Green Algae

Secondary article

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Article Contents

Introduction

The green algae comprise a large and diverse group of organisms that range from the microscopic (e.g. *Chlamydomonas*) to the macroscopic (e.g. *Acetabularia*). In addition to exhibiting a considerable range of structural variability, green algae are characterized by extensive ecological diversity. Green algae are found in virtually all aquatic (both freshwater and marine) and some terrestrial habitats. Although most are free-living, a number of green algae are found in symbiotic associations with other organisms (e.g. the lichen association between an alga and a fungus). Some green algae grow epiphytically (e.g. *Characiochloris*, which grows on other filamentous algae or higher aquatic plants), epizoically (e.g. *Basicladia*, which grows on the backs of turtles), or even endophytically (e.g. *Chlorochytrium*, which grows inside the thallus of the aquatic duckweed plant, *Lemna*). A handful of green algae, all of which have lost the ability to photosynthesize, can be listed as human pathogens that generally cause epidermal infections. The major groups of green algae are briefly described in the following sections. (***see*** Algal ecology.) (***see*** Algal symbioses.)

Major Groups

The green algae have been placed at a variety of formal linnean ranks. Many traditional authors support divisional (phylum) status for all organisms generally referred to as the green algae (i.e. the divisions Chlorophyta and Charophyta). The divisions Chlorophyta and Charophyta are comprised of five principal groups (i.e. classes) that are characterized by life history, biochemistry and ultrastructural features of the flagellar apparatus and/or the mitotic and cytokinetic apparatus (Mattox and Stewart, 1984; Mishler *et al.*, 1994; van den Hoek *et al.*, 1995; Graham and Wilcox, 2000). Recent molecular phylogenetic analyses have also shed considerable light on diversity and relationships among green algae (Mishler *et al.*, 1994; Friedl, 1997; Lewis, 1997; Chapman *et al.*, 1998). The Chlorophyta, Charophyta and Embyrophyta (i.e. the embryo-producing land plants) form a monophyletic group of green-pigmented plants that bear chlorophyll *a* and *b* in chloroplasts (see *Prototheca* for an exception to this generalization). The taxonomic and phylogenetic status of the green plant group is supported by both molecular and nonmolecular evidence (Graham, 1993; Graham and Wilcox, 2000). This group of green organisms has been termed the Viridaeplantae or Chlorobionta. Neither the euglenoids nor the chlorarachniophytes, both of which have apparently acquired a green chloroplast by a secondary endosymbiosis, are included in the green plant lineage (Graham and Wilcox, 2000). Furthermore, the Chloroxybacteria (e.g. *Prochloron*), which possess chlorophyll *a* and *b* organized on thylakoids, are true prokaryotes, and are not, therefore, included in the green plant lineage. The green algal division Chlorophyta forms one branch of the green plant lineage and the green algal division Charophyta is part of the other branch of the green plant lineage that also includes the embryophytes. Thus, the charophytes and embryophytes form a monophyletic group that has been termed the Streptophyta (Chapman *et al.,* 1998; Graham and Wilcox, 2000). (***see*** Algal taxonomy: historical overview.) (***see*** Molecular phylogeny reconstruction.) (***see*** Algae: phylogeny and evolution.) (***see*** Algal chloroplasts.) (***see*** Protist systematics.)

Table 1 illustrates the phylogenetic hierarchy of major green algal groups, as currently assessed by phylogenetic analysis of molecular and morphological evidence.

The Chlorophyta

The Chlorophyta are characterized by motile cells that exhibit a cruciate (cross-shaped) arrangement of four sets of microtubules that anchor the flagellar apparatus.

