

Chromista

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As a group, the chromists show a diverse range of forms from tiny unicellular, flagellates to the large brown algae known as kelp. Molecular studies have confirmed the inclusion of certain organisms once considered fungi, as well as some heterotrophic flagellates. Despite their diversity of form and feeding modes, a few unique characters group these organisms.

Introduction

The five-kingdom system of Robert H. Whittaker (see Whittaker, 1959, 1969), although a major improvement over the simple two-kingdom system of plants and animals, still left much room for criticism (see South and Whittick, 1987, for a review). While the kingdom Monera, with its distinct prokaryote organization of the nucleus, is still considered the most natural and unambiguous kingdom of this system, the remaining kingdoms have all undergone some or other taxonomic scrutiny. The plant, animal and fungi kingdoms, all multicellular eukaryotes, have each been defined by their nutritional modes. Several researchers have criticized the use of these characters, arguing that they defined adaptive traits and not taxa. These names are thus entirely unsuitable for revealing phylogenetic relationships among organisms. The kingdom Protista or Protoctista is the hardest to define, as it is the least homogeneous group. It is somewhat of a mix-and-match containing all eukaryotes that do not fit into the plant, animal or fungi kingdoms.

Towards the eight- and six-kingdom systems

The problems encountered with the five-kingdom system led to the continued use of the plant, animal and fungi kingdoms. The former kingdom Monera, the least problematic kingdom, was split into the kingdoms Eubacteria (true or present-day bacteria including the Cyanobacteria) and the Archaeobacteria (ancient bacteria). Despite being readily accepted, many still have problems with the placement of the Cyanobacteria (or blue-green algae) in a bacterial kingdom. Time saw the erection of the new kingdom Chromista, proposed to include the kelps and other brown algae (phaeophytes), the diatoms (bacillariophytes), the golden-brown algae (chrysophytes), certain moulds (oomycetes) and even heterotrophic flagellates (the silicoflagellates). At this point, the eight-kingdom system of classification was born.

Advances in molecular phylogeny, however, saw the development of a six-kingdom system (Cavalier-Smith, 1993) with the proposal for the erection of the kingdom Protozoa separate from the kingdom Chromista. The kingdom

Advanced article

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Monera (as the kingdom Bacteria) was resurrected, with the kingdom Protozoa occupying a pivotal position between the ancestral prokaryotic kingdom Bacteria and the four derived eukaryotic kingdoms, Animalia, Plantae, Fungi and Chromista (Cavalier-Smith, 1998).

The chromists represent an independent evolutionary lineage that appears to have diverged from the same common ancestor as plants, animals and fungi. The suggestion of a divergent algal group, however, being placed in a newly erected kingdom, was met with much criticism because the precise relationship of the chromists to the other eukaryotes is still problematic. However, the Chromista as a group was registered and named under the International Code of Botanical Nomenclature (Golding, 1996).

The name Chromista means 'coloured', and although some chromists like the Oomycota, Sagenista and various chrysophytes and silicoflagellates are colourless, the majority are photosynthetic. Despite their photosynthetic capacity, chromists are not all closely related to plants or even other algae. Unlike plants and green algae that possess chlorophyll *b* in addition to chlorophyll *a*, the Chromista possess chlorophyll *a* and *c*. Furthermore, unlike plants that store energy in the form of starch, the main food reserves of the Chromista are the oil leucosin and the polysaccharide chrysolaminarin, a β -1,3-linked glucan that is formed in vesicles located outside the chloroplast. Photosynthetic chromists often also carry various accessory pigments (fucoxanthin in some, vaucherixanthin in others) that give them their characteristic golden to brown to orange coloration.

But it is not their photosynthetic and accessory pigments that characterize the Chromista, but rather an unusual suite of diagnostic features found in no other group. The group originally got its name from the fact that they all possess flagellated cells at some stage of their life cycles, and the flagella are typically of two types (subsequently referred to as the heterokont-type flagella, **Figure 1**). One type of flagellum is covered with thin, stiff, tubular hairs, and is usually directed into the direction of swimming. The other type is shorter, lacks the coating of stiff hairs, and is usually directed away from the direction of motion. The anterior flagellum is referred to as a tinsel, pleuronematic

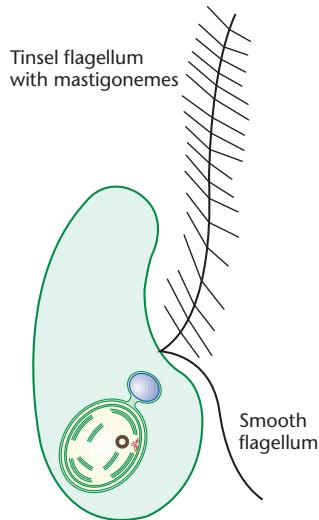


Figure 1 The typical heterokont-type flagellar system.

or flimmer flagellum, while the thin hairs are called mastigonemes. Whenever present, the mastigonemes have a unique tripartite structure. The posterior flagellum is referred to as a whiplash flagellum.

