Phycology

Introductory article

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The study of algae is generally called 'phycology', from the Greek word phykos meaning 'seaweed'. Just what algae are is difficult to define, because they belong to many different and unrelated classes including both prokaryotic and eukaryotic representatives. Broadly speaking, the algae comprise all, mainly aquatic, plants that can use light energy to fix carbon from atmospheric CO_2 and evolve oxygen, but which are not specialized land plants like mosses, ferns, coniferous trees and flowering plants. This is a negative definition, but it serves its purpose.

Article Contents

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General Features

Algae range in size from microscopic unicells less than 1 μm in diameter to kelps as long as 60 m. They can be found in almost all aqueous or moist habitats; in marine and freshwater environments they are the main photosynthetic organisms. They are also common in soils, salt lakes and hot springs, and some can grow in snow and on rocks and the bark of trees. Most algae normally require light, but some species can also grow in the dark if a suitable organic carbon source is available for nutrition. Algal photosynthesis may well account for half of the total global primary production and constitutes the basis of almost all aquatic food webs. Furthermore, the nitrogen-fixing cyanobacteria (blue-green algae) are an important source of fixed nitrogen, which is necessary for the nutrition of other plants and animals. The name 'algae' is not a taxonomic term, but rather describes a very broad collection of organisms, both prokaryotic and eukaryotic. These 'algae' are generally photosynthetic, but do not have roots or leafy shoots and lack true vascular tissue. **See also**: Algal ecology

Several species form important symbioses with animals, plants or fungi. For example, lichens are actually symbiotic associations of specific fungi and algae. A few cyanobacteria form symbiotic associations with several kinds of plants, enhancing their growth by providing fixed nitrogen. Others form symbioses with invertebrates such as sponges. The aquatic fern *Azolla* contains filaments of the nitrogen-fixing cyanobacterium *Anabaena azollae* in special chambers in the leaves. An important alga/animal symbiosis is that between certain reef-forming corals and the dinoflagellates *Symbiodinium* spp. There are many other examples of algal/invertebrate symbioses among the Protozoa, Porifera, Coelenterata and Mollusca. **See also**: Algal symbioses; Lichens; Porifera sponges

Uses

Algae are not only important as primary producers in nature, providing oxygen and food for other organisms, but several species are also of economic importance. Some kinds are consumed as food by humans. These include the red alga *Porphyra* (also known as nori or laver), an important ingredient of Japanese foods such as sushi. Other algae commonly eaten in the Orient are the brown algae *Laminaria* and *Undaria* and the green algae *Caulerpa* and *Monostroma*. The new science of molecular biology has depended largely on the use of algal polysaccharides, which are essential for the culture of bacteria and fungi and in the purification and separation of proteins and nucleic acids. Brown algae or kelps such as *Macrocystis*, *Laminaria*, *Durvillea* and *Sargassum* are sources of alginates, which can serve as thickening agents and colloidal stabilizers in the food, cosmetic, textile, pharmaceutical and paper industries. The total world production of alginates is about 21 500 tonnes, equivalent to an algal harvest of about 575 000 tonnes fresh weight. The principal genera harvested are *Macrocystis* and *Nereocystis* (Pacific coast of North America), *Laminaria* and *Ascophyllum* (Europe), *Durvillea* (Australasia) and *Laminaria* and *Undaria* (China). **See also**: Algal metabolism; Brown algae

Many red algae are abundant seaweeds of great economic importance, especially as sources of gelling agents such as agar and carrageenan, which are used in the food and cosmetic industries and in microbiological laboratories. Agar is obtained from genera such as *Gelidium*, *Gracilaria* and *Pterocladia*, with a total worldwide production of about 7000 tonnes. Carrageenan is mainly produced from *Chondrus crispus* (Irish moss) and *Mastocarpus stellatus* in Europe, and from *Eucheuma* and *Kappaphycus* species in the Philippines, with an annual production exceeding 13 000 tonnes. Many of these algae are farmed by mariculture when supplies of 'wild' material are inadequate to meet the high demand. Notably, the annual harvest of cultivated *Porphyra* or 'nori' is now worth about a billion dollars.