Table 1 Phylogenetic hierarchy of major green algal groups

Viridaeplantae/Chlorobionta
Streptophyta
Embryophyta
Charophyta
Charophyceae
Chlorophyta
Chlorophyceae
Trebouxiophyceae
Ulvophyceae
Prasinophyceae

Flagella are inserted apically in motile cells of the Chlorophyta. Two sets of flagellar microtubules always form pairs of microtubules, whereas the remaining two sets of microtubules vary in number. Each of these sets of microtubules have been termed flagellar roots. The two-stranded flagellar roots are always inserted opposite one another, as are the multistranded flagellar roots. This cruciate arrangement of flagellar roots has also been referred to as 180° rotational symmetry (Chapman *et al.*, 1998). Most members of the Chlorophyta exhibit a closed mitotic spindle in which the nuclear membrane remains largely intact during mitosis (exceptions are found among the Prasinophyceae) (Graham and Wilcox, 2000). Plasmodesmata have been found in several chlorophycean lineages (i.e. Chaetophorales and Oedogoniales) and in the Charophyceae (Graham and Wilcox, 2000). Peroxisomes in all but a few prasinophyte species have been found to contain the photorespiratory enzyme, glycolate dehydrogenase (Graham and Wilcox, 2000). In those organisms that produce a sexual stage, the bulk of the Chlorophyta exhibit zygotic meiosis where the zygote is the only diploid phase. However, the class Ulvophyceae includes many representatives in which alternation of generations or gametic meiosis characterizes the life history. In addition, the Chaetophorales in the class Chlorophyceae have been reported to exhibit an isomorphic alternation of generations, but this observation remains to be fully tested (van den Hoek *et al.*, 1995). The four classes within the Chlorophyta are briefly described below. (***see*** Chlorophyta (green plants).) (***see*** Algal reproduction.) (***see*** Plant peroxisomes and glyoxysomes.) (***see*** Algal flagella.)

Class Chlorophyceae

The Chlorophyceae are predominantly freshwater forms, although some species (e.g. *Dunaliella*) are found in brackish to marine environments. The class is currently diagnosed principally on the basis of ultrastructural features of the mitotic, cytokinetic and flagellar systems (Mattox and Stewart, 1984; Mishler *et al.*, 1994; Graham and Wilcox, 2000). Except for the Chaetopeltidales (e.g. *Chaetopeltis*), the Chlorophyceae are generally thought to lack body and flagellar scales on motile stages. The Chlorophyceae are characterized by a centric mitotic spindle that collapses during telophase. A system of microtubules, called a phycoplast, develops parallel to the plane of cell division. Basal bodies in the flagellar apparatus of motile cells either exhibit no relative offset (i.e. are directly opposed) or are offset, relative to one another, in a clockwise fashion. These flagellar apparatus features are currently regarded as apomorphic for the class Chlorophyceae. Molecular phylogenetic analyses also generally support the monophyly of the Chlorophyceae (Mishler *et al.*, 1994; Chapman *et al.*, 1998). (***see*** Biogeography of freshwater algae.) (***see*** Cell motility.)

Class Trebouxiophyceae

The Trebouxiophyceae have their origins with the class Pleurastrophyceae (Mattox *et al.*, 1984), which is no longer valid because the type genus, *Pleurastrum*, has been shown to be a member of the class Chlorophyceae (Friedl, 1997). Like the Chlorophyceae, the Trebouxiophyceae are predominantly freshwater organisms, but include a few marine species. Of particular interest is the observation that a number of trebouxiophycean organisms (including *Trebouxia*) are found in lichen associations. The class is currently diagnosed exclusively on the basis of 18S ribosomal deoxyribonucleic acid (rDNA) sequence analysis (Friedl, 1997; Chapman *et al.*, 1998). Cytologically, the Trebouxiophyceae exhibit features that are thought to be plesiomorphic. These plesiomorphic features include a metacentric spindle that collapses during telophase, a phycoplast system of cytokinetic microtubules, and basal bodies offset in a counterclockwise arrangement (Friedl, 1997). No body or flagellar scales have been detected on motile cells of the Trebouxiophyceae. Molecular phylogenetic analyses generally support the monophyly of the Trebouxiophyceae (Lewis, 1997; Friedl, 1997; Chapman *et al.*, 1998), but the degree of support varies from analysis to analysis. On the basis of a shared phycoplast system of cytokinetic microtubules, the Chlorophyceae and Trebouxiophyceae are thought to be sister taxa (**Figure 1**) within the Chlorophyta (Friedl, 1997; Lewis, 1997; Chapman *et al.*, 1998). (***see*** Phylogeny based on 16S rRNA/DNA.) (***see*** Classification.)