Secondly, their chloroplasts and nuclei are inside the rough endoplasmic reticulum (ER) instead of free in the cytoplasm, i.e. the chloroplast is bounded by a double membrane, but has an extra layer of ER (also two-layered) that is often continuous with the nuclear envelope (**Figure 2**). Inside the chloroplast, the thylakoids are stacked in groups of three called lamellae, although this feature in itself is not a diagnostic feature. Furthermore, the chloroplast contains a light sensitive ‘eyespot’ of pigmented granules called the stigma. The chloroplast DNA is not bound by a membrane and usually arranged in the shape of a ring called a nucleoid (or nucleomorph or cryptonucleus) and is thus a degenerate nucleus. The nucleoid is a simple single-strand DNA molecule coiled around an RNA core and has also been known as a bacterial chromosome or a chromatin body.

A third character common to the Chromista is their mitochondrial architecture. Mitochondria are generally spherical organelles that have an outer membrane surrounding an inner membrane that folds (cristae) into a scaffolding for oxidative phosphorylation and electron transport from enzymes. While most mitochondria have flat shelf-like or plate-like cristae, the chromists have tubular cristae.

Another character that a number of chromists share is the components of their cell walls. Although not all chromists can do this, many manufacture silica or calcium carbonate skeletons from their Golgi apparatus. The majority of those that do not possess silica or calcium carbonate skeletons deposit various cellulosic compounds around

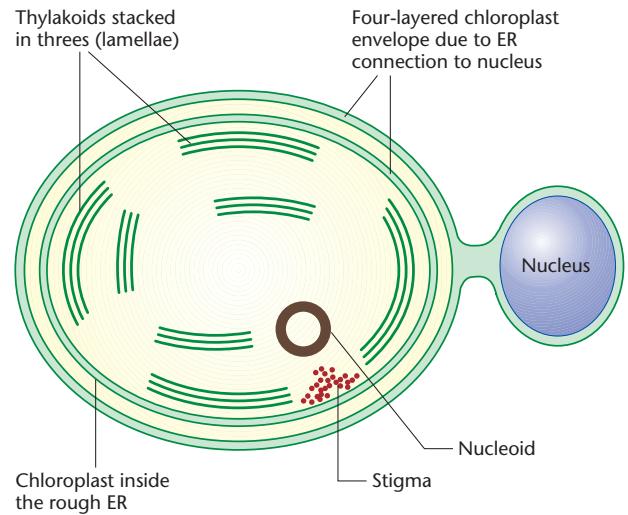


Figure 2 The chromist chloroplast and nucleus are both located inside the double membrane of the rough endoplasmic reticulum (ER).

their cells; this gives them form and rigidity while remaining flexible.

How did the chromists arise?

It is now generally accepted that present day chromists arose from a single endosymbiotic merging event between two eukaryotes into a single cell, this through the process of secondary endosymbiosis (refer to Margulis (1981) for her theory on endosymbiosis, see Cavalier-Smith, 1982, 1987; Gray, 1989; Battacharya, 2000). It has been postulated to have occurred during the later stages of the symbiotic origin of mitochondria and chloroplasts. The evidence is based largely on the presence of unusual organelle structures, such as the nucleoid (or nucleomorph or cryptonucleus), a naked (membrane-free) structure containing DNA in the shape of a ring, located within the ER. This minute, well-hidden structure codes for 80S ribosomes that are distinct from those of the cytoplasm and is inferred to be a reduced nucleus of the former endosymbiont.

The second line of evidence involves the double membrane of the ER surrounding the chloroplasts. The two membranes of the chloroplast ER are very different in evolutionary origin and must therefore have very different physiological and developmental properties. The outer rough membrane belongs to the host while the smooth inner membrane is in fact the lineal descendant of the plasma membrane of the eukaryotic symbiont that provided the chromist chloroplast. Even today, this smooth inner membrane seems to undergo budding to generate vesicles, reminiscent of a free-living cell undergoing pinocytosis (Golding, 1996).

