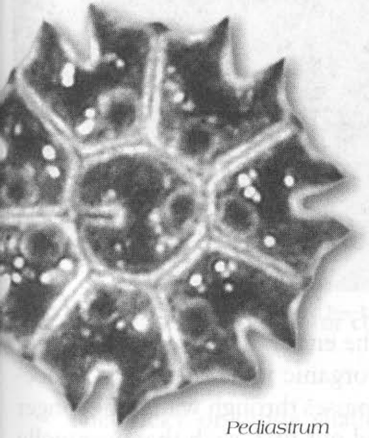
Chapter 1



Pediastrum

Introduction to the Algae

Occurrence, Relationships, Nutrition, Definition, General Features

From tiny single-celled species one micrometer in diameter to giant seaweeds over 50 meters long, algae are abundant and ancient organisms that can be found in virtually every ecosystem in the biosphere. For billions of years algae have exerted profound effects on our planet and its biota, and they continue to do so today. Still, in many habitats algae often go unnoticed unless environmental conditions become favorable for the development of conspicuous and sometimes massive proliferations of their numbers—a situation often brought about by human activity. People from many cultures, ancient and modern, have used algae for a variety of purposes. With the advent of biotechnology, algae are poised to play greater, albeit often subtle, roles in the day-to-day lives of human beings. In the following passages we provide a brief overview of algal habitats and activities that demonstrates algae occur in both expected and highly surprising places. This survey will set the stage for a circumscription of the algae, i.e., a definition for this enigmatic group of organisms.

An Overview of the Occurrence and Activities of Algae

Algae in the Marine Habitat

On land the largest and most striking plants are the trees. Together with their herbaceous relatives, their foliage makes green the most conspicuous color of the biosphere. Underwater there are "trees" of similar height that are less widely appreciated because most humans spend little time in their realm. Brown undulating forests of 50-meter-long giant kelps, as tall and crowded as their terrestrial counterparts, dominate significant stretches of submerged temperate coastlines (Fig. 1–1). Like trees, kelps use pho-

Figure 1–1 Kelp forest off the Chilean coast. The predominant alga pictured is *Macrocystis*. (Photograph courtesy R. Searles)

tosynthesis to convert the energy of sunlight into chemical energy, but the green of their chlorophyll is masked by large amounts of brown pigments. These **accessory pigments** aid in the collection of light not absorbed directly by chlorophyll molecules and channel the light energy to chlorophyll *a*—the only pigment that is able to effectively convert the energy of absorbed light into high energy bonds of organic molecules. This is necessary because as light passes through water, the longer wavelengths are filtered out first, such that eventually all that remains is a faint blue-green light that cannot be absorbed by chlorophyll.

Figure 1–2 Nearshore underwater marine algae (primarily the calcified brown alga *Padina*) in the Bahamas. A gorgonian coral is in the foreground.

Brown seaweeds are not limited to temperate waters, as they also form luxuriant thickets beneath polar ice sheets rarely noticed by anyone but phycologists or algologists—scientists who study these and other algae. The depth record for algae is held by dark purple-colored crusts of yet unnamed red algae discovered in tropical waters by phycologists using submersibles. These organisms live at depths greater than 250 meters, where the light intensity is only 0.0005% that of surface light. The accessory pigments of these algae—whose role is the same as that for those found in the kelps—are essential for the survival of photosynthetic organisms in such low-irradiance environments. In contrast, algae that live in high-irradiance habitats typically have pigments that help protect against photodamage. It is the composition and amounts of accessory and protective photosynthetic pigments that give algae their wide variety of colors and, for several algal groups, their common names such as the brown algae, red algae, and green algae. (We should caution, however, that attempting to identify a particular alga by color alone could be problematic, since, for example, there are red-colored green algae and brown or purple-colored red algae; other characteristics and features must also be considered.)

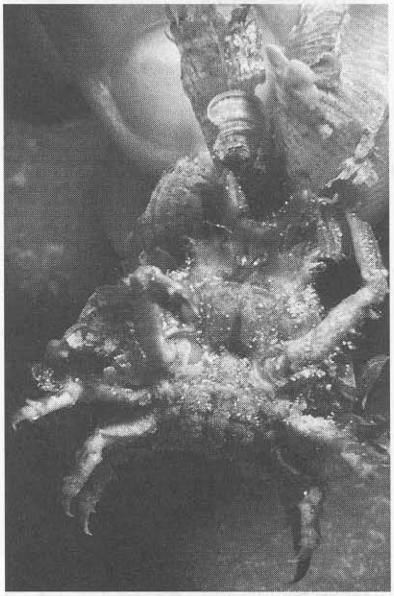


Figure 1–3 A small decorator crab with various attached algae.

