1998). This approach seems

Table 2: Composition of the Archezoa

	1983	1983	1987	1989	1990	1991	1993	1995	1996	1997	1998	1999
Diplomonads	X	X	X	X	X	X	X	X	X	X	X	X
Retortamonads	X	X	X	X	X	X	X	X	X	X	X	X
Oxymonads	X	X	X	X	X	X	X	X	X	X	X	X
Microspora	X	X	X	X	X	X	X	X	X			
Hypermastigids	X	X	X								X	X
Trichomonads	X	X	X								X	X
Mastigamoebids			X	X	X	X	X	X				
Pelomyxa		X	X	X	X	X						
Entamoeba		X	X	X	X							
Phreatamoeba						X	X					
Trimastix											X	

Note: In terms of the list presented in this publication, hypermastigids and trichomonads form part of the parabasalids, and the mastigamoebids, *Pelomyxa* and *Phreatamoeba*, are pelobionts (after Cavalier-Smith 1983, 1987*a*, 1987*b*, 1989, 1990, 1991*a*, 1991*b*, 1992, 1993, 1995, 1996–1997, 1999, 1998, 1999; Cavalier-Smith and Chao 1995, 1996).

to allow groups to be defined by one or more evolutionary events or hypotheses as to what evolutionary events might have taken place. One of these defining elements would define a monophyletic group, whereas others (which may or may not be used) may identify the evolutionary events associated with the emergence of subsets that are excluded from the group. Synapomorphic definitions exclude the speculative element of these definitions and make the inclusion of paraphyletic taxa less likely.

Synapomorphic Definition. Taxa can be defined by reference to those evolutionary innovations (apomorphies) associated with the emergence of the group. Eukaryotes may be defined as living things with nuclei or derived from such organisms. Most characters appeared once in evolutionary lineages (there are exceptions caused by symbioses or other forms of lateral transfer). All characters therefore have the capacity to define monophyletic and holophyletic groups. Groups defined by these criteria include all descendants of the first common ancestor with the synapomorphic character, even if the synapomorphic feature has been lost.

The advantages of using synapomorphic definitions were envisaged as being, first, that they clearly determine criteria for admission to the taxon; second, that they create monophyletic and holophyletic taxa that can be easily located within phylogenetic classification; third, that they are consistent with the dominant philosophy of phylogenetic reconstruction and classification; fourth, that the meaning of the name is independent of the composition of the grouping (the meaning of "the stramenopiles" is independent of whether the actinophryid heliozoa or opalines are included or excluded); and, fifth, that the resulting nomenclature is stable if the principle by which the name was defined is respected (but can be destabilized if it is equated with a circumscriptive or compositional definition). The disadvantages of synapomorphic descriptions are that they give little indication of the contents of the group; that they may mislead or confuse those unversed in phylogenetic systematics in cases where synapomorphic characters are transformed or lost within a group; and that they cannot be used universally because synapomorphies for many taxa are unknown and may indeed be nonexistent.

A taxon defined by reference to synapomorphy is destabilized (falsified?) only by agreement that the defining character is homoplasious. This would indicate that the group so defined is polyphyletic.

The synapomorphic definition can be made more utilitarian by adding a "binomial" dimension to place it within the context of a broader phylogeny. This can be done by defining the in-group with reference to the next most extensive group of organisms that includes the in-group. This ideally will link the in-group to the sister group. This next most inclusive cluster is here referred to as the "extended in-group." As an example, we might define the ciliates as the alveolates with nuclear dimorphism or derived from alveolates with nuclear dimorphism. In this case, the ciliates are the in-group, the alveolates are the next most inclusive (resolved) clade, and nuclear dimorphism is the synapomorphy of the in-group. Because the relationship between sister group and the in-group may change as phylogenetic insights develop, stability can only be protected by recognizing that the extended in-group is not part of the synapomorphic definition but an adjunct to it.

Synapomorphic definitions have been applied to the stramenopiles and to the minimal group containing the euglenids and kinetoplastids (Simpson 1997). The latter group (Euglenozoa) has also been defined in other ways. The approach has yet to be universally applied to all major types of eukaryotes listed elsewhere (Patterson 1994). I have tried to do that here.

The term "stramenopiles" was introduced as a test case for the use of synapomorphic definitions among protists. The concept has been widely used by protistologists, especially in the context of phylogenetic schemes to which it is well suited (e.g., Sogin et al. 1996; Beakes 1998). Alternative concepts (heterokonts, chromists, etc.) are also widely used. The "stramenopiles" has survived compositional adjustments—as it was designed to. The concept therefore appears robust and utilitarian but not persuasive. It has been confused somewhat by being regarded as equal or equivalent to traditional concepts (e.g., Lipscomb et al. 1998).

The "Archezoa" was initially defined as "containing those protozoan phyla that totally lack mitochondria (i.e., the Parabasalia [20], Metamonadina [2], the Microspora [5])" (Cavalier-Smith 1983, p. 1028) and by the statement that "I suggest also that the various amoebae such as *Entamoeba* and *Pelomyxa palustris* which lack mitochondria be removed from the phylum Sarcodina to form a further phylum of Archezoa called Archamoebae" (Cavalier-Smith 1983, p. 1029). Largely on the basis of the use of the "i.e." in the original definition, this was interpreted to mean that the Archezoa was defined by composition (Patterson 1988). This has been disputed (Cavalier-Smith 1998) with the suggestion that the definition is "phylogenetic." The group is paraphyletic and defined by two evolutionary events—the first being the emergence of eukaryotes and the second being the appearance of mitochondria. The group was defined as a subset of the "Protozoa," but this too is confusing because during the life of the Archezoa, the same author has conceived of the protozoa as excluding Archezoa (e.g., Cavalier-Smith 1990). The composition and rank of the group has been unstable (table 2). Despite the ambiguities, this term is in fairly wide use within evolutionary protistology.

Ultimately, the use of ranks, definitions, and hierarchy should serve to add value to concepts and to reduce ambiguity. What debate currently exists tends to defend past practices rather than to concentrate on the needs of the future. A progressive debate is still needed to identify weaker practices and replace them with better practices. At this time, and in the absence of agreement, I have segregated the major different approaches of defining taxa and applied them independently, and in a summary form, to all groupings for which sister groups are not widely accepted.

Eukaryotic Taxa without Known Sister Groups

The listing below is an elaboration of Patterson (1994) but is still an abbreviated and summary treatment. References have been kept to the minimum needed to provide an entrée into the literature. Taxa are listed on the basis of two criteria. First, there is no agreement as to what is their sister taxon. Second, they have a clear—usually ultrastructural—identity. Taxa without clear identities are relegated to simple lists. Those taxa with clear sister group relationships have been subordinated even if they have distinctive ultrastructural identities (this applies primarily to members of the stramenopiles, alveolates, euglenozoa, and opisthokonts). This resulting list provides the component elements for the comprehensive tree of eukaryotes.

In addition to the taxa with discrete identities, there are approximately 220 genera that have been described but which still lack a contemporary identity and are unplaceable within a phylogenetic classification. Taxa are listed in broad adaptive groups (table 3).

Acantharea

Circumscription: One of several groups of "radiolaria"—large marine unicells with radiating axopodia and an inorganic skeleton (in the case of Acantharea composed of 10/20 spicules made of strontium sulphate). Cell with central endoplasm and peripheral ectoplasm separated by a fibrous capsular wall, outside face of cytoplasm coated with a fibrous cortex that is joined to spicules by contractile myonemes. Often with symbionts. No propulsive organelles in trophic form but may have flagellated stage and/or amoebas and/or cysts in life cycle.

Ultrastructural identity: Not well established because of difficulty of good preservation. Mitochondria with tubular cristae. Axopodia arising from unspecified sites in the cytoplasm but having an open hexagonal or larger polygonal arrays of microtubules; periplasmic cortex axopodia details, extrusomes, and so forth. With concentric extrusomes. Mitosis involves an eccentric spindle located inside an intact nuclear envelope.

Synapomorphy: Tubulocristae protists with strontium sulphate skeleton with symmetry based on 20 radial elements.

Composition: About 150 species in 50 genera in four or five major subtaxa defined by skeletal characteristics.

Reference: Febvre 1990.

Actinophryids

Circumscription: One of several groups of organisms previously placed together as the heliozoa; round bodies with radiating stiff arms (axopodia); cell surface naked, no flagellated stage known. With one or many nuclei; siliceous plates or other siliceous aggregates form one layer of an encysted state. Affinities not known; possibly related to the pedinellids, a group of stramenopiles.

Ultrastructural identity: Mitochondria with bleblike (tubular) cristae. Axopodia supported by axonemes with microtubules in double polygonal spiral and nucleating on nucleus or amorphous material. Two types of extrusomes: one larger homogeneous and osmiophilic, the other smaller and more heterogeneous. Dictyosomes typically associated with nuclei. Mitosis with microtubules penetrating from the cytoplasm, nuclear envelope mostly fragments.

Synapomorphy: Tubulocristate protists with double polygonal spiral arrangement of microtubules in axopodia.

Composition: Probably with only two genera, *Actinophrys* and *Actinosphaerium* (the latter probably having *Echinosphaerium* and *Camptonema*) as synonyms.

Reference: Smith and Patterson 1986.

Alveolates

Circumscription: A significant group containing many species of "algae" and "protozoa"—both free-living and parasitic. Grouping suggested initially by the presence of the alveoli (see "synapomorphy"). Began to appear in discussions in the early 1980s; the grouping was confirmed by Gajadhar et al. (1991); the colloquial name was formally introduced into the literature by Cavalier-Smith. With three major subsets, the ciliates distinguished by nuclear dimorphism and cilia arranged in kineties. The dinoflagellates mostly with nuclei with unusual condensed chromosomes, and the apicomplexa—a group dominated by intracellular and extracellular parasites but including the agent for malaria. Structurally very complex.