Class Ulvophyceae

The Ulvophyceae include green algae that range from simple unicells to the largest macrophytes. With a few notable exceptions, the majority of ulvophytes are marine. The branched, filamentous genus *Cladophora* is one ulvophyte that has both freshwater and marine species. Cytologically, the Ulvophyceae exhibit a centric spindle that persists through telophase and the motile cells possess flagellar apparatus components that are arranged in a counterclockwise orientation. Many of the motile cells of the Ulvophyceae possess body and flagellar scales. A phycoplast system of microtubules has been observed in the ulotrichalean ulvophyte, *Gloeotilopsis*, but the issue of the taxonomic range of this character within the Ulvophyceae remains a matter of contention (Chapman *et al.*, 1998). Most green algal taxonomists do not yet list the phycoplast as a characteristic of the Ulvophyceae, as it has not been demonstrated in most species that have been studied to date. Except for the ulvophycean genus, *Cephaleuros*, none of the Ulvophyceae are thought to produce a phragmoplast system of microtubules (see Charophyta). The Ulvophyceae are frequently characterized as comprising two groups, the ulotrichalean ulvophytes (e.g. *Ulothrix*) and the siphonous ulvophytes (e.g. *Acetabularia*). The two groups differ from one another in

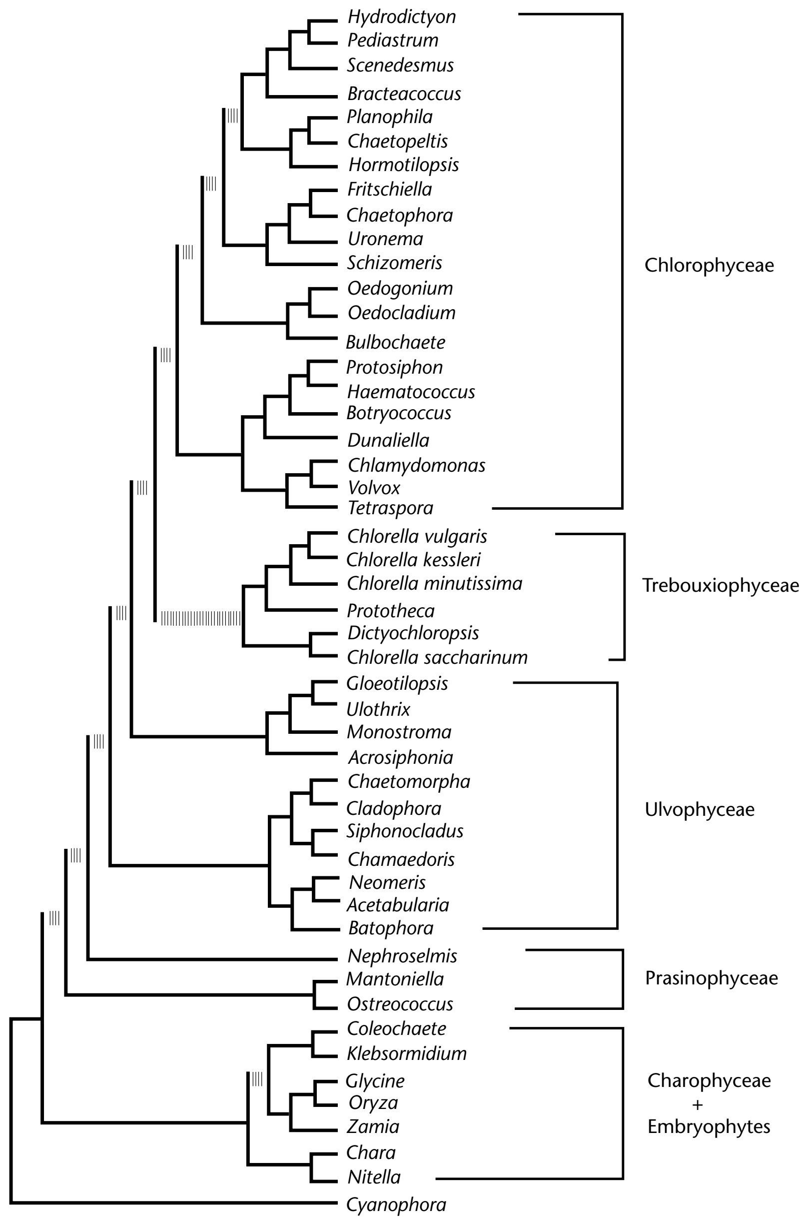

Figure 1 Consensus phylogeny of selected exemplars from the green algae (plus embryophytes) based on maximum parsimony analysis of equally weighted 18S rDNA sequence data (Buchheim, unpublished observations). Weakly supported branches (as determined by bootstrap analysis) are identified as dashed lines.

life history and in form (van den Hoek *et al.*, 1995; Chapman *et al.*, 1998; Graham and Wilcox, 2000). From a phylogenetic perspective, the siphonous ulvophytes form a distinct group, as do the ulotrichalean ulvophytes (**Figure 1**), but global monophyly of the two ulvophyte groups is in dispute at both the molecular and morphological levels (Mishler *et al.*, 1994; Chapman *et al.*, 1998). (***see*** Biogeography of marine algae.)