The rocky or sandy shallows of temperate and tropical oceans harbor a vast array of brown, red, and green algal growths that may form thin and sometimes slippery films on rocks; diaphanous, lacy, or fleshy forms attached by holdfasts; or miniature jointed shrubs armored with limestone (Fig. 1–2). Myriad smaller algae, like the epiphytes found on rain forest trees, attach themselves to, or actually grow within, larger seaweeds, rocks, corals, and shells. Algae share the tidal zone with numerous invertebrate animals such as barnacles and snails, which often compete with them for space or consume them. Occasionally small clumps of seaweeds may appear to crawl slowly across the ocean floor or along a coral reef—closer inspection reveals "decorator" crabs that have adorned themselves with a fashionable selection of brown, green, or red algae as a camouflage (Fig. 1–3).

Tropical fringes are typically populated with a breathtakingly diverse array of submersed reef-forming corals, whose very existence and form are dependent upon intracellular tenants—microscopic golden algal cells known as **zooxanthellae**—that generate food and oxygen in exchange for metabolic by-products (carbon dioxide and ammonia) released by the coral cells. Zooxanthellae allow corals to thrive in the typically low-nutrient conditions of tropical waters. Because of their obligate association with these photosynthetic algae, reef-building corals are limited to shallow, well-illuminated waters less than 20 meters or so in depth. Beneficial algae also occur within the cells and tissues of a wide variety of other marine animals such as nudibranchs, anemones, giant clams, ascidians, and sponges, as well as inside the cells of radiolarians and foraminiferans, which are but two types of the multitudinous simple organisms known as **protists**, an informal group to which the algae also belong.

Sandy tropical shallows may also contain extensive microbial mats composed of an interwoven community of cyanobacteria (also known as chloroxybacteria, blue-green algae, or cyanophytes), diatoms, and other microorganisms. In a few places—notably Shark Bay, Australia and tidal channels close to Exuma Island in the Bahamas—generations of calcium carbonate-depositing, sediment-trapping, cyanobacteria have built layered hummocks up to two meters high (Fig. 1–4). These hummocks represent modern versions of more widespread fossil formations known as **stromatolites**, which are commonly associated with the occurrence of earth's earliest life-forms.

In addition to these conspicuous marine algal communities with their relatively large seaweeds, coral formations, or algal aggregations, the surrounding ocean waters—occupying approximately 70% of the Earth's surface—teem with some 5000 species of tiny floating or swimming emerald, ruby, topaz, and turquoise jewels known as **phytoplankton** (Fig. 1–5). Although individually visible to humans only with the aid of a microscope, large populations can give ocean waters green or rusty hues. Color variations reflect differences in the types and amounts of blue-green, red, orange, and golden accessory pigments accompanying the green of chlorophyll. Like those giving larger seaweeds their brown, purple, or red coloration, these variously colored pigments also

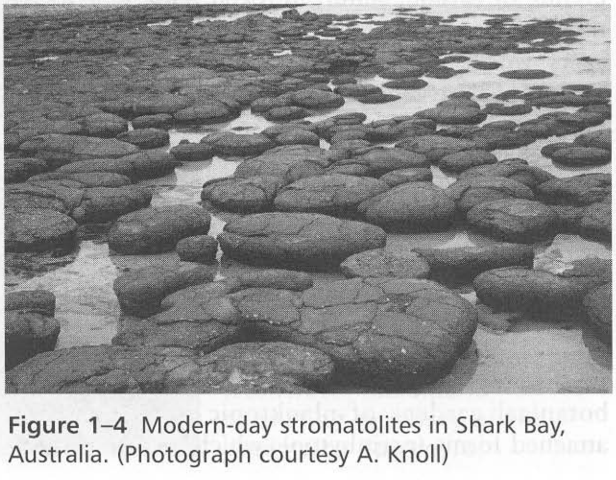


Figure 1–4 Modern-day stromatolites in Shark Bay, Australia. (Photograph courtesy A. Knoll)