Ultrastructural identity: Mitochondria tubulocristate, cell surface underlain by a system of abutting sacs—the alveoli. Dictyosomes often reduced. Contains several lineages each with discrete ultrastructural identities (i.e., ciliates, apicomplexa, and dinoflagellates). Group has various idiosyncrasies such as eyes, ingestion devices, cytoproct, and extrusomes. Flagella when present (whether as flagella or cilia) typically with at least one cross-striated fibrous root.

Synapomorphy: Tubulocristate protists with cortical alveoli (cortical alveoli defined as abutting sacs without attached ribosomes and not contiguous with other membranous systems and that form a continuous layer under the plasma membrane broken only by penetration of ingestion and egestion organelles, extrusomes, etc.).

Composition: Includes the Apicomplexa (inclusive of the predatory flagellates *Acrocoelus*, *Colpodella*, and the parasitic *Perkinsus*, which get from one host to another as swimming forms), the ciliates (Ciliophora), and the dinoflagellates. Some consider affinities with one other flagellate, *Colponema*. However, the identity of this genus and the alveolate nature of the subsurface sacs in this genus still need to be clarified. Haplosporidia also excluded as structural evidence does not support molecular insights of an affinity between these and the alveolates.

References: Mignot and Brugerolle 1975; Gajadhar et al. 1991; Patterson and Zölffel 1991; Cavalier-Smith 1993.

Ancyromonas

Circumscription: Heterotrophic gliding flagellates, small (<10 μm), with one recurrent flagellum and one anterior flagellum. Mostly documented at light microscopical level some ultrastructural information (Mylnikov 1990) under the generic name *Heteromita*.

Ultrastructural identity: Mitochondria with flat cristate. Cell surface supported by materials both within and external to the cell membrane. Two flagella, bases at right angles, three microtubular roots. Ball and cone style extrusomes present.

Synapomorphy: None specified.

Composition: Single genus with probably only three species.

References: Mylnikov 1990; Patterson and Simpson 1996.

Apusomonads

Circumscription: Gliding biflagellated heterotrophic protists with organic dorsal sheath. One flagellum projecting anteriorly, ventral side is naked and may produce pseudopodia. Probably consume bacteria. Argued by Cavalier-Smith and Chao (1995) to be related to the opisthokonts = (animal + choanoflagellate) + (fungi + chytrid) clade; a conclusion that seems to be premature.

Ultrastructural identity: Mitochondria tubulocristate, dorsal face of cell supported by an organic and intracellular theca. Flagella with two basal bodies located almost orthogonally and giving rise to microtubular roots, two of which seem to determine the margins of the ventral face of the cell.

Synapomorphy: Not specified but probably will refer to internal dorsal organic sheath.

Composition: Two genera: *Apusomonas* and *Amastigomonas*.

References: Patterson and Larsen 1991; Cavalier-Smith and Chao 1995.

Biomyxa

Circumscription: Amoeboid protist, with stiff pseudopodia that may branch and anastomose, may produce cysts and exist as uninucleate or multinucleate amoebas. Historically classified either as a member of the ill-defined proteomyxids or the equally ill-defined athalamid granuloreticulosea. Affinities with foraminifera possible but need to be confirmed.

Ultrastructural identity: Ultrastructural studies not coupled with light microscopical studies, so there is some debate as to the identity of the organism(s) studied by electron microscopy. Mitochondria tubulocristate. With dark inclusions; microtubules in the pseudopodia are not in geometric arrays

Synapomorphy: None specified.

Composition: Small and uncertain number of species.

References: Anderson and Hoeffler 1979; Patterson et al. 1999.

Caecitellus

Circumscription: Biflagellated gliding protist, heterotrophic, one flagellum projecting anteriorly, one trailing, with a posterio-lateral ingestion apparatus. Argued by some to be related to bicosoecids.

Ultrastructural identity: Tubulocristate mitochondria, two flagella giving rise to four microtubule roots; no hairs, scales, or other excrescences attached to flagella or cells surface. One of two studies shows osmiophilic structures in support of a mouth linked to roots arising from the basal bodies.

Synapomorphy: As yet unspecified but probably will relate to the structure of the feeding apparatus.

Composition: One species, *Caecitellus parvulus*.

References: Patterson and Zölffel 1991; Patterson et al. 1993; O'Kelly and Nerad 1998.

Carpediemonas

Circumscription: Cell with two flagella arising at the head of a ventral groove, heterotrophs, and free-living. Mostly from anoxic or organically enriched sites.

Ultrastructural identity: Amitochondriate, with two flagella and with three associated basal bodies, giving rise to three major microtubular roots, two of which support the margins of the ventral groove with associated nonmicrotubular material. Recurrent flagellum with three vanes. No

Table 3: Protista without contemporary identity

Free-living heterotrophic flagellates	Parasitic protists	Algal protists	Amoeboid protists	Nature uncertain
Acinetactis	*Amoeboaphelidium*	*Adinomonas*	*Actinocoma*	*Asthmatos*
Allantion	*Amylophagus*	*Archaeosphaerodiniopsis*	*Actinolophus*	*Endostelium*
Allas	*Aphelidiopsis*	*Aurospora*	*Aletium*	*Euchitonia*
Alphamonas	*Barbetia*	*Berghiella*	*Actinastrum*	*Euglenocapsa*
Amphimonas	*Bertarellia*	*Bjornbergiella*	*Actinelius*	*Heliomonas*
Artodiscus	*Bertramia*	*Boekelovia*	*Amphitrema*	*Hermisenella*
Aulomonas	*Cibdelia*	*Camptoptyche*	*Apogromia*	*Ligniera*
Bodomorpha	*Cingula*	*Chalarodora*	*Asterocaelum*	*Magosphaera*
Bodopsis	*Cristalloidophora*	*Chlamydomyxa*	*Astrolophus*	*Pansporella*
Bordnamonas	*Cytamoeba*	*Copromonas*	*Balamuthia*	*Perkinsiella*
Campanoeca	*Dermocystidium*	*Cyanomastix*	*Belaria*	*Phagomyxa*
Cladomonas	*Dinemula*	*Dinoasteromonas*	*Belonocystis*	*Polymyxa*
Clautriavia	*Diplophysalis*	*Dinoceras*	*Branchipocola*	*Sorosphaera*
Codonoeca	*Ducelleria*	*Glaucocystopsis*	*Chamydophyrs*	*Spongastericus*
Cruzella	*Echinococcidium*	*Goniodinium*	*Chlamydomyxa*	*Spongocyclia*
Cyathomonas	*Ectobiella*	*Heteromastix*	*Cichkovia*	*Spongospora*
Cyclomonas	*Elleipsisoma*	*Hillea*	*Cinetidomyxa*	
Dallingeria	*Embryocola*	*Histiophysis*	*Clathrella*	
Dimastigamoeba	*Endamoeba*	*Isoselmis*	*Dictyomyxa*	
Dingensia	*Endemosarca*	*Melanodinium*	*Dinamoeba*	
Dinoasteromonas	*Endobiella*	*Meringosphaera*	*Dobellina*	
Dinomonas	*Endomonas*	*Monodus*	*Elaeorhanis*	
Diplocalium	*Endospora*	*Nephrodinium*	*Endamoeba*	
Diplomita	*Eperythrocytozoon*	*Pachydinium*	*Endalimax*	
Diploselmis	*Globidiellum*	*Peliainia*	*Enteromyxa*	
Errera	*Gymnococcus*	*Petasaria*	*Flamella*	
Fromentella	*Haematotractidium*	*Phialonema*	*Gymnophrydium*	
Heliobodo	*Hyalochlorella*	*Pleuromastix*	*Hartmannina*	
Kamera	*Ichthyophonus*	*Pseudoactiniscus*	*Heterogromia*	
Kiitoksia	*Immnoplasma*	*Strobilomonas*	*Hyalodaktylethra*	
Macappella	*Labyrinthomyxa*	*Syncrypta*	*Iodamoeba*	
Metopion	*Lymphocytozoon*	*Tetragonidium*	*Janickina*	
Metromonas	*Lymphosporidium*	*Thaulirens*	*Kibisidytes*	
Microcometes	*Mononema*	*Thaumatodinium*	Lagenidiopsids	
Micromonas	*Myrmicisporidium*	*Thylakomonas*	*Leptophrys*	
Monochrysis	*Naupliicola*	*Triangulomonas*	*Leukarachnion*	
Parabodo	*Neurosporidium*		*Liegeosia*	
Paramastix	*Ovicola*		*Lithocolla*	
Paramonas	*Palisporomonas*		*Malpighiella*	
Peltomonas	*Paradinemula*		*Martineziella*	
Phanerobia	*Paraplasma*		*Megamoebomyxa*	
Phloxamoeba	*Parastasia*		*Microgromia*	
Phyllomitus	*Parastasiella*		*Myxodictyum*	
Phyllomonas	*Physcosporidium*		*Penardia*	
Platytheca	*Piridium*		*Pleurophrys*	
Pleurostomum	*Polysporella*		*Podactinelius*	
Proleptomonas	*Protenterospora*		*Podostoma*	
Quadricilia	*Protomonas*		*Pontomyxa*	
Rhizomonas	*Protomyxa*		*Protogenes*	
Rigidomastix	*Pseudoaphelidium*		*Protomonas*	
Sainouron	*Pseudosporopsis*		*Raphidiophryopsis*	

Table 3 (*Continued*)

Free-living heterotrophic flagellate	Parasitic protists	Algal protists	Amoeboid protists	Nature uncertain
Salpingorhiza	*Rhabdospora*		*Reticulamoeba*	
Schewiakoffia	*Rhinosporidium*		*Rhizoplasma*	
Stenocodon	*Rhyncodinium*		*Servetia*	
Stephanomonas	*Sergentella*		*Stygamoeba*	
Toshiba	*Serpentoplasma*		*Thalassomyxa*	
Trichonema	*Spermatobium*		*Theratromyxa*	
	Sphaerasuctans		*Topsentella*	
	Spiriopsis		*Trizona*	
	Spirogregarina		*Urbanella*	
	Toxocystis		*Wagnerella*	
	Trophosphaera			
	X-cells			

extrusomes, no discrete ingestion apparatus but with dictyosomes.