Prasinophyceae

The Prasinophyceae are a heterogeneous, nonmonophyletic assemblage of flagellate and coccoid unicells that include both freshwater and marine representatives. Flagellated forms vary from uniflagellate to 16-flagellated cells. Most prasinophytes lack true cell walls, but instead possess scaly surfaces. Both body scales and flagellar scales are present in many prasinophytes and this feature has been used as a taxonomic marker (van den Hoek *et al.*, 1995; Chapman *et al.*, 1998). A number of prasinophytes have been shown to possess a unique light-harvesting complex that differs from that in all other organisms (Graham and Wilcox, 2000). Most prasinophytes fall at the base of the chlorophyte branch (**Figure 1**). *Mesostigma*, a freshwater prasinophyte, is currently thought to be the most basal member of the Streptophyta lineage (Charophyta and Embyrophyta). The current consensus is that the Prasinophyceae will certainly be broken up into several distinct classes and some of its members transferred to other classes within the green algae (Graham and Wilcox, 2000). (*see* Algal cell walls.) (*see* Algal photosynthesis.) (*see* Light-harvesting complex.)

The Charophyta

The Charophyta are characterized by motile cells that exhibit an asymmetric set of flagellar roots. One flagellar root is associated with a multilayered structure or MLS. Flagella in motile cells of the Charophyta are inserted subapically. Most members of the Charophyta exhibit an open mitotic spindle in which the nuclear membrane disappears during mitosis (some prasinophytes also have open mitotic spindles). The mitotic spindle persists throughout mitosis. In addition to the mitotic/cytokinetic features, most motile stages of the charophytes possess body and flagellar scales. All charophytes have peroxisomes that produce glycolate oxidase and catalase. The four classes within the Chlorophyta are briefly described below.