The unicellular green alga *Dunaliella salina*, which becomes red in hypersaline media, is grown commercially in Australia, China and the USA as a source of the carotenoid

β-carotene, which has been recommended as a nutritional supplement and is widely used as a natural colourant for foods. The cyanobacterium *Spirulina* is extensively cultured in Thailand, the USA, China, India, Japan, Chile and Australia and is sold as a food supplement with sales approaching 1 billion dollars annually. The chlorophyte *Chlorella* is also cultured for human consumption and has a large world market. Other species of microalgae are being developed as sources of polyunsaturated fatty acids to supplement human and animal diets. **See also**: Green algae

The silica walls of diatoms fossilize well, and in many parts of the world there are extensive deposits of their shells from the Tertiary era known as 'diatomaceous earth' or 'Kieselguhr'. The fine holes and small size of these silica walls make them an excellent filter material for swimming pools and for the food and chemical industries. **See also**: Algal calcification and silicification; Diatoms

Nitrogen-fixing cyanobacteria (e.g. *Anabaena*, *Nostoc*) are used as natural fertilizers in India and other parts of Asia, where they reduce the need for expensive synthetic fertilizers in rice farming. Some algae are also proving to be potential sources of new pharmaceutical products, including antibiotics and agents to combat cancer and viral diseases. A number of algal compounds are currently under development by drug companies. **See also**: Nitrogen fixation; Photosynthesis and respiration in cyanobacteria

Several green algae, selected largely for the ease with which they can be cultured in the laboratory, have been used for investigating fundamental processes such as photosynthesis, light perception, flagellar motility, cell differentiation and sexuality. A few species of *Chlorella*, *Chlamydomonas*, *Volvox* and *Euglena*, in particular, have contributed much to our basic knowledge of such phenomena.

Noxious Algae

Although most algae are beneficial, some produce powerful toxins, and when they form 'blooms' they can cause major environmental problems by sickening or killing fish, birds, cattle and other animals drinking the water. Moreover, when the cells die and decay they may use up so much of the oxygen in the water that they cause more deaths of aquatic life. The formation of such blooms in lakes and rivers is promoted by nutrient pollution, and increased human pollution of water bodies means that they are becoming more common throughout the world. In fresh waters, the culprit is usually a cyanobacterium, *Microcystis* sp., while in the sea the main bloom-forming toxic algae are certain diatoms and dinoflagellates, which cause the so-called 'red tides'. Brevitoxin, produced by certain marine dinoflagellates, is one of the most toxic and complicated organic compounds produced by any organism. It has only recently been synthesized artificially. When such algae are consumed by shellfish, these animals can in turn become poisonous. In many parts of the world the incidence of toxic algae is monitored, and, when they are abundant, inshore fisheries may be closed to reduce the threat to human health. When the algal bloom dies out, the shellfish eventually clear themselves of the toxic algae and then become once more fit for human consumption. **See also**: Harmful algal blooms; Protozoa

Some seaweeds, introduced to foreign shores, have become troublesome weeds (e.g. certain species of *Sargassum* and *Caulerpa*). **See also**: Biogeography of marine algae

Classification

Although earlier classifications of algae were based mainly on their pigments, more recent ultrastructural and molecular biological studies have led to considerable changes and reassessments of the phylogenetic relationships of the various algal divisions to one another and to other organisms. For example, since the blue-green algae (which used to be called Cyanophyta) are prokaryotic, they have been renamed Cyanobacteria and alternatively can be classified among the bacteria. **Table 1** presents a resumé of the main distinguishing features of the presently recognized divisions of algae, and some details of the structure, life histories and general biology of the main groups are given below. **See also**: Algal pigments; Algal taxonomy: historical overview; Prokaryotic systematics: a theoretical overview

The systematic positions of the various groups of algae have undergone many changes in the last century, and with the onset of new methods for evaluating phylogenetic relationships (e.g. electron microscopy, molecular biology) more changes are being proposed. At present there is no complete consensus. Furthermore, differences between the Botanical and Zoological Codes of Nomenclature mean that sometimes different names may be applied to the same algal groups. The classification scheme used here follows that of van den Hoek *et al*. (1995) for the most part. For convenience, **Table 2** compares it with some other classifications. **See also**: Protozoan taxonomy and systematics