An Overview of the Major Chromist Subtaxa

The Chromista (Cavalier-Smith, 1986, 1989) has also variously been referred to as the Heterokonta (van den Hoek, 1978 (as Heterokontophyta); van den Hoek *et al.*, 1995; Baldauf *et al.*, 2000), the Stramenopiles (Patterson, 1989), and the Chromobionta (Jeffrey, 1971; see also South and Whittick, 1987; Green *et al.*, 1989). Patterson (1989) defines the Stramenopiles as 'tubulocristate protists with tripartite tubular hairs or derived from such organisms'. The Heterokonta are specifically characterized by flagellated cells that have two unequal flagella (one tinsel or hairy, the other smooth and whiplash) that are laterally inserted. The name Chromobionta was derived from the Chromophyta, a group collectively comprising the haptophytes (see below) and the heterokonts (a reference to their golden pigmentation). Essentially it included all protists possessing chlorophylls *a* and *c*, lacking chlorophyll *b*. The obvious problem with the Chromobionta was that it included the dinoflagellates, a group that lacks many of the typical heterokont features. From the characterizations, it is evident that each of these names has, however, been used to define specific groups of protists.

Despite their common features, there is still no full agreement as to how the taxa within the Chromista are interrelated. There has, however, been much support for the use of the term Chromista as defined by Cavalier-Smith (1997). Although the Chromista as a kingdom is comprised of some 13 321 species from 11 divisions or phyla (depending on the phylogenetic source), we will only be concentrating on the more popular (those that have been well studied) taxa. One thing is certain though, the ultrastructure, biochemistry and molecular analyses of the following taxa indicate their affinities to each other and that they

belong to the Chromista with a suite of general chromist characters that are easily recognizable (Table 1).

Haptophyta

Also called the Prymnesiophyta, or coccolithophorids, the Haptophyta are still included with the Chromista by many authors despite growing evidence to the contrary. Typically unicellular flagellates, the haptophytes were once classified with the chromists (as heterokonts) on the basis of their photosynthetic pigments (more specifically the accessory pigments diadinoxanthin and fucoxanthin) and together they were classified as the Chromophyta. This was particularly in reference to their golden coloration. The Haptophyta, however, lack several of the morphological and molecular characters common to the Chromista. First, they do not possess the typical heterokont-type flagella. Secondly, they possess a unique organelle, the haptonema, a flagellum-like organelle that is attached to the cell near the point of insertion of the true flagella. It is this organelle from which the group's name was originally derived.

Sagenista

Like the haptophytes, it is well established that the Sagenista is a basal group of protists. While there is much debate about the phylogeny of this group, there appears to be consensus as to the paraphyletic origin of this group. Although the specific relationships are unclear, the Sagenista is generally divided into two groups, namely the Bicocea (also referred to as the Bicoflagellota or Bicocoecida) commonly referred to as the bicosoecids, bicosecids or bicoecids, and the Labyrinthulomycota (or Labyrinthulea) or labyrinthulids.

The bicoecids comprise a small collection of both pho-

Table 1 Characters common to the taxa of the Chromista

Characteristics of the Chromista	
Main pigments	Chlorophyll <i>a</i> and Chlorophyll <i>c</i> , α and β carotene, xanthophylls (fucoxanthin in some, vaucherixanthin in others); chlorophyll <i>b</i> is never present
Food reserves	Chrysolaminarin (β 1,3-linked glucan), formed in vesicles outside the chloroplast
Chloroplast features	Membrane two-layered but with an extra two layers of endoplasmic reticulum that is continuous with the nuclear envelope; the thylakoids are stacked in groups of three (lamellae)
Chloroplast endoplasmic reticulum	Present
Cell wall	Varies, sometimes includes silicon
Flagella	Present in at least some stage of the life cycle; one flimmer or tinsel and one smooth (whiplash); collectively referred to as the heterokont-type flagella
Mitochondrial cristae	Tubular

tosynthetic and heterotrophic unicells. Although poorly studied, it is known that photosynthetic unicells possess chlorophyll *a* and *c*, the typical heterokont-type flagella, and the tubular cristae in their mitochondria, features that they share with the majority of the chromists. Cavalier-Smith (1989) believes the bicoecids represent the primitive protist that first entered into a symbiosis with a chlorophyll-*c*-containing symbiont to form the Chromophytes.