Charophyceae

The Charophyceae include those green algae traditionally linked with embryophytes (i.e. the land plants). The Charophyceae include *Chara* and *Nitella*, *Coleochaete*, *Klebsormidium*, *Spirogyra* and all desmids (e.g. *Micrasterias*). Charophycean algae that exhibit an embryophyte-like cytokinetic apparatus (i.e. a phragmoplast) are thought to be the closest, extant relatives of the embryophytes. Both *Chara* and *Coleochaete* exhibit a phragmoplast system of microtubules that forms perpendicular to the plane of cell division and is thought to be the template for plasmodesmata development. The monophyly of the Charophyceae has been challenged on the basis of both molecular and morphological evidence, but the issue remains a matter of debate. (*see* Embryophyta (land plants).) (*see* Plant mitosis, cytokinesis and cell plate formation.)

Economic and Ecological Importance

The green algae include a number of economically and ecologically important plants. The organisms presented below represent a sampling of some of the distinctive diversity within the green algae.

Botryococcus

A member of the chlorophycean lineage (**Figure 1**), *Botryococcus* is a coccoid unicell that secretes lipids, called botryococcenes, which have been touted as a source of renewable, carbon-based energy for the future (Graham and Wilcox, 2000). Furthermore, it is thought that *Botryococcus* may have been a significant contributing source in the development of oil shale and coal (Graham and Wilcox, 2000). (*see* Algal storage products.)

Chlamydomonas

A member of the chlorophycean lineage (**Figure 1**), *Chlamydomonas* is a biflagellated unicell that exhibits an ability to reproduce both asexually and via the formation of isogametes (anisogamy and oogamy are evident in some species). *Chl. reinhardtii* remains one of the most useful organisms for the study of basic physiological processes, including photosynthesis and carbon uptake (van den Hoek *et al.*, 1995; Graham and Wilcox, 2000). (*see* Algal metabolism.)

Volvox

A globose colony of *Chlamydomonas*-like cells, *Volvox* is the largest of the colonial flagellates. It is a member of the chlorophycean lineage (**Figure 1**) and is a close ally of *Chlamydomonas* (Chapman *et al.*, 1998). *Volvox* colonies are comprised of hundreds to thousands of cells per organism, depending on the species (Graham and Wilcox, 2000). Like *Chlamydomonas*, *Volvox* has been used extensively by the research community as a model organism. Unlike *Chlamydomonas* (a unicell), *Volvox* can be and has been used to study the control of multicellular development. The discovery of transposable elements in *Volvox* has dramatically enhanced its usefulness for the study of development at the molecular level and it is likely that this distinctive alga will play a more prominent role in developmental research. (*see* Adhesive specificity and the evolution of multicellularity.)

Chloromonas

A member of the chlorophycean lineage (**Figure 1**), *Chloromonas*, is a biflagellated unicell that is known to be a close ally of both *Chlamydomonas* and *Volvox* (Buchheim *et al.*, 1997). Many species of *Chloromonas* (and some species of *Chlamydomonas*) are distinctive in their ability to grow in snow. Snow that is coloured bright green or red often harbour these 'snow algae'. Moreover, these photosynthetic organisms may be a key component of an extraordinary microcosm of organisms that are capable of exploiting a habitat too extreme for the vast majority of life. (*see* Arctic ecosystems.)

Bracteacoccus

This is a coccoid member of the chlorophycean lineage (Lewis, 1997). Although *Bracteacoccus* grows well in liquid culture, it is noted for its typical habitat – the so-called algal crusts found in arid regions of the world (Lewis, 1997).

Fritschiella

This is a branched, filamentous organism associated with the green algal order, Chaetophorales, in the chlorophycean lineage (Booton *et al.*, 1998). *Fritschiella* exhibits a heterotrichous form of filamentous development, in that it possesses a distinct prostrate system of filaments and an erect system of filaments. The habit of *Fritschiella*, which grows on wet or moist soil surfaces, is reminiscent of the mosses. As such, it has been touted as a possible sister group to the embryophytes (which include the mosses). However, ultrastructural evidence from the mitotic and cytokinetic apparatus indicates that *Fritschiella* is not part of the immediate sister group to the embryophytes (**Figure 1**).