Prokaryotic algae

Cyanobacteria (blue-green algae) and Prochlorophyta

The cyanobacteria are prokaryotic organisms that have no membrane-limited nuclei, Golgi apparatus, mitochondria, endoplasmic reticulum or plastids. The DNA lies free in the cytoplasm, often accompanied by the photosynthetic membranes, the thylakoids. Like other plants, and unlike other photosynthetic bacteria, the cyanobacteria can produce oxygen during photosynthesis. Although they have no evident sexual reproduction, genetic recombination by transformation or conjugation may occur. The cells are generally blue-green to violet, but some may appear greenish, red or black, depending on the relative abundances of their pigments, chlorophyll *a*, phycocyanin and phycoerythrin in the cells and other dark-coloured substances in

Table 1 The main distinguishing features of the presently recognized divisions of algae

	Main pigments	Main storage products	Cell forms	Cell covering	Habitats and number of species	Selected genera
Prokaryotes						
Cyanophyta (Cyanobacteria) 'blue-green algae'	Chlorophyll *a* Phycocyanin Phycoerythrin	Cyanophycean starch (α-1,4-linked glucan), cyanophycin (alanine and arginine polymer)	Unicellular, filaments and colonial. No flagellate cells	Peptidoglycan wall with external lipo-polysaccharide layer. May also have mucilaginous sheath	Freshwater, marine and terrestrial (~ 2000 species)	*Anabaena* *Microcystis* *Nostoc* *Spirulina*
Prochlorophyta	Chloropyll *a* Chloropyll *b*	Starch-like polysaccharide	Unicellular and filaments. No flagellate cells	As for cyanobacteria	Marine and fresh-water (4 species)	*Prochloron* *Prochlorococcus* *Prochlorothrix*
Eukaryotes						
Glaucophyta	Chlorophyll *a* Phycocyanin	Starch (outside chloroplast)	Unicellular, some flagellates	Cells surrounded by layer of vesicles con-taining scales or fibrillar material	Freshwater (~ 5 species)	*Cyanophora* *Glaucocystis*
Rhodophyta 'red algae'	Chlorophyll *a* Phycoerythrin Phycocyanin	Floridean starch (α-1,4-linked glucan)	Unicellular, filament-ous and thalloid (no flagellate stages)	Cell wall of cellulose fibrils (Florideo-phyceae) or xylan fibrils (Bang-iophyceae) in mucilagi-nous matrix that may contain agar or carrageenan. Some calcified	Mainly marine (~ 5500 species)	*Bangia* *Ceramium* *Chondrus* *Eucheuma* *Gelidium* *Gracilaria* *Lithophyllum* *Mastocarpus* *Porphyra* *Porphyridium* *Pterocladia*
Cryptophyta	Chlorophyll *a* Chlorophyll *c* Phycoerythrin Phycocyanin	Starch (outside chloroplast) and lipid	Mainly unicellular, one filamentous genus. Two uniequal flagella	Stiff proteinaceous periplast, usually of rectangular or polygonal plates	Marine and freshwater (~ 200 species)	*Chroomonas* *Cryptomonas*
Heterokontophyta						
Chrysophyceae	Chlorophyll *a* Chlorophyll *c* Fucoxanthin	Chrysolaminaran (*β*-1,3-linked glucan)	Mainly unicellular or colonial, a few simple multicellular or, Two flagella, one smooth, the other hairy	Naked or with siliceous scales on surface	Mostly freshwater (~ 1000 species)	*Ochromonas* *Synura*