Like the bicoecids the labyrinthulids (more commonly known as slime nets), also have flagellated stages in their life cycle that possess the typical heterokont-type flagella. Although they have traditionally been classified with the fungi, it is their flagellar features that group them with the chromists. Their common name is derived from the fact that they are unique in their ability to produce or secrete an anastomosing slime net or membrane outside their cells. Hardly any characters unite the bicoecids and the labyrinthulids and many authors have opted to separate these two groups.

Oomycota

The Oomycota, or quite literally ‘egg fungi’ (also referred to as Pseudofungi), is a small division of fungus-like, filamentous protists commonly known as water moulds and downy or powdery mildews. Although some are unicellular, the majority are multicellular and mycelial (branched filamentous coenocyte) in nature. The Oomycota have been classified as chromists because their free-swimming zoospores possess the heterokont-type flagella. Furthermore, food is stored in the form of mycolaminarin, an energy storage molecule similar to that found in diatoms and brown algae.

For some time, however, the oomycetes were classified as fungi because of their essentially filamentous growth and feeding mode similar to that of the fungi. Unlike fungi, however, which have cell walls composed of chitin, the oomycetes’ cell walls are composed of cellulose, similar to that found in the brown algae. Also, the free-living stage of the oomycetes has a diploid chromosome complement while that of the fungi is haploid.

Bacillariophyta

Commonly known as diatoms, the bacillariophytes are unicellular or colonial, but are never organized into more complex thalli. Only the male gametes are flagellated with the flagella typically of the heterokont type. Like most chromists, they also possess chlorophyll *a* and *c*. The chief distinguishing feature of the Bacillariophyta, however, is the cell wall, which is siliceous and composed of two overlapping halves, rather similar to a shoebox or Petri dish. This type of cell is termed a frustule.

The two kinds of pennate and centric diatoms are classified into two orders, the Pennales and Centrales. The

frustules of pennate diatoms are usually elongate and bilaterally symmetrical in valve view. There is usually an elongate structure (the raphe) visible at the surface of each valve; this is actually a slit in the frustule, at the centre of which is a thickening called the central nodule. At each end of the raphe there are also thickenings called polar nodules. Mucilage extruded through the raphe or polar regions may be used for movement, attachment or protection from abrasion. There are many features present on the surface of the frustule, many of which are best resolved using the scanning electron microscope. It is these patterns (marginal projections and minute holes called punctae) that are used to separate taxa within the Bacillariophyta.

Silicoflagellata

The Silicoflagellata are uncommon, mostly planktonic marine flagellated algae that are represented by both photosynthetic and heterotrophic forms. They are characterized by having internal skeletons (distinctly star-shaped) over which the cell body wraps itself. The skeletons are constructed by a secretion of silicon dioxide either in the form of a network or framework (resembling simple radiolarians), or in the form of multiple scales. They possess the typical heterokont-type flagella; the long flagellum (called an undulipodium) is used to propel the cell while the other flagellum is much reduced and barely visible; in many reviews, this reduced flagellum is regarded as lacking. Most reports of reproduction indicate a predominance of asexual reproduction by simple mitotic division.

Many authors classify the silicoflagellates as a class under the Chrysophyta (also referred to as the Dictyochophyceae). Others have, however, suggested the elevation of this group, arguing that the Chrysophyta are almost exclusively freshwater algae, while the silicoflagellates are almost exclusively marine. Is this character, however, enough to warrant such a move?

Chrysophyta

Although the Chrysophyta (golden or golden-brown algae) are now generally believed to be paraphyletic, or possibly even polyphyletic (see Sandgren *et al.*, 1995), many still treat the subtaxa belonging to this group as a composite entity. Their distinct golden or golden-brown coloration is derived from their yellow, brown and orange accessory pigments (carotenoids and xanthophylls). Fucoxanthin is particularly important in imparting colour to this group although it is entirely absent from the Xanthophyceae.

Their apparently unifying characters are the presence of chlorophyll *a* and *c*, and the possession of the heterokont-type flagella. However, a small minority of chrysophytes are colourless and are essentially heterotrophic. To complicate matters further, the chrysophytes are considered by

some to not be truly autotrophic because it is believed that nearly all chrysophytes can become facultatively heterotrophic during adverse conditions. Similarly, not all chrysophytes possess flagella, and some that do, lack the typical heterokont-type flagella; instead, they have isokont flagella, i.e. flagella of equal length.

Some of their other unifying characters are the composition of the cell wall constituents, and their food storage products. In many chrysophytes, the cell wall is composed of cellulose while in others silica is the main cell wall component. Food is generally stored as oils or as the polysaccharide laminarin that is also very typical of the brown algae.