Selenastrum

A crescent-shaped, coccoid green alga, *Selenastrum* is frequently encountered in plankton samples from ponds and lakes. It is readily grown in culture and has been shown to exhibit demonstrable responses to environmental toxins. Consequently, *Selenastrum* has been adopted by many governmental agencies, including the US Environmental Protection Agency, as an organism of choice in the testing protocols for environmental toxins (Graham and Wilcox, 2000). (*see* Environmental impact assessment.)

Chlorella

Chlorella is distinguished by a general lack of superficially distinguishing features! It lacks any known motile stages and reproduces by autosporogenesis – the formation of nonmotile spores within a parental sporangium. The simplicity of the organism and its ease of growth have made *Chlorella* a favourite of plant physiologists interested in studying plant processes such as photosynthesis.

Prototheca

In common with *Chlorella*, *Prototheca* is a unicellular, coccoid organism that does not produce any known motile stage. It is allied within the class Trebouxiophyceae (**Figure 1**). Although *Prototheca* possesses plastids with starch (and thus is a plant-like organism), it is distinctive in that it lacks photosynthetic pigments and is thus heterotrophic. Given its phylogenetic neighbours (e.g. *Chlorella*), it is clear that *Prototheca* has lost the ability to produce photosynthetic pigment. It has been described as an opportunistic pathogen of humans (Graham and Wilcox, 2000).

Dunaliella

Dunaliella is a unicellular, flagellated ally of *Chlamydomonas* in the class Chlorophyceae (**Figure 1**), despite the fact that *Dunaliella* normally grows in saline to hypersaline environments and lacks a cell wall. It has been used extensively by scientists studying adaptations to saline environments and scientists interested in the production of carotenoid pigments. In fact, *Dunaliella* is currently grown in aquaculture for industrial-scale production of β-carotene, an essential component of the human diet (Graham and Wilcox, 2000). (*see* Halophiles.)

Ulothrix

This is an unbranched, filamentous member of the class Ulvophyceae (**Figure 1**). Moreover, *Ulothrix* lends its name to a group within the Ulvophyceae, the ulotrichalean ulvophytes. The ulotrichalean ulvophytes exhibit complex life histories in which haploid and diploid phases, called gametophytes and sporophytes, are produced. This type of life history is called alternation of generations. *Ulva* is one of several macroscopic relatives of *Ulothrix* that produces gametophytes and sporophytes that are morphologically indistinguishable. *Ulothrix*, a freshwater representative, is an exception to the general rule that most ulvophytes are marine organisms. Cytologically, *Ulothrix* and other ulotrichalean organisms are uninucleate. (*see* Gametophyte and sporophyte.)

Acetabularia

A macroscopic green algal member of the ulvophycean lineage (**Figure 1**), *Acetabularia* is commonly called ‘Neptune’s wineglass’ because of its shape – a central stalk capped by radiating arms that form a bowl in most species. *Acetabularia* is an ally of a group of ulvophycean called ‘siphonous’ green algae, most of which have a multinucleate phase. These siphonous algae are generally characterized by complex, macroscopic morphologies, yet the thalli are not organized into distinct cells (i.e. the thalli lack crosswalls). Thus, the thalli of *Acetabularia* are essentially large, unicellular organisms. As a consequence of this distinctive feature, geneticists have exploited *Acetabularia* in studies of algal development. In contrast to the Ulotrichales, many members of the siphonous lineage are effectively multinucleate.

Nitella

Nitella is a close ally of *Chara* in the charophycean lineage (**Figure 1**). Both *Nitella* and *Chara* are macroscopic green algae. The cells that comprise *Nitella* thalli are notably large (up to 15 mm in length) and the cytoplasm exhibits pronounced cyclosis, thus *Nitella* has frequently been used in teaching laboratories to illustrate this remarkable phenomenon. Moreover, it has been the organism of choice for the study of intracellular movement at the molecular level. Similarly, the large vacuoles of *Nitella* have been exploited in the study of basic vacuolar function.

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