continued

Table 1 Continued

	Main pigments	Main storage products	Cell forms	Cell covering	Habitats and number of species	Selected genera
Xanthophyceae	Chlorophyll *a* Chlorophyll *c*		Unicellular (coccoid, flagellate or amoeboid), some colonial, uninucleate and multinucleate filaments. Two flagella, one smooth, one hairy	Mainly of cellulose fibrils, sometimes impregnated with silica, often in two overlapping halves	Mainly freshwater and terrestrial, some marine (~600 species)	*Tribonema* *Vaucheria*
Eustigmatophyceae	Chlorophyll *c* Violaxanthin		Unicellular and coccoid. One or two flagella	Polysaccharide walls	Freshwater and marine	*Nannochloropsis*
Bacillariophyceae 'diatoms'	Chlorophyll *a* Chlorophyll *c* Fucoxanthin		Unicellular and colonial. No flagella except in spermatozoids	Wall of two siliceous valves with bilateral or radial symmetry	Freshwater and marine (~100 000 species)	*Navicula* *Nitzschia* *Skeletonema* *Thalassiosira*
Raphidophyceae	Chlorophyll *a* Chlorophyll *c* Fucoxanthin (marine spp.) Diadoxanthin, Vaucheriaxanthin Heteroxanthin (freshwater spp.)		Unicellular. Two flagella, one smooth, other hairy	No cell walls	Freshwater and marine (~40 species)	*Chattonella* *Fibrocapsa*
Dictyochophyceae	Chlorophyll *a* Chlorophyll *c* Fucoxanthin		Unicellular with one hairy flagellum	Mucilaginous envelope	Marine (2 species)	*Dictyocha*
Phaeophyceae 'brown algae'	Chlorophyll *a* Chlorophyll *c* Fucoxanthin		Multicellular. Two laterally inserted flagella in reproductive cells	Wall of cellose microfibrils, stiffened by calcium alginate in a mucilaginous matrix	Marine (~2000 Species)	*Ascophyllum* *Dictyota* *Durvillea* *Ecklonia* *Ectocarpus* *Fucus* *Laminaria* *Macrocystis* *Nereocystis* *Sargassum* *Undaria*

Dinophyta 'dinoflagellates'	Chlorophyll *a* Chlorophyll *c*	Starch (outside chloroplast) and lipid	Predominatly unicellular, some coccoid filamentous. Two flagella, one transverse in a furrow, the other longitudinal	Cell surrounded by layer of flat, polygonal vesicles, which may be empty or, more usually, contain cellulose plates	Mainly marine (~2000 species)	*Alexandrium* *Amphidinium* *Ceratium* *Gymnodinium* *Noctiluca* *Symbiodinium*
Haptophyta (Prymnesiophyta) Haptophyceae	Chlorophyll *a* Chlorophyll *c*	Chrysolaminaran	Unicellular with 2 flagella. Each cell also has a 'haptonema'	Cell covered with cellulose scales and/or calcified scales (coccoliths)	Mainly marine (~500 species)	*Chrysochromulina* *Emiliania* *Pleurochrysis*
Euglenophyta 'euglenoids' Euglenophyceae	Chlorophyll *a* Chlorophyll *b*	Paramylon (β-1,3-linked glucan)	Unicellular with single flagellum	Cell surrounded by proteinaceous strips wound helically around the cell	Mainly freshwater (>800 species)	*Astasia* *Euglena* *Phacus*
Chlorophyta 'green algae'						
Prasinophyceae	Chlorophyll *a* Chlorophyll *b*	Starch (in chloroplasts)	Unicellular: 1–8 flagella	Covered with organic scales composed mainly of 3-deoxy-manno-2-octulosonic acid	Marine and freshwater (~180 species)	*Pyramimonas* *Tetraselmis*
Chlorophyceae			Coccoid, unicellular or colonial flagellates, multcellular or multinucleate filaments. Usually with 2–4 flagella	Flagellate cells with glycoprotein envelope, non-flagellate cells with polysaccharide walls, which may contain some cellulose	Mainly freshwater, but also terrestrial and marine forms (~1000 species)	*Chlamydomonas* *Chlorella* *Dunaliella* *Oedogonium* *Oocystis* *Volvox*
Ulvophyceae			Unicellular, multicellular or multinucleate filamentous. 2 or 4 flagella in reproductive cells	Wall with microfibrils of polymers of a range of sugars embedded in a complex mucilaginous matrix	Almost all marine (~270 species)	*Acrosiphonia* *Enteromorpha* *Monostroma* *Ulva*
Cladophorophyceae			Multinucleate filaments. Reproductive cells with 2–4 flagella	Wall mainly of cellulose	Mainly marine (~420 species)	*Chaetomorpha* *Cladophora* *Valonia*
Bryopsidiophyceae			Mainly giant multinucleate cells. Reproductive cells with 2–4 flagella	Wall mainly of cellulose	Mainly marine (~150 species)	*Caulerpa* *Codium* *Halimeda* *Udotea*