Because of the heterogeneous nature of the Chrysophyta as a group, several subtaxa formerly included in the Chrysophyta have been given separate recognition. There is, however, no consensus as to how these taxa are interrelated or their placement within the phylogeny of the Chromista for that matter. The following taxa, once regarded as subtaxa, are now considered separate (but close) to the Chrysophyta: Eustigmatophyceae (also referred to as Eumastigophyceae), Parmophyceae, Raphidophyceae (also referred to as the Raphidophyta), chloromonads, Sarcinochrysidophyceae (also referred to as the Sarcinochrysidophyceae), and many more (Table 2).

Xanthophyta

The Xanthophyta (variously also referred to as the Xanthophyceae, Tribophyceae and the Heterocontae) are commonly called yellow-green algae. Unlike the other

chromists, the xanthophytes lack the accessory pigment fucoxanthin, the pigment responsible for the golden-brown to orange coloration of its sister taxa. The dominant pigment in the Xanthophyta is chlorophyll *a*, which generally gives the alga a green coloration. This, combined with the fact that members of the group often produce copious amounts of carotenoids, gives the xanthophytes their distinctly yellow-green coloration. Those xanthophytes that have reduced carotenoid concentrations are quite easily mistaken for green algae.

A suite of distinct features characterizes the Xanthophyta. They are primarily freshwater and soil algae (often also occurring on and within plant surfaces) with only a few planktonic marine forms. Although most occur as either flagellated unicells, coccoid or filamentous forms, some occur as palmelloid colonies while their most distinctive forms are based on a coenocytic or siphonous organization. Like all chromists, they possess chlorophyll *a* and *c* (in only small amounts), the zooids have the typical heterokont-type flagella (although these are apically inserted) and food reserves stored as chrysolaminarin. In many xanthophytes, the cell wall is absent. The constituents of those that do possess cell walls are still completely unknown although some have been reported to be cellulose impregnated with silica. Their cysts, however, are formed from silica, the cyst walls often, but not always, being composed of two overlapping halves.

The phylogeny of the xanthophytes like so many of the other taxa is by no means adequate. The xanthophytes typically lack the nucleoid present in most chromists, suggesting a secondary acquisition of the chloroplast. While

Table 2 Some of the classes formerly classified under the Chrysophyta that have been given separate recognition

Class	Chief features
Parmophyceae	Unicellular, very tiny, lack flagella, walls with siliceous plates, sometimes treated as an order of the Chrysophyceae
Sarcinochrysidophyceae	Unicellular, colonial, filamentous to slightly more complex, possibly represent the ancestral group from which the brown algae evolved; occur mainly in estuarine and coastal marine water, often high up on rocky shores
Xanthophyceae	Unicellular or colonial, but many species made up of multinucleate siphons (filaments with no cellular crosswalls); more common in freshwater than in the sea, but important in salt marshes
Eustigmatophyceae	All unicellular, coccoid cells that may or may not have flagella, mainly found in freshwater or soil
Raphidophyceae	Unicellular flagellates without cell walls, flagella are apically inserted, one is directed backward in a ventral groove; includes both freshwater and marine species
Dictyochophyceae	Only two living species known, both are marine, unicellular, there is a single long tinsel flagellum and a reduced barely visible smooth one; silica skeleton outside of cell membrane gives them the name silicoflagellates, known as fossils dating back about 120 million years

there is still much debate as to the placement of the Xanthophyta, the group as a whole has even been suggested to require revision at the generic, familial and ordinal levels. This is in view of the fact that molecular evidence now suggests that the characters used to separate the Xanthophyta at the ordinal level appear to no longer be valid (McElhinney *et al.*, 2002).

Phaeophyta

The Phaeophyta (also referred to as the Phaeophyceae and on occasion the Chromophyta and the Chromophycota) are the brown algae. The Phaeophyta, being the largest of the chromists, only occur as multicellular forms. They range from filamentous species (e.g. *Ectocarpus*) to complex parenchymatous species reaching up to 60 m or more in length, as exemplified by the giant kelps (*Macrocystis*) of the Californian coast. There are between 1500 and 2000 species known at present, assigned to approximately 265 genera. Only six genera are represented in freshwater, the rest being entirely marine.