Synapomorphy: Excavate flagellates with three basal bodies.

Composition: One species has been named (*Carpediemonas membranifera*); contains second species yet to be named.

References: Ekebom et al. 1996; Simpson and Patterson 1999.

Centroheliozoa

Circumscription: The centrohelids, one of several groups previously assigned to the Heliozoa that are now regarded as polyphyletic. Round bodied with stiff radiating arms (axopodia) supported internally by microtubules and with extrusomes that are quite easy to see. Cell surface naked or with organic or siliceous spines and/or scales. Some species with symbiotic algae. No flagellated stages known, may form cysts.

Ultrastructural identity: Mitochondria with lamellate flat cristate. Microtubules of radiating axonemes in hexagon with triangle arrangement and arising from a multilamellate microtubule organizing center, extrusomes with ball-and-cone organization. Radiating system of lacunae near cell surface. Many conventional dictyosomes dispersed in cytoplasm. Siliceous elements of periplast created within silicon deposition vesicles.

Synapomorphy: Platycristate heliozoa with multilamellate microtubule organizing center faced with hemispherical structures giving rise to axonemes of microtubules arranged in hexagons and triangles.

Composition: About 85 species; Family Heterophryidae (*Cienkowskya*, *Oxnerella*, *Sphaerastrum*, *Heterophrys*), Family Raphidiophryidae (*Parasphaerastrum*, *Polyplacocystis*, *Raphidiophrys*, *Raphidocystis*,) Family Acanthocystidae *Pseudoraphidocystis*, *Pseudoraphidiophrys*, *Pterocystis*, *Echinocystis*, *Choanocystis*, *Acanthocystis*).

References: Smith and Patterson 1986; Mikrjukov 1996*a*, 1996*b*.

Cercomonads

Circumscription: Biflagellated gliding protists, anterior flagellum beating stiffly, posterior flagellum trailing, body more or less capable of producing pseudopodia, may be amoeboid. Argued by some to be related to *Chlorarachnion* but both probably belong to a more extensive group (including cercomonads, *Chlorarachnion*, some slime molds, thaumatomonads, *Hyperamoeba*) of tubulocristate flagellates with a tendency to an amoeboid body form, but which has yet to be properly defined. Common and widespread.

Ultrastructural identity: With tubular cristae in mitochondria. Dictyosomes. Two flagella without excrescences or paraxonemal structures; basal bodies inserting almost at right angles, interconnected with nonmicrotubular material and giving rise to several microtubular roots (*Massisteria* excepted). With darkly staining membrane-bound paranuclear body. With electron-dense or concentric extrusomes. Nuclear envelope breaks down during mitosis, spindle microtubules arise at basal bodies.

Synapomorphy: Tubulocristate protists with paranuclear body.

Composition: Several genera: *Cercomonas*, *Massisteria*, *Bodomorpha*, *Heteromita*.

References: Patterson and Zölffel 1991; Karpov 1997.

Chlorarachniophytes

Circumscription: Reticulate amoeboid organisms with cytoplasmic strands linking cell bodies, uniflagellated dispersal stage, with photosynthetic compartment formed from a eukaryotic algal symbiont probably derived from green algae. Recent molecular work suggests close relationship with the euglyphid filose testate amoebas but in the absence of a synapomorphy and the ramicristate nature of the mitochondrial cristae; they are here kept separated, ranked up to level of division. Also, see cercomonads.

Ultrastructural identity: Mitochondria with tubular cristae. Dictyosomes present. With concentric extrusomes. Flagella of flagellated stage without hairs, scales, or other excrescences, also without paraxonemal structures. Basal bodies anchored by microtubular roots. Plastids with variable number of thylakoids per lamella and with associated nucleomorph and with pyrenoids.

Synapomorphy: None known but may be definable by the plastid symbiosis.

Composition: Four genera, six species.

References: Bhattacharya et al. 1995; McFadden et al. 1997.

Coelosporidium

Circumscription: Parasites of digestive system of cladocera, initially existing as unicellular amoebas located extracellularly but subsequently penetrating into cells and into the body cavity and becoming multinucleate before producing spores (cysts). Affinities uncertain but suggestions of links to *Nephridiophaga* or to the trichomycete fungi (see nephridiophagids).

Ultrastructural identity: Mitochondria present but appearance of cristae ambiguous in the one published ultrastructural study, probably platycristate. Many dictyosomes. Cell with stacks of endoplasmic reticulum associated with lipid droplets. Spore wall perforated.

Synapomorphy: None specified.

Composition: Probably monotypic.

References: Manier et al. 1976; Lange 1993.

Collodictyon

Circumscription: Heterotrophic flagellates, four similar flagella inserting at the head of a broad ventral groove, ingesting algae via the groove.

Ultrastructural identity: Mitochondria with tubular cristae, dictyosomes present, cells without walls, scales, or other excrescences.

Synapomorphy: None at this time. The one ultrastructural study to date lacks detail, possibly related to *Diphylleia.*

Composition: Several species.

Reference: Klaveness 1995.

Copromyxids

Circumscription: Cellular slime molds, spores released from treelike structures (sorocarps), which form from aggregation of encysting cells with or without a pseudoplasmodium—a coordinated mass of motile aggregated cells.

Ultrastructural identity: Mitochondria with tubular cristae. Other details not available.

Synapomorphy: Not specified—currently tubulocristate protist behaving as cellular slime mold.

Composition: Two genera, *Copromyxa* and *Copromyxella.*

Reference: Blanton 1990.

Cryothecomonas

Circumscription: Biflagellated heterotrophic flagellate moving by swimming or gliding, with one anteriorly directed and one posteriorly directed flagellum, body surface coated in delicate theca except at site of emergence of flagella and in area of food ingestion. Theca not visible by light microscopy. Feeding by ingestion by ventral face of body often involving pseudopodia.

Ultrastructural identity: Mitochondria with tubular cristate, two flagella inserting as inclined basal bodies interconnected by a striated band, giving rise to several microtubular arrays, one of which links basal bodies to nucleus, transition zone with constriction, cell with dictyosomes and osmiophilic bodies. Cell surface with thin organic coating. During mitosis, the nuclear envelope disintegrates, spindle microtubules arise from basal bodies.

Synapomorphy: Not specified—this is a tubulocristate flagellate with body enclosed by delicate mucoid theca and a large ventral groove, but neither feature is unique to this taxon.

Composition: One genus, several species.

References: Thomsen et al. 1991; Drebes et al. 1996.

Cryptomonads

Circumscription: Biflagellated autotrophic, mixotrophic and heterotrophic flagellates, flagella inserting in an anterior groove/channel lines with refractile ejectisomes. Variously colored photosynthetic compartments, in some taxa at least, formed from secondary symbioses with eukaryotes, the symbiont being located in a membrane-bound compartment and provided with a reduced nucleus (the nucleomorph). Two genera of heterotrophs, one (*Goniomonas*) possibly primitively so.

Ultrastructural identity: Mitochondria cristae flattened, mitochondrion often extensive. Coiled ribbon extrusomes (ejectisomes) associated with flagellar pocket (gullet) and with cell surface. Geometrically positioned plates of fibrous cytoskeletal material underlie the membrane. Plastidic taxa with plastid inside a fold of the nuclear envelope and with nucleomorph where studied. No eyespot. Both flagella with stiff bipartite hairs. Small scales may be attached to cell body. Flagella insert into near parallel basal bodies, usually with multilamellate root structure (rhizostyle) in addition to several microtubular roots. Nuclear division with spindle developing from basal bodies and penetrating the dividing nucleus, the membrane of which completely breaks down.

Synapomorphy: Flagellar groove/channel with associated ejectisomes and/or double row of flagellar hairs on both flagella and/or cortical plates.

Composition: With about 25 genera, two of which are heterotrophic.

References: Roberts 1984; Gillott 1990.

Desmothoracids

Circumscription: One subset of the group previously referred to as heliozoa. Amoeboid body giving rise to stiff pseudopodia (the heliozoan stage) located in an organic lorica, often stalked. Heliozoan stage produces biflagellated motile stage, which can then give rise to an amoeboid form with stiff but motile pseudopodia. Heterotrophic.

Ultrastructural identity: Mitochondria with tubular cristae, microtubules in support of pseudopodia not in organized geometric arrays or in open hexagons, and no microtubule organizing center is known. Many dictyosomes. Extrusomes concentric core and girdle (kinetocyst). Flagellated stage not studied in any detail.

Synapomorphy: Tubulocristate protists with a heliozoan stage located in a fenestrated organic lorica.

Composition: Three genera: *Clathrulina* (=*Elaster*?), *Hedriocystis*, and *Cienkowskya* (=*Monomastigocystis*).

References: Bardele 1972; Smith and Patterson 1986.

Dimorphids

Circumscription: Helioflagellates, with two or four similar flagella, very elongate kinetosomes. Flagellates in trophic stage with axopodia radiating from an amorphous microtubule organizing center located between kinetosomes and nucleus. Microtubules tending to be in square packing. With tubular mitochondrial cristae.

Ultrastructural identity: Mitochondria with tubular cristae possibly ramicristate. With concentric extrusomes. Dictyosomes present. Microtubules supporting pseudopodia in clusters, tightly packed sometimes in square pattern, arising from an amorphous structure associated with flagellar basal body. Flagella with hairs, scales, or other excrescences also without paraxonemal structures. Basal bodies very long, with fibrous and nonmicrotubular anchorage materials and linked to nucleating site for pseudopodial axonemes.