continued

Table 1 Continued

	Main pigments	Main storage products	Cell forms	Cell covering	Habitats and number of species	Selected genera
Dasycladophyceae			Giant multinucleate cells. Biflagellate reproductive cells	Wall mainly of a fibrillar β-1,4-linked mannan	Marine and almost all tropical ($\sim$50 species)	*Acetabularia* *Dasycladus*
Trentepohliophyceae			Uninucleate filaments. Reproductive cells with 2–4 flagella	Polysaccharide walls with outer layer of sporopollenin	Subaerial ($\sim$80 species)	*Trentepohlia* *Cephaleuros*
Pleurastrophyceae			Coccoid, sarcinoid or filamentous. Reproductive cells with 2 flagella	Walls with sporopollenin like substances	Mainly subaerial	*Myrmecia* *Trebouxia*
Clorophyta 'green algae'						
Klebsormidiophyceae			Coccoid, sarcinoid or filamentous Reproductive cells with 2 flagella	Walls mainly of crystalline cellulose	Freshwater and moist subaerial	*Coleochaete* *Klebsormidium*
Zygnematophyceae (unicellular known as 'desmids')			Coccoid or filamentous. No flagellate stages	Walls mainly of crystalline cellulose	Only freshwater ($\sim$6000 species)	*Closterium* *Mougeotia* *Spirogyra*
Charophyceae ('stoneworts and brittleworts')			Complex thalli with multinucleate cells. Biflagellate male gametes	Walls of crystalline cellulose	Freshwater and brackish waters ($\sim$90 species)	*Chara* *Nitella*

Table 2 Comparison of the classification system used in this article with that used by Corliss for the Protozoa

This article	Corliss
Kingdom Eubacteria	
Division Cyanophyta	
Class Cyanophyceae[a]	
Class Prochlorophyta[a]	
Kingdom Eukaryota	Empire Eukaryota
	Kingdom Protozoa
Division Euglenophyta	Phylum Euglenozoa
Division Dinophyta	Phylum Dinozoa
Division Heterokontophyta	Kingdom Chromista
Class Chrysophyceae	Phylum Chrysophyta
Class Xanthophyceae	
Class Eustigmatophyceae	
Class Bacillariophyceae	Phylum Diatomae
Class Raphidophyceae	Phylum Raphidophyta
Class Dictyochophyceae	Phylum Dictyochae
Class Phaeophyceae	Phylum Phaeophyta
Division Cryptophyta	Phylum Cryptophyca
Division Haptophyta	Phylum Haptomonada
	Kingdom Plantae
Division Glaucophyta	Phylum Glaucophyta
Division Rhodophyta	Phylum Rhodophyta
Division Chlorophyta	
Class Prasinophyceae	
Class Chlorophyceae	
Class Cladophorophyceae[b]	
Class Bryopsidophyceae	
Class Dasycladophyceae	
Class Trentepohliophyceae[b]	
Class Pleurastrophyceae[c]	
Class Klebsormidiophyceae	
Class Ulvophyceae	Phylum Ulvophyta
Class Charophyceae[d]	Phylum Charophyta
Class Zygnematophyceae[d]	

[a]Recent molecular data indicate the Cyanophyta and the Prochlorophyta should be merged.
[b]Recent data suggest that these two classes should be merged with Ulvophyceae.
[c]This class is polyphyletic and is likely to be distributed among several other classes of the Chlorophyta.
[d]This Charophyceae and the Zygnematophyceae are sister taxa to the higher plants (the Streptophyta) and should probably not be included with the Chlorophyta.

their extracellular coverings. Their cells, with diameters ranging from about 0.2 to 200 μm, may exist singly, sometimes in a slimy matrix, or in filaments of indefinite length with or without a polysaccharide sheath. Some cyanobacteria form large colonies or extensive mats. In one subclass the filaments may comprise two kinds of cells, some being pigmented and photosynthetic, whereas others have thick walls with clear contents and internal knob-like projections at the ends where they connect to adjacent cells. These latter cells are 'heterocysts', in which elemental nitrogen is fixed into ammonium. Most of the filamentous forms can move by gliding over the surface of a substratum. Some planktonic species have gas vacuoles, which help them to float. **See also**: Bacterial cells; Bacterial intracellular membranes; Cyanobacterial heterocysts; Photosynthesis and respiration in cyanobacteria

The cyanobacteria have a long fossil record. Some have been found mineralized in rocks over 3 billion years old. These algae are thought to have been the dominant forms of life in the Proterozoic era (between 2.5 and 2 billion years ago). Certain kinds of cyanobacteria occur as fossils in layered structures called stromatolites, and living stromatolites of similar construction can still be seen in Shark Bay, Western Australia. **See also**: Algae: phylogeny and evolution; Fossil record

The Prochlorophyta differ from the Cyanobacteria mainly in their pigments and the fact that their thylakoids are paired or stacked rather than single. Recent molecular data indicate a close relationship between these two groups of prokaryotic algae, and it now seems hardly justifiable to retain the prochlorophytes as a separate division. *Prochloron*, the first of the prochlorophytes to be described, grows symbiotically in ascidians, while the two genera discovered more recently are free living. Filaments of *Prochlorothrix* occur in lakes, while the tiny *Prochlorococcus* has been found to be very abundant in oceanic plankton.