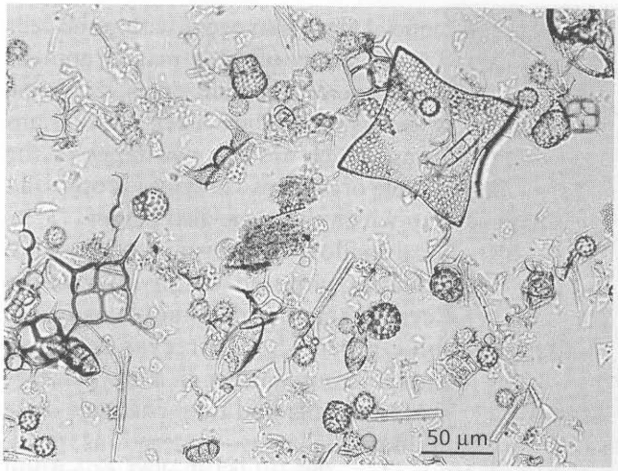


Figure 1–5 Sedimented phytoplankton from the late Cretaceous and early Cenozoic Arctic Ocean, including silicoflagellate and diatom remains. (Specimen courtesy D. Clark)

assist in harvesting light for photosynthesis and in photoprotection. Enormous variation in phytoplankton shape and size has resulted from multiple adaptive solutions to two important problems: sinking to depths where the low levels of light limit photosynthesis and growth, and herbivory—the consumption of algae by animals and protists.

Populations of marine phytoplankton can become so large that they are detectable by satellite remote sensing technology. Such **blooms** are in fact one of the more dramatic vegetational features of the planet when viewed from space (Fig. 1–6). Collectively, marine microalgae have been modifying the earth's atmosphere for more than 2.7 billion years (Buick, 1992), and they continue to exert a powerful influence on modern atmospheric chemistry and biogeochemical cycling of carbon, sulfur, nitrogen, phosphorus, and other elements (Chapter 2). Hundreds of millions of years' worth of past phytoplankton growth and sedimentation have generated important oil and limestone deposits. Algal plankton also form the base of marine food chains, supporting both microbial and animal plankton (zooplankton), upon which economically important marine fisheries and ecologically significant marine mammal and bird populations are dependent.

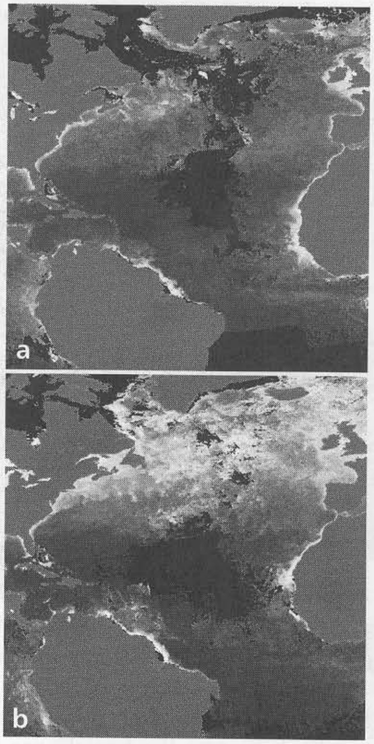


Figure 1–6 Two NASA satellite images of the North Atlantic taken in (a) winter and (b) spring. Brighter areas represent higher concentrations of chlorophyll and, hence, phytoplankton. Totally black areas are regions for which data were not collected.

The Algae of Freshwaters

Freshwater lakes, ponds, and streams contain similar botanical gardens of planktonic microalgae and attached forms (**periphyton**), which are often themselves festooned with epiphytes (Fig. 1–7). Although not exhibiting the phenomenal size range of their marine relatives, freshwater algae nonetheless display a wide diversity of form and function. As in the

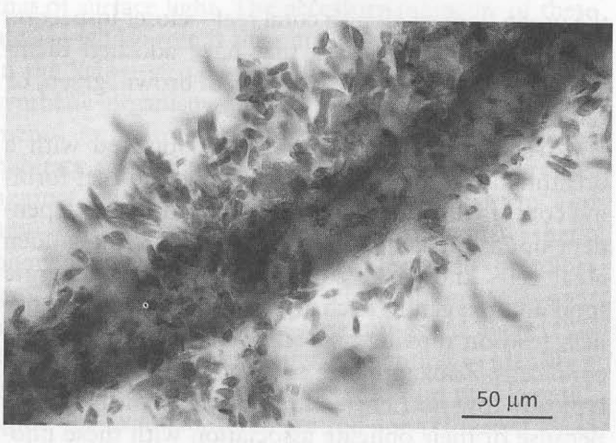


Figure 1–7 A specimen of the freshwater green alga *Oedogonium* with large numbers of epiphytic diatoms.