Synapomorphy: Tubulocristate protists with axopodial axonemes nucleating on an amorphous site linked to kinetosomes.

Composition: Two genera, *Dimorpha* and *Tetradimorpha*.

Reference: Brugerolle and Mignot 1984.

Diphylleia

Circumscription: Flagellate with two similar flagella inserting almost apically at the head of a broad groove that is used for the ingestion of food. Heterotrophic, freshwater.

Ultrastructural identity: Mitochondria with tubular cristae, with two flagella arising from two inclined basal bodies; flagella without hairs or other excrescences but with short fibrous intraflagellar inclusions; flagellar transition zone narrowed. Basal bodies giving rise to a dorsal root from which arise cortical microtubules, and two ventral microtubular and fibrous roots that support the margins of the ventral groove. No extrusomes but with dictyosome.

Synapomorphy: None specified.

Composition: (=*Aulacomonas*), monotypic.

References: Brugerolle and Patterson 1990; Patterson and Zölffel 1991.

Diplomonads

Circumscription: Amitochondriate flagellates with nuclei associated with a group of four kinetosomes, giving rise to two to four flagella each. Most with two nuclei and two sets of flagella. Flagella sometimes arising at anterior end of feeding groove (i.e., the taxa are excavate), others with cytoskeletal suckers for attachment to surfaces, some (*Octomitus*) with neither groove nor suckers. All heterotrophs, free-living or parasitic.

Ultrastructural identity: Without mitochondria, kinetid with four basal bodies giving rise to two or three major microtubular roots. Cell surface naked, no dictyosomes. Nuclear envelope largely intact during mitosis but spindle penetrates from the cytoplasm.

Synapomorphy: None specified, unless the duplex nucleo/kinetid structure is ancestral, but this hypothesis needs to be assessed.

Composition: About nine genera.

Reference: Vickerman 1990.

Discocelis

Circumscription: Small flattened gliding flagellates, heterotrophic, with two emergent flagella; asymmetric cell shape in part caused by an internal organic cytoskeletal "velum," marine; some similarities to apusomonads.

Ultrastructural identity: Mitochondria with tubular cristae, with two flagella and two basal bodies closely associated with the nucleus, basal bodies giving rise to several microtubular ribbons. Flagella without hairs or other excrescences. With peripheral concentrically structured extrusomes. With finely striated thin organic layer (velum) underlying the cell membrane.

Synapomorphy: Tubulocristate eukaryote with cytoskeletal velum.

Composition: One genus, several species.
Reference: Vørs 1988.

Ebriids

Circumscription: Biflagellated protists, with internal solid siliceous, branching or fenestrated, skeleton. Heterotrophic, able to produce pseudopodia. Marine. Considered by some to be a dinoflagellate, but there is no strong case for this. Few species living but with a good fossil record.

Ultrastructural identity: Few ultrastructural data are available, identity attributable to siliceous inclusion.

Synapomorphy: Flagellated protist with internal solid siliceous skeleton with branching or fenestrated appearance.

Composition: About three extant species in two genera.

Reference: Taylor 1990.

Ellobiopsids

Circumscription: Parasites of marine invertebrates, attached externally. Multicellular with trophic and generative sections. Release of biflagellated distributive stages follows multiple fission.

Ultrastructural identity: With very limited ultrastructural information, identity based largely on life history. Mitochondria with tubular cristae, trophic form with internal thick pellicle penetrated by membranous invaginations. Flagella without paraxonemal structures or hairs. Centriolar complexes embedded within folds of the nuclear envelope.

Synapomorphy: Not specified.

Composition: *Ellobiopsis* and *Thalassomyces*, possibly also *Parallobiopsis*, *Rhizellobiopsis*, and *Elllobiocystis*.

Reference: Whisler 1990.

Entamoebidae

Circumscription: Amitochondriate parasitic amoebas with pseudopodia as clear semieruptive bulges from anterior of cell. Forms cysts. Amitochondriate status probably secondary.

Ultrastructural identity: Mitochondria absent, dictyosomes present. Small osmiophilic bodies sometimes adhering to inner surface of cell membrane. Cytoplasm with helical arrays (said to be of ribosomes), mitosis with entirely intranuclear spindle with amorphous intranuclear microtubule organizing center.

Synapomorphy: Amitochondriate amoebas with intranuclear spindle.

Composition: *Entamoeba* (three species); possibly also *Endolimax* (monotypic), *Iodamoeba* (monotypic).

References: Albach and Booden 1978; Espinosa-Cantellano et al. 1998.

Euglenozoa

Circumscription: Flagellates with two flagella inserting into an anterior pocket. Two basal bodies giving rise to three microtubular rootlets, free living or parasitic, autotrophs, heterotrophs, and mixotrophs. Mostly with discicristate mitochondria and possibly distantly related to other taxa (*Stephanopogon*, Hemimastigophora, nucleariids, and Heterolobosea) with discicristate mitochondria.

Ultrastructural identity: Well studied, with two flagella, flagella typically inserting parallel or nearly so, giving rise to three microtubular ribbons, one of which associated with actual or presumptive ingestion device. Flagella with paraxonemal rods, the dorsal (anterior) flagellum with a tubular paraxonemal rod, and the ventral (recurrent) flagellum with a paraxonemal rod with a lattice structure. Flagella often with fine hairs. Extrusomes with lattice walls when extruded and a cruciate pattern when not. Mitochondrial cristae typically disc shaped with short pedicel; some (kinetoplastids) with aggregates of DNA. Cell surface naked or with strips of cytoskeletal material (euglenids). Nuclear envelope intact during mitosis, spindle microtubules internal.

Synapomorphy: Discicristate protists with heteromorphic paraxonemal rods (dorsal flagellum with tubular rod, ventral with lattice structure).

Composition: Four subtaxa: euglenids; kinetoplastids, including *Hemistasia* (and its probable synonym *Entomosigma*), and *Rhynchobodo* (and its synonym *Cryptaulax*); *Postgaardi*; and diplonemids.

References: Simpson 1997; Bernard et al. 1999.

Eumycetozoa—see ramicristates

Fonticula

Circumscription: Cellular slime molds, plate like cristae, usually classified with acrasids (Heterolobosea). Spore-forming body created through aggregation of amoebas. Amoebas are unlike those of acrasids because of subpseudopodia—hence their cautious classification as a separate group.

Ultrastructural identity: Mitochondria with discoidal cristate.

Synapomorphy: Not specified.

Composition: Isolated genus.

Reference: Blanton 1990.

Glaucophytes

Circumscription: Eukaryotes with cyanelles (reduced cyanobacteria) but with a wide array of trophic forms (flagellates, nonmotile coccoid organisms, palmelloid). Presence or absence of a cellulosic cell wall, presence or absence of a mucilage sheath. Given the variation, monophyly, which is largely based on the cyanelles, requires confirmation.

Ultrastructural identity: Considerable variation, mitochondria with flat cristae. With flattened sacs under cell membrane, which in some species may produce scales. Dictyosomes present and may be associated with the nucleus or with the flagellar apparatus, cyanelles present with or without a surrounding wall. Differing numbers of multilayered structures associated with the flagellar anchorage system if flagella are present. Flagella if present may have fine hairs. Nuclear envelope breaks down during mitosis, basal bodies/centrioles not used to nucleate spindle microtubules.

Synapomorphy: None available but probably platycristate protists with cyanelles with subsurface layer of sacs.

Composition: *Cyanophora* (two species), *Glaucocystis* (10 species), *Gloeochaete* (probably monotypic), and (?) *Glaucosphaera* (one species). *Cyanidium* and relatives included by some are assigned to the red algae.

References: Mignot et al. 1969; Kies and Bremer 1990.

Granuloreticulosa

Circumscription: Amoeboid organisms, mostly marine. With pseudopodia, which extend from the cell body as a series of strands which divide and anastomose. The structure of the net is always changing, and granular cytoplasm moves actively in both directions along the strands, which internally have microtubules. The appearance and behavior of the pseudopodial network is held by many to be synapomorphic. The group is dominated by the foraminifera, the trophic cells of which occupy multichambered or agglutinated tests. Some organisms that live in a single chambered test (the Monothalamida) and some without tests (Athalamids) may be included. Because branching dynamic pseudopodial networks may be found in some taxa that may not be granuloreticulosea (such as *Micrometes*, a flagellate, *Biomyxa*, gymnophreids, *Gymnophrydium*, vampyrellids, leptomyxids, various slime molds, etc.), the monophyly of the group is still uncertain. Consequently, some taxa assigned by others to this group, such as the Komokiacea and *Biomyxa*, are excluded here—even though there are undoubtedly some monothalamid and athalamid relatives of the foraminifera. The foraminifera includes taxa with complex life cycles (phases involving production of gametes separated by phases involving asexual reproduction); with or without flagellated swarmers; with or without nuclear dimorphism. Many species with endosymbiotic algae.

Ultrastructural identity: Mitochondria with tubular cristae. Nuclear envelope may be supported by fibrous sheath. Pseudopodia containing microtubules but not in geometric arrays, also with dark osmiophilic bodies. Flagellated stage generally unstudied, but it is now generally agreed that the flagella are without tripartite hairs (cf. Patterson 1989). Wall of testate forms variable in composition and make-up.

Synapomorphy: Usually said to be branching/anastomosing dynamic filamentous pseudopodial system, but this needs to be confirmed.

Composition: About 40,000 species; most are foraminifera.

Reference: Lee 1990.

Gymnophrea

Circumscription: Small- to medium-sized amoebas with branching bodies from which extend fine pseudopodia with extrusomes and which may branch and anastomose. Cytoplasmic movements not strongly noticeable. Heterotrophic. Two short flagella. Flagellated zoospores may be produced.

Ultrastructural identity: Mitochondria with flat cristae. Perinuclear dictyosomes. With two short flagella, basal bodies parallel, anchorage not well characterized. With concentric extrusomes. Microtubules occur in the pseudopodia.