Eukaryotic algae

Division Rhodophyta (red algae)

Most red algae are multicellular, mainly marine, growing attached to intertidal or subtidal rocks. A few are unicellular (e.g. *Porphyridium*), while others are filamentous. The filaments may be simple, branched or closely packed and held together by a gelatinous matrix to form diverse and often spectacular thallus shapes. In the Florideophyceae the individual cells in each filament, and sometimes also those of neighbouring filaments, are connected by 'pit plugs'. The cell walls are generally composed of cellulose fibrils (but in *Porphyra* and *Bangia* the fibrillar material is a polymer of xylose) embedded in an amorphous material typically composed of sulfated galactose residues. Some red algae (e.g. in the Corallinales) have cell walls indurated with calcium carbonate. **See also**: Algal cell walls

The life history of most of the red algae is unique in that it has three phases: (1) a haploid free-living gametophyte, (2) a diploid phase, the carposporophyte, which is parasitic on the female gametophyte and (3) a second diploid phase, the free-living tetrasporophyte.

Division Heterokontophyta

The Heterokontophyta include organisms whose flagellate cells have one long 'hairy' flagellum generally directed forward during swimming, and a shorter smooth flagellum that points backwards. The hairy flagellum has two rows of lateral hairs called mastigonemes, composed of glycoprotein. In this division the chloroplast is enclosed not only by its own double membrane, but also by a part of the endoplasmic reticulum. This division includes a morphologically diverse group of organisms ranging from small naked unicells and silica-walled diatoms to the complex multicellular brown algae, as well as several classes of colourless protozoans and even some organisms hitherto classed as fungi. **See also**: Algal chloroplasts; Algal flagella; Algal taxonomy: historical overview; Diatoms

Class Phaeophyceae (brown algae)

The brown algae, mostly seaweeds, are among the most conspicuous algae especially in temperate areas, where they flourish in the intertidal regions and may also form extensive beds offshore. In the tropics, the brown alga *Sargassum* is abundant in shallow reef waters and can be found free-floating in the Sargasso Sea. Brown algae range in size from microscopic filamentous forms such as *Ectocarpus* to large kelps up to 60 m in length. The structure and differentiation of the thallus may be complex. For example, kelps such as *Laminaria* and *Ecklonia* have a holdfast, which attaches to a rocky bottom, a stipe (stem) and upper leafy parts, the laminae or blades, where most of the photosynthesis occurs. Several genera such as *Sargassum* and *Fucus*, and the kelps *Macrocystis* and *Nereocystis*, have gas-filled bladders that aid in holding up the thallus when submerged. **See also**: Biogeography of marine algae; Brown algae

As in the red algae, the cell wall consists of cellulose fibrils and amorphous polysaccharides, which in brown algae are characteristically alginates. These are polymers of two sugar acids, D-mannuronic acid and L-guluronic acid, which make some of the brown algae economically valuable.

Class Bacillariophyceae (diatoms)

Diatom cells are characterized by having lacy silicified walls, called frustules, consisting of two, often overlapping, sections somewhat like Petri dishes. They exhibit a wide range of shapes and ornamentations with bumps and spines, and many openings that allow the exchange of nutrients and waste products with the external environment. They may be single-celled or colonial, and are either bilaterally symmetrical (the Pennales) or radially symmetrical (the Centrales). The inelastic nature of the silicified lateral walls is responsible for the fact that on each division the cells of most species become a little smaller, in average dimensions, until eventually the cells of a population tend to die out unless they undergo some kind of reproduction during which they regain their original maximum size. Unlike many other unicellular algae, they are typically diploid. **See also**: Algal calcification and silicification; Diatoms

Diatoms are common members of the freshwater and marine phytoplankton, while many species are epiphytic or benthic. Their abundance means that they are significant producers of organic matter, accounting for some 20–25% of the total primary production in the ocean.