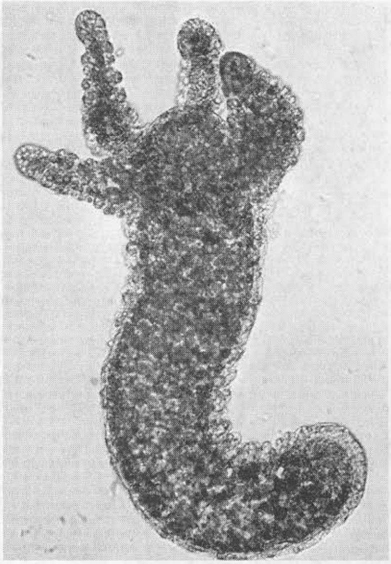


Figure 1–8 *Hydra* containing endosymbiotic green algae known as zoochlorellae.

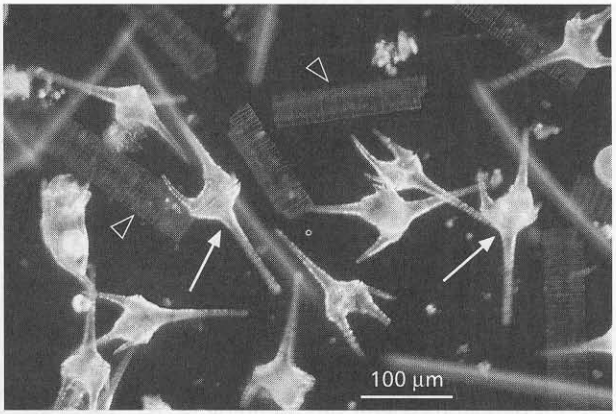


Figure 1–9 Freshwater phytoplankton from a southern Wisconsin lake. The predominant organisms in this sample include the dinoflagellate *Ceratium hirundinella* (arrows) and the filamentous diatom *Fragilaria* (arrowheads).

oceans, it is not uncommon to find that certain photosynthetic freshwater algae colonize the cells and tissues of protozoa or coelenterates like the familiar *Hydra* (Fig. 1–8). Cyanobacteria living within the tissues of water ferns (see Fig. 3–31) can be a major contributor to the nitrogen economy of rice cultivation in paddies and thus influence the nutrition of millions of human beings. Freshwater phytoplankton (Fig. 1–9) and periphyton (also known as benthic algae) form the base of the aquatic food chain, without which freshwater fisheries could not exist. In addition to oceanic and freshwater environments, some algae have adapted to extreme habitats such as hot springs and brine lakes.

Algal Blooms

Conspicuous blooms of microscopic algae (Fig. 1–10) occur in marine and freshwaters, often in response to pollution with nutrients such as nitrogen and/or phosphate. Nutrient pollution can usually be traced to human activities, such as discharge of effluents containing sewage or industrial wastes, or the use of agricultural fertilizers. Surface algal scums or weedy

Figure 1–10 Algal bloom in a freshwater marshland consisting primarily of the green alga *Spirogyra*.

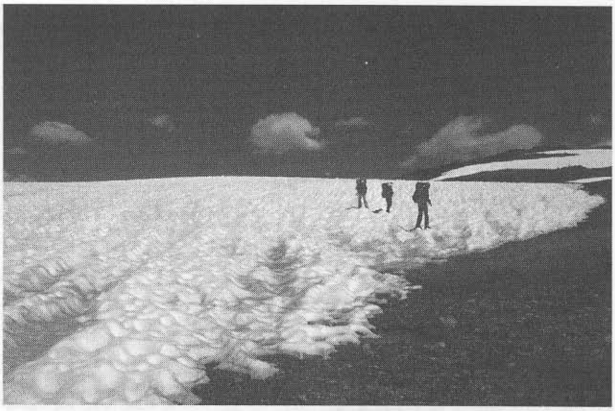


Figure 1–11 The darkened areas on this Colorado snowfield are reddish patches of "snow algae." Although members of the green algae, they are red because of the high levels of photoprotective pigments within their cells.