Synapomorphy: None defined.

Composition: Two genera: *Gymnophrys* and *Borkowia*.

Reference: Mikrjukov and Mylnikov 1998*b*.

Gymnosphaerida

Circumscription: Heliozoa with axonemes arising from a central nucleating site; uninucleate or multinucleate, naked or with adhering siliceous spicules. Cell may be differentiated into a stalk and head. With extrusomes and tubulocristate mitochondria.

Synapomorphy: Tubulocristate heliozoa with axopodial axonemes having hexagonal packing arrangements and arising from an amorphous nucleating structure.

Composition: *Gymnosphaera*, *Hedraiophrys*, and *Actinocoryne*—all monotypic.

References: Febvre-Chevalier 1980; Jones 1980.

Haplosporids

Circumscription: Sporozoan parasites of mostly marine invertebrates. Trophic cells uninucleate or multinucleate, intracellular, and no flagella. Spore walls develop intracellularly from haplosporosomes, and the spore has a distinctive lid and often extraneous filaments. Held by some to be related to the alveolates, but there is no evidence of alveoli.

Ultrastructural identity: Mitochondria with tubular cristae. Dividing nucleus with internal spindle and the nuclear envelope remains intact. There is a residuum of parallel microtubules from the mitotic spindle, and this “kernstab” persists through interphase.

Synapomorphy: Tubulocristate protists with lidded spore and/or persistent spindle (Kernstab) in nondividing nucleus.

Composition: Three genera with about 35 nominal species. Proliferative kidney disease organism X (pkx) is included, though some regard this as being allied to myxospora.

References: Seagrave et al. 1980; Perkins 1990; Siddall et al. 1995.

Haptophytes

Circumscription: Marine flagellates, almost all with plastids with chlorophylls *a* and *c*, with two flagella and one additional locomotor/feeding organelle, the haptonema. Some mixotrophic, one species exclusively heterotrophic. Many with inorganic (calcareous) scales (coccoliths). Some with polymorphic life cycles. Cytological organization similar in many respects to stramenopiles with chloroplasts, and they have been classified with that group by some. They lack the synapomorphy of stramenopiles, and at this time molecular evidence does not support derivation from that group.

Ultrastructural identity: Mitochondria with tubular cristae. Dictyosomes present. Plastids with lamellae comprised of three thylakloids, no stigma; plastid in an extension of endoplasmic reticulum—the periplastidial endoplasmic reticulum. Haptonema with enclosed microtubules not in 9 + 2 arrangement. Two flagella, without hairs, scales, or other excrescences, with up to four major microtubular roots and some nonmicrotubular materials. Mitosis with spindle nucleating in cytoplasm and nuclear envelope breaking down.

Synapomorphy: Tubulocristate flagellates with haptonema.

Composition: Several hundred species, with some dispute as to the status of one subset, the Pavlovales.

References: Hibberd 1976*b*; Bhattacharya et al. 1993; Green and Leadbeater 1994.

Heterolobosea

Circumscription: Heterotrophic amoebas, amoebo-flagellates (collectively the vahlkampfiids or schizopyrenids), flagellates (*Percolomonas*), and slime molds (the acrasids). Two genera have no flagellated stage, but the majority of species have the capacity to convert from amoebas to flagellates or to encyst. Flagellates have two to four flagella and usually an ingestion region with an adjacent ridge supported by microtubules. Amoebas move with eruptive pseudopodia. Common in soils, but the group contains a facultative pathogen of the human central nervous systems (*Naegleria*). The acrasid slime molds are one of two types of cellular slime molds in which resistant spores are released from an aggregated mass of cells and in which differentiation may occur.

Ultrastructural identity: Mitochondrial cristae discoidal (i.e., with pedicel) or sacculate, mitochondria may be partly enclosed by an extension of endoplasmic reticulum. Basal bodies parallel or nearly so, giving rise to several microtubular roots and sometimes a cross-striated nonmicrotubular root. Without dictyosomes with stacks of sacs, usually no extrusomes, cell surface naked. Nuclear envelope intact during mitosis, spindle microtubules internal.

Synapomorphy: To be resolved but either discicristate protists forming eruptive pseudopodia or discicristate protists with parallel basal bodies inserting on an electron-dense pad, possibly with a substantial cross-striated root.

Composition: Schizopyrenida, Acrasida, *Percolomonas*.

References: Page and Blanton 1985; Patterson and Zölffel 1991.

Hyperamoeba

Circumscription: Heterotrophic protist with amoeboid and gliding (uni)flagellated stages, flagellated stage uniflagellated, and reminiscent of pelobionts but with tubulocristate mitochondria. Cysts also produced. Flagellated stage reminiscent of protostelids and relatedness to eumycetozoa is probable.

Ultrastructural identity: Mitochondria with tubular cristae, some with central core, dictyosome present cristate. Two apical basal bodies give rise to four microtubular rootlets, two conical arrays of microtubules extend toward nucleus and center of cell.

Synapomorphy: Tubulocristate protist with double cone of microtubules arising from anterior pair of basal bodies.

Composition: Probably one species.

References: Patterson and Zölffel 1991; Karpov and Mylnikov 1997.

Jakobids

Circumscription: Flagellates with two flagella located at the anterior end of a ventral feeding groove (i.e., are excavate), with mitochondria, freely swimming or loricate.

Ultrastructural identity: Mitochondria with flat or tubular cristae, flagellar apparatus with two basal bodies giving rise to two major microtubular roots, which support the margins of the ventral groove. Other cytoskeletal microtubules arise directly or indirectly from the basal bodies, no extrusomes. Mitosis not described.

Synapomorphy: Excavate mitochondriates with two basal bodies.

Composition: *Jakoba*, *Reclinomonas*, and *Histiona*.

Reference: O'Kelly 1993.

Kathablepharids

Circumscription: Relatively large biflagellated flagellates, heterotrophic, ingesting larger food particles (other protists) often by means of anteriorly located mouth, with long flagella that appear thicker than most flagella because they (and the body) are covered with a layer of organic matter structured as if comprised of tiny scales in regular arrays. Cells typically with extrusomes in a line along one face of the body.

Ultrastructural identity: Mitochondria tubulocristate, dictyosomes are well developed. Two flagella, acutely inclined or near parallel basal bodies give rise to microtubular and microfibrillar structures, with regularly arrayed organic material attached to flagellar membrane and to cell membrane. Microtubules also underlie cell surface, extrusomes rolled ribbon type, with anterior ingestion device being an expanded cone of microtubules, the wall of which may incorporate a cylinder of microtubular ribbons. The nuclear envelope disperses during mitosis, and microtubules of the spindle arise in the cytoplasm. Discrete microtubule organizing centers have not been observed.

Synapomorphy: Tubulocristate protists with body and flagella coated in an organic layer apparently formed of fine scales in regular arrays.

Composition: *Kathablepharis* (=*Katablepharis*), *Leucocryptos*, and *Platychilomonas*.

References: Lee and Kugrens 1991; Vørs 1992*c*; Lee et al. 1993; Clay and Kugrens 1999.

Komokiacea

Circumscription: Large marine benthic organisms with a cytoplasmic mass surrounded by agglutinated material. Only known as large amoeboid organisms producing branching pseudopodial strings with which detritus and food is collected. Mostly reported from deep-sea habitats. Very few observations have been made on live cells. Initially classified within the foraminifera, but there is no evidence of a single-chambered or multichambered test. Assigned to the Granuloreticulosea on the basis of one observation of "granulo-reticulate" pseudopodia—but as pointed out under Granuloreticulosea, this character is not restricted to that group.

Ultrastructural identity: No clear ultrastructural identity, this group is distinguished by unusual gross morphology only.

Synapomorphy: None known.

Composition: About 12 genera in two families (Komokiacea and Baculellidae).

References: Tendal and Hessler 1977; Cedhagen and Mattson 1991.

Luffisphaera

Circumscription: Marine organisms, small rounded body enclosed in a case of scales and spines. Scale and spine morphology are used to identify species. Heterotrophic.

Ultrastructural identity: Tubulocristate mitochondria. Most ultrastructural information relates to nature of spines, which have a mesh structure. Dictyosomes present. No specified cytoskeletal material, no evidence of flagella.

Synapomorphy: None specified but distinguished by mesh-structured spines and scales.

Composition: Several species.

References: Belcher and Swale 1975; Vørs 1993.

Microsporidia

Circumscription: Intracellular parasitic protozoa, heterotrophic, minute, no flagella, no mitochondria, no dictyosomes. Infect animals and other protozoa. Trophic stages are uninucleate or multinucleate plasmodia, may be diplokaryotic (i.e., nuclei are paired). There is evidence for meiosis. Distinguished from other sporozoa by the distinctive spores that contain a coiled filament that everts to inject infectious organisms into host cells. Argued by some to be the most primitive eukaryotes, by others to be allied to the true fungi.

Ultrastructural identity: No mitochondria, dictyosomes, or flagella. Spores with coiled introverted filaments through which the infectious cell is injected into hosts, spores also with layered system of sacs—the polaroplast also involved in discharge of infectious organism. Nucleus intact during mitosis, microtubules of mitotic spindle lie within the nucleus but nucleate on amorphous structures external or attached to nuclear envelope.

Synapomorphy: Spore with introverted polar filament.

Composition: Fairly large group containing the rudimicrosporidia and the true microsporidia (chytridiopsids, and the microsporida with about 20 families).

References: Larsson 1986; Canning 1990.

Ministeria

Circumscription: Small marine heterotrophic protist, spherical with 20 symmetrically distributed stiff radiating pseudopodia, one species vibratile suggesting the presence of a flagellum.

Ultrastructural identity: Mitochondria with flat cristae. Little further information available.

Synapomorphy: Platycristate protist with 20 stiff radiating pseudopodia.