Division Dinophyta (dinoflagellates)

The dinoflagellates are mainly unicellular, although there are a few filamentous forms. The nucleus has a unique structure, with the chromosomes almost always highly condensed in a sort of prophase. The cells swim with two dissimilar flagella, a transverse flagellum, usually coiled in a groove around the body of the alga, and a longitudinal flagellum directed backwards that serves as a kind of rudder. The cell of many species is covered by a definite number of polygonal plates composed of cellulose. The free-living cells are normally haploid. After pairing (which is rarely observed), the diploid zygotes become thick-walled spores, which can survive for long periods in dark and cold conditions so that many of them can overwinter. **See also**: Algal flagella

About 90% of the dinoflagellates are marine, being particularly abundant in warmer waters. Most are planktonic, although benthic forms occur. Many are phagotrophic, and can catch and eat plankton cells even larger than themselves. Some form symbioses with a wide range of invertebrates, especially reef-building corals, where the cells (called zooxanthellae) live within the cells of their animal hosts, to which they provide photosynthetically fixed carbon compounds. This additional nutrition contributes to the spectacular success of corals in shallow tropical waters, where they may form extensive reefs. Some jellyfish, and the giant clam *Tridacna*, also harbour symbiotic zooxanthellae. **See also**: Algal symbioses

Dinoflagellates can form large blooms known as red or brown tides. Some are phosphorescent, producing a lovely show along warm marine shores and lagoons, but a few are very toxic as mentioned above. **See also**: Harmful algal blooms

Division Haptophyta

The haptophytes are unicellular flagellates with paired, yellow-brown chloroplasts and a peculiar anterior filament, the haptonema, which sometimes serves for attaching the cells to a substrate or for catching prey. Among the most extensively studied is *Emiliania*, often common in marine phytoplankton. Many haptophytes have more or less calcified scales: the chalk downs and the white cliffs of Dover are the accumulated fossil deposits of their coccoliths. **See also**: Phytoplankton

Division Chlorophyta (green algae)

The Chlorophyta show a great diversity in form, life history and habitat, and this is reflected in the many classes currently recognized (**Table 2**). Green algae of one kind or another have successfully colonized almost all possible wet habitats. They are common in marine and fresh waters, some genera grow in soil, on trees and on rocks, while a few species have adapted to flourish in extreme habitats such as snow (e.g. *Chlamydomonas nivalis*) or salt lakes (e.g. *Dunaliella salina*). Almost all freshwater green algae are haploid, with only the zygote being diploid, whereas many kinds of marine algae such as *Ulva* have free-living haploid and diploid stages. Most *Caulerpales* have only diploid thalli. **See also**: Algal ecology; Green algae

The Chlorophyta have a wide range of flagellar arrangements and modes of nuclear and cell division. Like the red and brown algae, their cell walls have a structural, fibrillar component, generally of cellulose, embedded in an amorphous matrix. The walls also contain some protein, as do those of higher plants.

Most chlorophytes have flagellate stages in their life history. However, in the Zygnematophyceae (which include *Spirogyra* and the desmids) it seems that the ability to form flagellated cells has been totally lost, sexual reproduction involving the conjugation of amoeboid gametes. Several interesting evolutionary trends are found in the Chlorophyta. In one branch of the Chlorophyceae (Volvocales) the trend has been to form larger and larger colonies of flagellated cells, culminating in the spherical colonies of the freshwater green alga *Volvox*. The marine Bryopsidophyceae, on the other hand, have large multinucleate (coenocytic) tubes that branch and intertwine to form the thallus, as in *Halimeda* and *Udotea*, or form a creeping stolon from which upright photosynthetic, more or less leaf-like shoots arise, as in *Caulerpa*. The coenocytic condition has also arisen in several other chlorophyte classes, among which the Dasycladales are probably the oldest and most remarkable. Their giant vegetative cells, which may reach 20 cm in length, have only a single nucleus until shortly before reproduction. For this reason, *Acetabularia* has been extensively investigated in experimental studies of interrelations between nucleus and cytoplasm. **See also**: Algae: phylogeny and evolution; Protozoan sexuality