shoreline growths often have pernicious effects on aquatic ecosystems. Water transparency may become so reduced that organisms such as corals, aquatic plants, and periphyton no longer receive sufficient light for photosynthesis. It has been estimated that 50% or more of marine and freshwater algal blooms produce poisons that affect neuromuscular systems, are toxic to the liver, or are carcinogenic to vertebrates. These toxins can cause massive fish kills, death of birds, cattle, dogs and other animals, and serious illness, or death, in humans (Carmichael, 1997). One recently discovered bloom-forming marine microalga is a deadly "ambush predator"—single-celled dinoflagellates known as *Pfiesteria* secrete a highly toxic compound into the water to kill fish, after which they consume the decaying flesh. *Pfiesteria* was apparently detected only recently because normally small populations had relatively cryptic effects. The recent appearance of larger and more harmful populations of this alga in Chesapeake Bay is correlated with increases in water pollution associated with local agricultural activities (Burkholder, et al., 1992) (see Chapter 3).

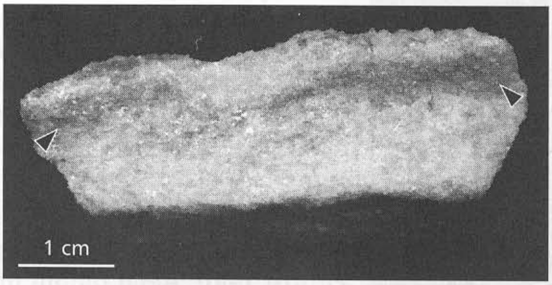


Figure 1–12 A band of cryptoendolithic algae (arrowheads) growing within sandstone. (Specimen courtesy R. Bell)

Figure 1–13 *Umbilicaria*, a large lichen with a membranous thallus, growing on a shaded cliff with the fern *Polypodium*.

Terrestrial Algae

A considerable number of algae have adapted to life on land, such as those occurring in the snows of mountain ranges (Fig. 1–11), in "cryptobiotic crusts" typical of desert and grassland soils, or embedded within surfaces of rocks in deserts (Fig. 1–12), polar regions, and other biomes. The activities of soil and rock algae are thought to enhance soil formation and water retention, increase the availability of nutrients for plants growing nearby, and minimize soil erosion (Johansen, 1993).

Several species of terrestrial algae, together with fungi, form the distinctive life-forms known as lichens (Fig. 1–13). Lichens are ecologically important because of their role as pioneers in early stages of succession, where they help to convert rock into soil, slowly dissolving it with excreted acids. Lichens also help to stabilize fragile desert soils and are used as living barometers of air quality because of their sensitivity to air pollution.

Some terrestrial algae occur in surprising places. For example, algae can impart a greenish cast to the

Figure 1–14 Microalgal production facility. Algal cultures are grown in successively larger volumes and finally cultivated for biomass harvest in long raceways stirred by paddle wheels (foreground). (Photograph courtesy J. Kranzfelder)

fur of giant sloths and sometimes live within the hollow hairs of polar bears. Also, the pink color of flamingos is due to a red-colored algal accessory (carotenoid) pigment consumed as they feed. Algae also occur regularly within the tissues of various plants, including bryophytes, cycads, and the tropical flowering plant *Gunnera*, where they are found in the petioles of its giant leaves.

Human Uses of Algae

For millennia people throughout the world have collected algae for food, fodder, or fertilizer. More recently algae have begun to play important roles in biotechnology. For example, they have been used to absorb excess nutrients from effluents, thereby reducing nutrient pollution in lakes and streams. Algae also generate industrially useful biomolecules (Fig. 1–14), and serve as a human food source, either directly (Fig. 1–15) or indirectly, by supporting aquaculture of shrimp and other aquatic animals. Algae are increasingly being cropped in lab-based bioreactors, outdoor production ponds, and engineered offshore environments.