Composition: Two species.

References: Patterson and Zölffel 1991; Patterson et al. 1993.

Multicilia

Circumscription: Heterotrophic flagellates, small to medium, with irregular or regular rounded body with up to 30 flagella arising randomly over the surface. Heterotrophic, eating other protists.

Ultrastructural identity: Mitochondria with flat cristae. Each flagellum linked to a single basal body, basal body gives rise indirectly to an incomplete cone of microtubules and also ribbons of microtubules may link adjacent basal bodies. Fibrous cytoskeletal structures are also located adjacent to basal body. Multiple dictyosomes.

Synapomorphy: Platycristate flagellates with flagellar basal bodies anchored by an incomplete cone of microtubules.

Composition: Several species. *Polymastix* and *Tetracilia* are accepted as synonyms.

Reference: Mikrjukov and Mylnikov 1998*a*.

Myxospora—see opisthokonts

Nephridiophagids

Circumscription: Parasitic organisms associated with the malpighian tubules of insects; early development extracellular, later development involves plasmodia, which may bud. Spores are produced by parts of plasmodium and are concave or biconcave with a banded appearance when viewed by light microscopy. Previously linked with *Coelosporidium* but life cycle and ultrastructural differences now indicate that association is not appropriate.

Ultrastructural identity: Shape of mitochondrial cristae not established. Dictyosomes present. Nuclear envelope remains intact during nuclear division. Mitotic microtubules nucleating from amorphous materials external to nucleus. No centrioles reported as associated with spindle during mitosis.

Synapomorphy: None specified.

Composition: About 12 species previously assigned to five nominal genera.

Reference: Lange 1993.

Nucleariidae

Circumscription: Amoeboid organisms, with fine pseudopodia unsupported by microtubules, with or without hollow siliceous plates or spheres or spines, the walls of which are a meshwork. Uninucleate or multinucleate. No flagellated stages known. Mostly described from soils or freshwater.

Ultrastructural identity: Mitochondria with discoidal cristae. With dictyosomes. Pseudopodia without microtubules, supported by microfibrillar material. During mitosis, the nuclear envelope remains intact and microtubules lie within the nucleus. One species reported with a microfibrillar cytoskeletal sheath. No extrusomes.

Synapomorphy: None known, distinguished at this time as filose amoebas with discoid mitochondrial cristae.

Composition: *Nuclearia*, *Pompholyxophrys*, *Pinaciophora*, *Rabdiophrys*, and *Vampyrellidium*.

References: Patterson 1983; Patterson et al. 1999.

"Opisthokonts"

Circumscription: This group contains the true fungi and their protist relatives (the chytrids) and the animals and their protist relatives (the choanoflagellates). The close relationship of the multicellular taxa was initially indicated by molecular means. The group contains uniflagellated solitary and colonial protists with one flagellum at some stage in their life history, phagotrophs, saprophytes, mycelial organisms with spore-forming bodies but no flagella, multicellular heterotrophs formed from layers of cells (epithelia), and the sponges with a less structured arrangement of cells. Collagen, one of the components of the extracellular matrix of the animals has also been reported from some fungi. All of the flagellated taxa and flagellated cells swim with a single flagellum beating behind the cell. The term "opisthokonta" has been applied to this grouping (Cavalier-Smith and Chao 1995; Cavalier-Smith 1996). However, Cavalier-Smith and Chao do not use the term as a formal taxon because it would require that more "important" taxa are subordinated to less "important" taxa. Here, the opisthokonts is a taxon with the composition as indicated below on an interim basis. Unfortunately, the name should be revisited as the term Opisthokonta has previously been used by Copeland (1956) for the chytrids. Some other permanently or temporarily "opisthokont" protists—such as several nominal pelobionts or the unassigned *Phalansterium* or *Pseudaphelidium*—are not included, and it is not yet known if they form part of this group.

Ultrastructural identity: The diversity of organization within this group is great, extending from uniflagellated protists with or without the ability to make siliceous products to multicellular mycelial or epitheliate organisms. Apart from having platycristate mitochondria and being dictyosomate, this group has few discriminating characters that extend throughout this group. Nuclear division is variable within the fungi but in the animals, the envelope breaks down during mitosis.

Synapomorphy: Unspecified but probably may relate to the radiating and arcing anchorage structures associated with the single flagellum. Very few studies of the protistan (ancestral) members have been conducted, and until more detailed ultrastructural studies are carried out, such a determination would probably be premature. Most included taxa have secondarily lost this character.

Composition: The largest of the major eukaryote lineages with probably in excess of 1,000,000 species, in two major clusters: (chytrids + true fungi) + (choanoflagellates + Metazoa). These two clusters themselves require appropriately defined names. This taxon includes the Myxospora (previously thought of as a group of protozoa) as a subset of the Cnidaria. Some argue that the opisthokonts should include the Microspora.

References: Copeland 1956; Morris 1993; Wainright et al. 1993, 1994; Cavalier-Smith and Chao 1995; Cavalier-Smith 1998; Müller 1998.

Oxymonads

Circumscription: Mostly flagellates, all known species are commensals usually in intestines of termites, typically with four flagella in two pairs, and basal bodies giving rise to an organelle, the axostyle, which may be able to undulate.

Ultrastructural identity: No mitochondria, four basal bodies arranged in two separated pairs and giving rise to several major microtubular roots, some with associated nonmicrotubular roots. Axostyle, comprised of parallel sheets of microtubules, which in some species slide relative to each other and may have associated additional material. No extrusomes nor dictyosomes, cell surface naked.

Synapomorphy: Amitochondriate protists with axostyle constituted of multiple sheets of microtubules.

Composition: Fewer than 100 species located in several families (polymastigids, pyrsonymphids, and oxymonads).

Reference: Brugerolle and König 1997.

Parabasalids

Circumscription: Mostly flagellated protozoa, mostly commensals in insects or parasites. Some (hypermastigids) may have very large numbers of flagella and are usually symbionts in the intestines of wood-eating insects, others (trichomonads) may have an undulating membrane. An axostyle may be visible. A few species are free living.

Ultrastructural identity: No mitochondria. All cells (excepting aflagellated taxa) with at least one cluster of four basal bodies, which are the source of microtubular roots. Dictyosomes are well developed, often numerous, and may be associated with a nonmicrotubular rootlet, the parabasal fiber. Cell surface naked, no extrusomes. Mitosis with intact nuclear envelope and with spindle microtubules lying external to the nucleus.

Synapomorphy: Flagellated protists with a parabasal apparatus of dictyosomes anchored to a striated root.

Composition: Trichomonads, hypermastigids, and *Cochlosoma*.

References: Lee et al. 1985; Pecka et al. 1996.

Paramyxea

Circumscription: Parasitic heterotrophic protists typically found in the digestive system of marine invertebrates where they feed by osmotrophy. Initial infectious cell is amoeboid. Paramyxeids are regarded as multicellular because the daughter cells formed by division of the infectious cell may be contained within the initial cell; these continue to develop into multicellular spores. With a complex process of nuclear and cellular division.

Ultrastructural identity: Shape of mitochondria not confirmed. With a reduced (nine single microtubules) centriolar structure associated with the microtubules of the mitotic spindle; nuclear envelope disrupts during division.

Synapomorphy: Tubulocristate protists, during spore development endogenous budding accompanies cell division.

Composition: Several genera.

Reference: Desportes and Perkins 1990.

Pelobionts

Circumscription: Four genera of about 200 nominal species, mostly uniflagellated, without mitochondria or dictyosomes. Ribosomal RNA sequences places pelobionts away from the base of the tree, one other molecule and structural evidence suggest a more basal location. *Phreatamoeba* has been synonymized with *Mastigamoeba.*

Ultrastructural identity: Without mitochondria, dictyosomes, or fibrous cytoskeletal structures. Basal bodies are not paired and are supported by a cone of microtubules and, excepting taxa with nonmotile flagella, with a single radiating ribbon of microtubules. Flagella without paraxial structures. No extrusomes and no ingestion device. Some taxa with non–9 + 2 arrangement of microtubules in axonemes and without nine X triplet organization of microtubules in basal bodies.

Synapomorphy: (Primitively?) amitochondriate protists with unpaired basal bodies anchored with cone and ribbon of microtubules.

Composition: *Pelomyxa*, *Mastigamoeba*, *Mastigella*, and *Mastigina.*

References: Hinkle et al. 1994; Simpson et al. 1997; Stiller et al. 1998.

Phaeodarea

Circumscription: A group of marine radiolaria (protists with axopodia, skeletons, and no flagella in the trophic state). Most have a skeleton of amorphous silica with associated organic matter, cytoplasm separated into an inner area by a thick capsule, and an inner layer that is further divided by a cape of vesicles—the cape having three openings: an apical astropyle that seems to be associated with the formation of feeding pseudopodia and two parapyles from which axonemal microtubules arise. Contain aggregates of waste material: the phaeodium. Life cycle may be complex, and flagellated distributive stages are produced

Ultrastructural identity: Little studied, mitochondria probably tubulocristate.

Synapomorphy: Radiolaria with central capsule with three openings: an apical astropyle and two parapyles.

Composition: About 100 genera.

References: Cachon and Cachon 1985*a*; Cachon et al. 1990.

Phagodinium

Circumscription: A parasitic protist that invades synurophytes (stramenopiles) and consumes cytoplasm, cyst with three points (tridentate), may also produce biflagellated dispersive cells from a "sporangium."

Ultrastructural identity: Only a small amount of information is available. Mitochondrial cristae tubular. Cyst wall organic. With dictyosomes, starch, and other storage bodies.

Synapomorphy: Tubulocristate protist with tridentate cyst.

Composition: Monotypic.

Reference: Kristiansen 1993.

Phalansterium

Circumscription: Heterotrophic flagellates, forming colonies with cells embedded in an organic globular matrix, a single apical flagellum with tight-fitting continuous cytoplasmic collar.