The Chlorophyta have a long fossil record, the Prasinophyceae dating back at least 600 million years. The Bryopsidophyceae, Dasycladophyceae and Charophyceae are at least 400–500 million years old, and evidence suggests that all the higher plants, from mosses and liverworts to the angiosperms, evolved from green algae (possibly the Charophyceae) between 400 and 500 million years ago. **See also**: Geological time: principles

Evolution

Not all algae are photosynthetic. About half of the dinoflagellates, many of the euglenoids, and about half a dozen chlorophytes and diatoms, are colourless, and live heterotrophically like protozoa or fungi. However, the cells of most other algae have chloroplasts that enable them to photosynthesize and live autotrophically. In that plastids have their own DNA, separate from that of the cell nucleus, and can reproduce autonomously (no cell can produce chloroplasts *de novo*), they resemble prokaryotes. This observation led Merezhkovsky to suggest, some 100 years ago, that plastids originally evolved from intracellular symbionts, although for many years this idea was not taken seriously. However, a variety of recent techniques and discoveries, combined with molecular biological data, have shown almost conclusively that his hypothesis, which he called symbiogenesis, is probably correct. This means that, when we try to construct phylogenetic trees indicating how the various kinds of algae have evolved, we must consider separately the evolutionary pathways of the nuclear (eukaryotic) and the chloroplastic (prokaryotic) components. In fact, recent evidence indicates that, perhaps by ingesting or otherwise incorporating a cyanophyte-like cell, a heterotrophic, eukaryotic cell could have become the first alga. It might have been a red alga, since the plastids of rhodophytes have almost the same pigments as those of cyanophytes. Development of the ability to produce a second, accessory chlorophyll could have given rise to an ancestral green alga. Scientists are still speculating as to whether the different pigment systems of algae could have evolved like this, after the first symbiogenesis. Alternatively, pigment diversification may have preceded the postulated ingestion of several different plastid ancestors, giving rise to the ancestors of red, brown, green and other algal classes. These are challenging questions. More research, and specifically more molecular–biological analyses, will probably provide answers before long. **See also**: Algal chloroplasts; Algal photosynthesis; Algal pigments; Endosymbionts; Plant chloroplasts and other plastids

The situation has further complications. Electron-microscopic evidence indicates that viable plastids can be handed on, transferred by a second incorporation from one kind of eukaryote to another. Some euglenoids and cryptophytes apparently obtained their chloroplasts by ingesting and incorporating plastids from cells of a eukaryotic green alga. Other kinds of ingesting cells may already possess and retain their own kind of plastid, and in fact dinoflagellates with two dissimilar kinds of plastids in each cell have already been found, indicating that such transfers might have occurred more than once in evolution. **See also**: Molecular evolution: introduction

The branched genealogical trees of algae are apparently more entangled by anastomoses than those of any other class of organisms. Phycology can be complicated. That is what makes the study of algae so interesting.

Further Reading

Berger S and Kaever MJ (1992) *Dasycladales*. Stuttgart: Thieme Verlag.

Bold HC and Wynne MJ (1978) *Introduction to the Algae*. New York: Prentice-Hall.

Borowitzka MA and Borowitzka LJ (eds) (1988) *Micro-algal Biotechnology*. Cambridge: Cambridge University Press.

Clayton MN and King RJ (eds) (1990) *Biology of Marine Plants*. Melbourne: Longman Cheshire.

Fritsch FE (1935, 1945) *Structure and Reproduction of the Algae*, vols. I and II. Cambridge: Cambridge University Press.

Harris EH (1988) *The Chlamydomonas Source-book*. San Diego: Academic Press.

Lee RE (1989) *Phycology*, 2nd edn. Cambridge: Cambridge University Press.

Lembi CA and Waaland RJ (eds) (1988) *Algae and Human Affairs*. Cambridge: Cambridge University Press.

Lewin RA (ed.) (1993) *Origins of Plastids: Symbiogenesis, Prochlorophytes, and the Origins of Chloroplasts*. New York and London: Chapman & Hall.

Lobban CS and Harrison PJ (1994) *Seaweed Ecology and Physiology*. Cambridge: Cambridge University Press.

Round FE, Crawford R and Mann DG (1990) *The Diatoms: Biology and Morphology of the Genera*. Cambridge: Cambridge University Press.

van den Hoek C, Mann DG and Jahns HM (1995) *Algae. An Introduction to Phycology*. Cambridge: Cambridge University Press.