Algae have provided science with uniquely advantageous model systems for the study of photosynthesis

Figure 1–15 Harvesting the red alga *Porphyra*, grown on nets in an aquaculture operation for use as food. (Photograph courtesy B. Waaland)

and other molecular, biochemical, and cellular-level phenomena of wider importance. Examples include Melvin Calvin's elucidation of the light-independent ("dark") reactions of photosynthesis in the green alga *Chlorella*. Studies of algae have been essential to our understanding of basic photosynthetic processes, and they continue to break new conceptual ground. The relative simplicity, antiquity, and vast diversity of algae, coupled with excellent fossil records in some cases, have also made algae invaluable systems for deciphering organismal and organellar evolution and ecosystem function, and for understanding the effects of human disturbance upon the biosphere (see Chapter 4).

What Are the Algae?

Phylogenetic Relationships of Algae

In order to take a closer look in subsequent chapters at the essential roles of algae in nature and to consider the biotechnological utility of algae, it is first necessary to define these organisms. This is not an easy task, because algae clearly do not form a cohesive group. In the parlance of the field of biology known as **systematics**, which endeavors to understand how organisms are related to one another and to organize them into groups based upon their evolutionary (**phylogenetic**) relationships, we would say that algae are not **monophyletic**. The origin of a monophyletic group (or clade) can be traced to a single hypothetical common ancestor. The organisms commonly regarded as algae, however, appear to have originated on multiple occasions.

Evolutionary relationships among organisms can be visually represented as a **phylogenetic tree**. Various features, including cell structure, biochemistry, molecular (amino acid and nucleic acid) sequences, and molecular architectural data, can be used to infer such phylogenies. The phylogenetic tree depicted in Figure 1–16 shows the major algal groups and their relationships as deduced from nuclear-encoded small subunit (18S) ribosomal RNA gene sequences. As we will see in a more complete discussion of algal systematics in Chapter 5, 18S rDNA sequences offer particular advantages for discerning organismal relationships, particularly in highly diverse, ancient groups such as the algae. Molecular sequence information has provided evidence for the existence of eight to nine major clades or phyla (divisions) of algae. These are the cyanobacteria (chloroxybacteria), classified among the Eubacteria, and the eukaryotic phyla Glaucophyta (glaucophytes, sometimes classified with the red algae), Euglenophyta (euglenoids), Cryptophyta (cryptomonads), Haptophyta (haptophytes), Dinophyta (dinoflagellates), Ochrophyta (a diverse array of tiny flagellates, diatoms, chrysophyceans, brown algae and a host of other groups), Rhodophyta (red algae), and Chlorophyta (green algae). Summaries of the major features of each of these groups are found at the end of this chapter and in Table 1–1. As more information, particularly nucleic acid sequence data, becomes available, it is possible that the composition of these groups, their classification as phyla, or concepts of relative divergence times may change. However, inasmuch as the emerging molecular-based phylogenies correspond well with concepts of relationships based on the cellular structure and biochemistry of algal cells, it is likely that many of the relationships described here are substantially accurate. Two groups of plastid-containing protists, the apicomplexans and chlorarachniophytes (discussed in Chapter 7), may, after additional study, be defined as algal phyla.

A closer examination of Figure 1–16 reveals that some algal clades are actually more closely related to particular, well-defined groups of non-photosynthetic protozoa than to other groups of algae. One example is the close relationship of euglenoids (euglenids) with kinetoplastid protozoa (organisms with an unusual mitochondrion-associated DNA-containing body, the kinetoplast). This suggests that the familiar laboratory organism *Euglena*, which is characterized by bright green chloroplasts, has a closer kinship to *Trypanosoma*, the agent of human diseases such as sleeping sickness, than to other green-colored algae. Another striking example—golden-colored, plastid-containing dinoflagellates such as *Peridinium*, are more closely related to ciliate protozoa (e.g., *Paramecium*) and to malarial and toxoplasmodial parasites (also known as **apicomplexans**) than to some other algae with golden chloroplasts, such as diatoms. How is this possible? An explanation for these apparent anomalies relates both to the phenomenon known as **endosymbiosis**, in which one or more endosymbiotic organisms (**endosymbionts**) live inside the cells of a **host** organism, as well as to the widespread **horizontal transfer** (movement from one organism to another) of genes involved in photosynthesis. These topics will be covered in more detail in Chapter 7.