Ultrastructural identity: Mitochondria with tubular cristae, cells with a single apical flagellum with single basal body, anchorage involving concentric rings, which give rise to radiating microtubules. Well-developed dictyosomes associated with basal body. Flagellum with mucus but otherwise without hairs, scales, or other excrescences, no paraxonemal rods.

Synapomorphy: Tubulocristate protist with single apical flagellum anchored by a radially symmetrical array of microtubules.

Composition: One genus, several species.

Reference: Hibberd 1983.

Plasmodiophorids

Circumscription: Mostly parasitic, some phagotrophic consumers of cell contents of plants and oomycetes. Some with a highly unusual extrusome (stachel) used for penetrating food cells. Feeding cell may or may not be plasmodial, giving rise to multiple "zoospores" with two or four flagella; flagella without hairs, hence excluded from Oomycetes (stramenopiles) with which they are normally allied. With long-lived cysts with chitin in their walls.

Ultrastructural identity: Form of mitochondrial cristae is ambiguous, appearing either flat or sacculate (molecular evidence suggests plasmodiophorids are allied to tubulocristate eukaryotes). With a distinctive cruciate appearance of nucleus during mitosis of vegetative cells. Flagellar basal bodies long. May have complex extrusomes.

Synapomorphy: Eukaryotes with cruciate mitotic profiles in dividing vegetative cells.

Composition: About 40 species in 10 genera.

References: Barr 1983; Dylewski and Miller 1983; Beakes 1998.

Polycystinea

Circumscription: A group of marine radiolaria (protists with axopodia, skeletons, and no flagella in trophic state), usually with a skeleton of hydrated amorphous silica, developing from a four pronged spicule which may be dissolved by at least some species. Cytoplasm separated into an inner area by a capsule having differentiated regions (the fusules) through which the axopodia pass. Frequently with symbiotic dinoflagellates. Distributive stages have two flagella and some have strontium sulphate crystals, suggesting relationship with Acantharea.

Ultrastructural identity: Mitochondria with tubular cristae. Microtubules of axopodia form branching arrays or wide hexagons. Capsule a discrete organic structure with fusules as a pore with electron-dense material enveloping the microtubules of the axoneme. Microtubule organizing center amorphous/fibrous/granular. Mitosis with spindle inside nucleus but microtubule nucleating material external to nuclear envelope.

Synapomorphy: Tubulocristate eukaryotes, with capsule with fusules separating endoplasm and ectoplasm.

Composition: Spumellarids (fusules distributed over entire capsule) and nasellarids (fusules located at one apex).

References: Cachon and Cachon 1985*b*; Cachon et al. 1990.

Pseudodendromonads

Circumscription: Heterotrophic flagellates with two flagella and discrete ingestion area formed by loop of two microtubular roots, rather like bicosoecid stramenopiles to which—it is argued by some—they are related. May be solitary and swimming, attached by a stalk, or colonial and attached. May or may not have surface scales.

Ultrastructural identity: Mitochondria with tubular cristae, two flagella arising from two inclined basal bodies. Flagella with associated microtubular roots, one of which forms a hairpin structure that wraps around the cytopharyngeal region. Flagella without hairs or scales or other excrescences. Dictyosome usually associated with the nucleus. Nuclear envelope fragments during mitosis. Spindle microtubules arise within the cytoplasm. Some species with structures believed to be extrusomes. May be related to bicosoecids (stramenopiles) and *Caecitellus*.

Synapomorphy: Tubulocristate protist with hairpin rootlet of microtubules surrounding an ingestion region.

Composition: *Adriamonas*, *Pseudodendromonas*, and *Cyathobodo*

References: Mignot 1984; Verhagen et al. 1994; Strüder-Kypke and Hausmann 1998.

Pseudospora

Circumscription: Genus of heterotrophic protists with two flagella and amoeboid stages, which typically attack plant cells. Trophic cells amoeboid or plasmodial, distributive form is flagellated and produced after encystment of amoeboid stage. Usually assigned to a group of unclear identity, the pseudosporids.

Ultrastructural identity: Mitochondria with tubular cristae. Flagellar anchorage structures not well characterized. Flagella without hairs or other excrescences. Multiple dictyosomes. Cell surface naked. Mitosis not studied.

Synapomorphy: Not clear, group distinguished by feeding strategy and life history.

Composition: Single genus segregated to avoid retention of an ambiguous concept for pseudosporids or proteomyxids.

References: Swale 1969; Schweikert and Schnepf 1996.

Ramicristates

Circumscription: Amoeboid organisms with tubular cristae that branch. Amoebas are distinguished by moving and/or acquiring food by means of pseudopodia, which can be filose, lobose, branching, conical, or with subpseudopodia. This group contains the bulk of the naked lobose amoebas of previous classifications, the lobose and filose testate amoebas. Three groups—stereomyxids, dictyostelids (a type of cellular slime mold), and acanthamoebids have a lamellate microtubule organizing center. Dictyostelids and acanthamoebids use cellulose, the former in the stalks, which support spores and in the cysts of the latter. The true slime molds (the eumycetozoa = protostelids and myxomycetes) are included. In these, the individual cells aggregate into a syncitial plasmodium that moves with an ebb and flow pattern. The syncitium produces a fruiting body from which are released resistant distributive cysts (spores). The eumycetozoa have a biflagellated stage in life cycle—one of the few types of ramicristates with flagellated forms. *Leucodictyon* is another plasmodial organism with flagellated distributive stage.

Ultrastructural identity: Mitochondria with irregular tubular and branching cristae. Mitosis variable but typically with nuclear envelope either breaking down at poles or breaking down entirely. Spindle microtubules arising from amorphous material near the nucleus or from basal bodies if flagella are present.

Synapomorphy: Mitochondriate eukaryotes with branched tubular mitochondrial cristae.

Composition: The euamoebae (corresponding broadly with the naked lobose amoebas); centramoebae (i.e., with lamellate microtubule organizing center: Acanthamoebae, Stereomyxidae and Dictyosteliidae), the leptomyxids, *Trichosphaerium*, lobose testate amoebas (Testacealobosea), filose testate amoebas (Testaceafilosea), and *Gromia*, protostelids, and myxomycetes. This group contains the bulk of the naked lobose amoebas of previous classifications, the lobose and filose testate amoebas.

References: Roos 1975; Frederick 1990; Spiegel 1990, 1991; Grell 1991; Grell and Schüller 1991; Patterson 1994; Patterson et al. 1999.

Red algae

Circumscription: The red algae, unicellular to multicellular (up to 1 m) mostly free-living but some parasitic or symbiotic, with chloroplasts containing phycobilins. Cell walls made of cellulose with mucopolysaccharides penetrated in many red algae by pores partially blocked by proteins (complex referred to as pit connections). Usually with separated phases of vegetative growth and sexual reproduction. Common and widespread, ecologically important, economically important (source of agar). No flagella.

Ultrastructural identity: Mitochondria with flat cristae, sometimes associated with forming faces of dictyosomes. Thylakoids single, with phycobilisomes, plastids with peripheral thylakoid. During mitosis, nuclear envelope mostly remains intact but some microtubules of spindle extend from noncentriolar polar bodies through polar gaps in the nuclear envelope.

Synapomorphy: No clear-cut feature available; possibly pit connections

Composition: About 4,000 species, usually divided into two subclasses: the Bangiophyceae and the Floridophyceae.

References: Gabrielson et al. 1990; Ragan and Guttell 1995; Saunders and Kraft 1997.

Reticulomyxa

Circumscription: Naked large amoebas with reticulate pseudopodial system with bidirectional movement of cytoplasm; pseudopodial system is similar to that of the Foraminifera. Can produce cysts. Probably allied to or a member of the Granuloreticulosea; unfortunately the latter lacks a clear synapomorphy (see Granuloreticulosea).

Ultrastructural identity: Mitochondria with tubular cristae, pseudopodia with microtubules not in geometric arrays, and with electron-dense bodies believed to be extrusomes.

Synapomorphy: Not known.

Composition: Monotypic.

References: Ostwald 1988; Patterson et al. 1999.

Retortamonads

Circumscription: Heterotrophic flagellates, typically with two or four flagella, mostly commensal or parasitic but at least one free-living taxon known. Excavate, in the sense that the flagella sit at the head of a ventral feeding groove with ingestion occurring at the base of the groove.

Ultrastructural identity: Without mitochondria, flagella associated with four basal bodies arranged in a cruciate pattern or in separated pairs, giving rise to two major microtubular roots, which support the margins of the ventral feeding groove and are associated with some nonmicrotubular strands. Microtubules, which underlie the dorsal cell surface, arise from a band (lapel) of dense material near the basal bodies. Extrusomes not reported, no dictyosomes.

Synapomorphy, None known, possibly a cytoskeletal lapel dorsal to flagellar anchorage, or hook-shape of anterior part of right microtubular root.

Composition: Two known genera, *Chilomastix* and *Retortamonas*.

Reference: Bernard et al. 1997.

Rosette agent

Circumscription: Obligate intracellular parasite from spleen and kidneys of farmed chinook salmon, with multilayered cellulose-containing wall within host cells, and with distinctive transverse plates developing at fission. Sequence studies suggest affinity with several other parasites such as *Dermocystidium* and *Ichthyophonus*, and a colloquial name (DRIPS) is emerging for this cluster, although it currently lacks a structural synapomorphy.

Ultrastructural identity: Ultrastructural studies not detailed, mitochondria present. Cristal form not known, with a multilayered wall. No flagellum or discernible cytoskeleton.

Synapomorphy: None specified.

Composition: Currently monotypic.

References: Harrell et al. 1986; Kerk et al. 1995.

Spironemidae

Circumscription: Multiflagellated heterotrophic protists, usually elongate body. Flagella arranged in a small number of longitudinal rows (kineties). Body surface underlain by one large dorsal organic plate and one large ventral organic plate.