The Phaeophyta are undoubtedly members of the Chromista, sharing many of the characters that distinguish the group: they possess chlorophyll *a* and *c*, lack chlorophyll *b* and possess the accessory pigment fucoxanthin, the pigment responsible for its coloration. The products of photosynthesis (food reserves) are stored as laminarin. The chloroplasts are the typical chromist chloroplast having a two-layered membrane with an extra two layers of ER that is continuous with the nuclear envelope; the thylakoids are stacked in groups of three (referred to as lamellae). The only flagellate stages, however, are the spores and gametes. Motile stages are generally pear-shaped (pyriform), and have the typical heterokont-type flagella: namely, two laterally inserted flagella one of which points forward and the other backward. The anterior one is of the flimmer type, while the posterior one is smooth. In some species, male and female gametes are similar, while in others there is a separate egg and sperm cell (the sperm cell then being the only gamete to bear the heterokont-type flagella).

Besides occurring only as multicellular forms, the phaeophytes are unique with regard to a number of other features. Food is stored in a stalked pyrenoid that is attached to the chloroplast. The cell wall comprises phlorotannins and is made of cellulose strengthened by calcium alginate, a substance that is of considerable economic significance as it is extracted and used as a gelling and emulsifying agent in a large number of industries.

While the placement of the Phaeophyta within the Chromista is well established, the exact relationship of this group to other chromists is still vague. Many believe that they are most closely related to the Xanthophyta and then secondarily to the Chrysophyta. Much of the reported evidence stems from the sperm and zoospore ultrastructure although even this probably still needs verification.

Phylogenetic and Evolutionary Considerations

How many kingdoms?

The concept of kingdom, as well as of most other taxonomic levels, predates the realization that living organisms have undergone evolution and that phylogenies can be traced through a combination of morphology, anatomy, ultrastructure and (more recently) molecular sequences. Rather than modifying our taxonomic systems, we have attempted to mould phylogenies so that they fit into the kingdom–division (phylum)–class–order–family–genus–species series. Therefore, the squeezing of organisms into these categories is somewhat arbitrary. For example, the evolutionary distance between divisions varies enormously from seed plants to red algae, showing that the concept of ‘division’ is not used consistently in different groups.

The classification of organisms into kingdoms carries the implicit assumption that once lineages diverge, genetic information does not cross back again from other lineages. We now know that there are a number of ways that genetic material has crossed lineages, the most obvious one being the endosymbiosis of chloroplasts and mitochondria. Therefore, the concept of kingdom is an imperfect concept, and one that biologists are still trying to figure out how to deal with in the light of our current and steadily advancing knowledge.

It has long been recognized that the two-kingdom system was inadequate. In 1969, Robert H. Whittaker proposed a five-kingdom system as an alternative to the two-kingdom system. The Archaeobacteria and the Eubacteria are treated as subkingdoms under this system. Various authors have used either Protista or Protoctista for the kingdom that includes most eukaryotic algae. Under this system, photosynthetic organisms for example occur in three kingdoms: Monera, Protista and Plantae. In most treatments that use this system, the Chlorophyta are included in the Protista and not the plant kingdom, something that is clearly not supported by the current evidence.

The Monera were eventually split into the kingdoms Eubacteria and Archaeobacteria. A further kingdom, the Chromista, was proposed at the same time for the heterokont organisms, although this was – and remains – controversial. The kingdom Archaezoa was proposed for three phyla (Archaeomoeae, Metamonada, Microsporidia) which differ from all other eukaryotes in lacking mitochondria, peroxisomes, Golgi dictyosomes and cisternae, and probably also in having 70S rather than 80S ribosomes.

Molecular studies have prompted major revisions and are now showing that even the eight-kingdom and the recently proposed six-kingdom systems are not adequate. Some groups are paraphyletic, others are polyphyletic. Sequence, intron-location and functional data from nuclear

and mitochondrially encoded proteins suggest, too, that the red algae and the green algae are sister groups, further suggesting that the red algae are not plants (Ragan and Gutell, 1995). Current evidence is pointing towards the idea that there is a single eukaryotic kingdom (variously referred to as the Eukarya, or the Eukaryota), if indeed the concept of 'Kingdom' has any fundamental meaning at all in evolutionary phylogeny. Fusing the plants, animals, fungi and protists into a new Crown eukaryotic kingdom may resolve many of our ideas as to where taxa such as the red algae fit into the scheme of things. However, there is no consensus in this regard, and various problematic groups are still likely to be treated according to any of the above systems, or without regard to their position within kingdoms at all.

It must be borne in mind that the ideas expressed here are but an oversimplification of the ideas and research phylogenies of so many before us. By no means do we argue or even suggest that these taxonomic placements are final. Continued molecular and ultrastructural studies no doubt will clarify and ratify or rectify much of our present ideas on the phylogeny of the Chromista.

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