Ultrastructural identity: Mitochondria cristal form ambiguous but probably tubular or sacculate. With flagella arising from short basal bodies and anchored by longitudinal fibrous and microtubular elements. With dictyosomes. Cell surface folded, underlain by microtubules and organic layers. Concentric extrusomes.

Synapomorphy: Mitochondriate protist with flagella in kineties and with two subsurface organic plates.

Composition: Three genera: *Stereonema*, *Spironema*, and *Hemimastix*

Reference: Foissner and Foissner 1993.

Spongomonads

Circumscription: Heterotrophic flagellates, two flagella inserting at the apex of cells, which are embedded in a matrix of iron-rich mucoid globules, some forming large colonies.

Ultrastructural identity: Mitochondria with tubular cristae. With two flagella inserting in near parallel basal bodies, basal bodies with radiating fibrous anchorage structures and radiating microtubules, as well as cross-striated fibers running between and away from the basal bodies. Dictyosome located adjacent to nucleus and basal bodies.

Synapomorphy: Tubulocristate flagellates embedded in globular mucoid iron-rich matrix.

Composition: Two genera, few species.

References: Hibberd 1976*a*, 1983; Strüder-Kypke and Hausmann 1998.

Stephanopogon

Circumscription: Genus of marine flagellates with flagella in kineties on one or both faces, dorso-ventrally flattened with apical flattened mouth with or without barbs.

Ultrastructural identity: Mitochondria with discoidal cristae, flagella arising from unpaired basal bodies, each anchored by a cone of microtubules and linked to other basal bodies in a kinety by electron-dense strands. Bands of microtubules may also underlie surface of cell. Flagella without hairs, scales, or other excrescences, and without paraxonemal structures. Mouth with rods of microtubules arrayed in square-packed pattern and with membrane-bound bodies (extrusomes?) with densely staining contents. Larger extrusomes are associated with body surface.

Synapomorphy: Discicristate flagellates, kinetosomes in kineties anchored with a basket of microtubules and linked longitudinally by nonmicrotubular ribbons.

Composition: One genus, several species.

Reference: Patterson and Brugerolle 1988.

Sticholonche

Circumscription: Marine protists with four rows of flattened mobile axopodia, which insert in ball and socket joints in the nucleus. Rowing motion of axopodia propels the cell. Also referred to as taxopodids.

Ultrastructural identity: Mitochondria probably tubulocristate. Microtubules of axopodia with hexagonal packing, and with electron-dense basal ball located in a socket created of electron-dense material attached to outer face of nuclear envelope.

Synapomorphy: Tubulocristate (?) eukaryotes with mobile axopodia with ball and socket insertion in nucleus.

Composition: Two species.

References: Cachon and Cachon 1978; Smith and Patterson 1986.

Stramenopiles

Circumscription: A major assemblage of tubulocristate protists, including taxa with and without chloroplasts. Plastids if present with chlorophylls *a* and *c*. Most flagellated taxa with one short and one long flagellum but some with only one flagellum. The long flagellum usually carrying tripartite tubular hairs that reverse the thrust from the flagellum. In a few cells the hairs are absent and in one lineage they may be attached to the body surface. Cells may also be aflagellated, amoeboid, or mycelial, may be extremely large (some brown algal kelps). Cells may have scales, organic walls, or inorganic walls. Includes parasites, saprophytes, autotrophs, and heterotrophs; includes some taxa with great species diversity (e.g., diatoms).

Ultrastructural identity: This group has considerable diversity, with few features common to all species. Mitochondria have tubular cristae, usually with two flagella but one group of lineages have a single flagellum, and another lineage has many flagella arranged in rows (kineties). If two basal bodies are present, they are typically anchored by four microtubular roots. Plastids are present in many species, with three thylakoids per lamellae and with a stigma usually included within the plastid. Dictyosomes present. Extrusomes may be present or absent. Mitosis typically with fragmenting membrane and microtubules arising from external to the nucleus, most usually from the bases of the flagella.

Synapomorphy: Tubulocristate protists with tripartite tubular hairs, but there has been secondary loss of this character in some subsets.

Composition: *Aureococcus*, Bicosoecids, *Blastocystis*, brown algae, *Chlamydomyxa*, chromulinids, Chrysomeridales, *Commation*, diatoms, *Developayella*, *Diplophrys*, eustigmatophytes, Hibberdiales, Hydrurales, labyrinthulids and thraustochytrids, *Ollicola*, Oomycetes, Parmales, pedinellids, pelagophytes, *Pendulomonas*, phaeothamniids, *Pirsonia*, proteromonads, raphidophytes, *Reticulosphaera*, *Rhizochromulina*, silicoflagellates, slopalines, synurids, xanthophytes (inter alia).

References: Patterson 1989; Andersen 1991; Leipe et al. 1994; Saunders et al. 1995; Schnepf and Schweikert 1996; Silberman et al. 1996.

Telonema

Circumscription: Single genus of predatory flagellates, two flagella equal or nearly so arising from the apex of the cell, but cell swims with flagella directed behind the moving cell. Marine, fairly common.

Ultrastructural identity: Mitochondria cristae tubular. Two flagella arising from two almost parallel basal bodies, basal bodies give rise to complex microtubular sheath, with associated fibrous structures. Sheath underlines one side of cell, with discrete ingestion area located subapically adjacent to basal bodies. Dictyosomes present, occasional extrusomes present.

Synapomorphy: None specified, taxon distinguished by cytoskeleton (details unpublished).

Composition: Two species.

References: Patterson and Zölffel 1991; Vørs 1992*a*, 1992*b*; D. J. Patterson and N. Vørs (unpublished data).

Thaumatomonads

Circumscription: Heterotrophic flagellates, two flagella; glide or swim; able to produce pseudopodia with which food is ingested. All species studied ultrastructurally have inorganic external scales and perhaps spines. Some syncitial.

Ultrastructural identity: Ultrastructural studies more or less restricted to whole mount preparations and details of the scales. Spines appear hollow and have symmetrical extensions from the base, scales tend to have margins that are rolled over. In those species that have been studied in more detail, the scales form in association with tubulocristate mitochondria.

Synapomorphy: Probably formation of surface scales in association with mitochondria of all scaley species (but apparently naked species have yet to be examined).

Composition: Seven genera.

References: Swale and Belcher 1974; Beech and Moestrup 1986; Patterson and Zölffel 1991.

Trimastix

Circumscription: Amitochondriate excavate flagellate with four flagella inserting at the head of a ventral feeding groove in a cruciate pattern. Heterotrophic and free living.

Ultrastructural identity: Without mitochondria. Four basal bodies with three major microtubular roots, two supporting the margins of a ventral gutter and both with associated fibrous threads. Cell dorsally with supporting microtubules arising indirectly from one microtubular root. Cell surface naked, no extrusomes, dictyosomes in at least one species, recurrent flagellum with two opposed flagellar vanes. Mitosis not described ultrastructurally.

Synapomorphy: None specified.

Composition: Three species.

Reference: Brugerolle and Patterson 1997.

Vampyrellids

Circumscription: Amoebas with filose/tapering pseudopodia usually finely granular cytoplasm, pseudopodia rarely anastomosing. Mostly ingest the contents of algal and fungal cells, which they gain access to by perforating the cell walls. Feeding amoebas alternating with digestive cysts, cytoplasm frequently orange. Freshwater and marine. Cells uninucleate or multinucleate.

Ultrastructural identity: Mitochondria with tubular cristae. Dictyosomes present. No flagella or centrioles known. Cytoplasm with helical arrays (of ribosomes?) Mitotic nuclei with intact nuclear envelopes and intranuclear spindles.

Synapomorphy: Tubulocristate filose amoebas with alternation of motile amoebas and digestive cysts.

Composition: *Arachnula*, *Gobiella*, *Hyalodiscus*, *Leptomyxa*, *Vampyrella*, and *Vampyrelloides*.

Reference: Röpstorf et al. 1994.

Viridaeplantae

The green algae and plants, distinguished as platycristate taxa with or without flagella, with chloroplast containing chlorophylls *a* and *b*, eyespot when present in plastid, basal bodies anchored by cruciate system of rootlets. Coccoid, filamentous, palmelloid, amoeboid, or multicellular, most with cellulosic cells walls (prasinophytes are an exception). A major group and includes the multicellular plants. "Chlorophyta" is usually the term used to refer to nonplant elements of the clade.

Ultrastructural identity: Mitochondria with flat cristate, plastids in cells with thylakoids arranged in granae (stacks), two bounding membranes around the plastids; stigma if present within the plastid. With flagella typically anchored by cruciate array of microtubular roots and or a multilayered structure or derived from such structures; transition region with star and "H-piece." Mitosis may or may not involve loss of the nuclear envelope. Microtubules usually assist in controlling the orientation of new walls. The cell walls of "multicellular" species may or may not have pores called plasmodesmata.

Synapomorphy: Platycristate taxa with plastid thylakoids bearing chlorophylls *a* and *b* in stacks.

Composition: Typically about 11 categories (Classes?) of algae, one being the prasinophytes; plus (the Kingdom including) all green metaphyta.

Reference: van den Hoek et al. 1991.

Xenophyophores

Circumscription: Generally large (>1 cm) marine amoebas with an agglutinated test. Cell multinucleated; waste material (stercomata) accumulate around cell within test. Cytoplasm contains barite crystals. Very little information on cell organization, pseudopodia said to be filopodial or granuloreticulopodial. Widespread and possibly significant in deep sea sediments.

Ultrastructural identity: No information, identity based on gross morphology, stercomata, and barite crystals.

Synapomorphy: Large marine amoebas containing barite ($BaSO_4$) crystals, and with adhering stercomata.

Composition: Two subsets (psamminids and stannomids); 50 species in about 15 genera.

Reference: Tendal 1972.

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