Eukaryotic cells are defined by the presence of a double membrane-bound nucleus and, in most cases, other organelles such as mitochondria and chloroplasts (plastids). The plastid is the site of photosyn-

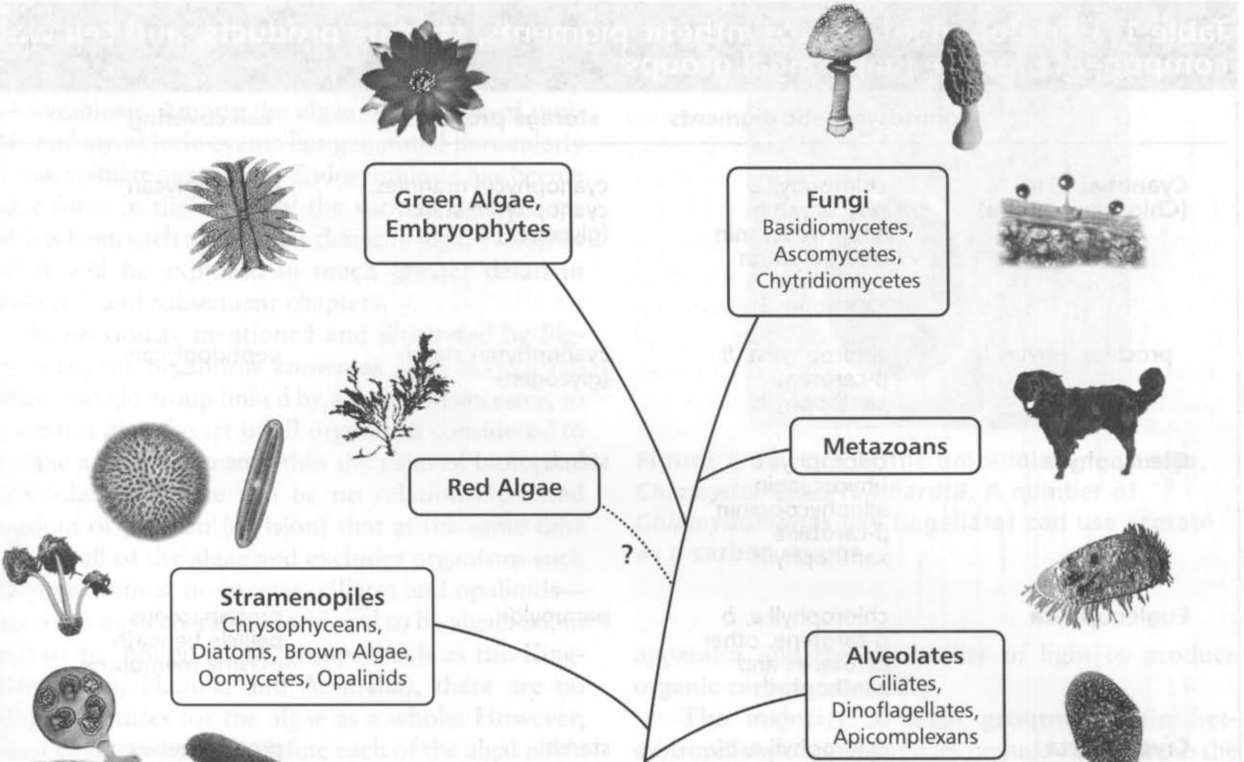


Figure 1–16 Relationships of eukaryotic algae and other eukaryotic groups, based on nuclear-encoded small subunit ribosomal RNA sequencing studies described by Schlegel (1994) and additional molecular sequence information. As new data become available, this phylogeny may change, and the placement of groups labeled with question marks may be better resolved.

thesis in eukaryotic algae. The term chloroplast, while appropriate for all algae because they all contain the green pigment chlorophyll, is applied principally to the usually green-colored plastids of euglenoids, green algae, and land plants. In view of the compelling evidence presented in Chapter 7, mitochondria and plastids are now considered to have originated by the endosymbiotic incorporation of bacteria into host cells. The transformation of free-living bacteria into mitochondria and plastids has been accompanied by

Table 1–1 Predominant photosynthetic pigments, storage products, and cell wall components for the major algal groups

	photosynthetic pigments	storage products	cell covering
Cyanobacteria (Chloroxybacteria)	chlorophyll *a* phycocyanin allophycocyanin phycoerythrin β-carotene xanthophylls	cyanophycin granules, cyanophytan starch (glycogen)	peptidoglycan
prochlorophytes	chlorophyll *a, b* β-carotene xanthophylls	cyanophytan starch (glycogen)	peptidoglycan
Glaucophyta	chlorophyll *a* phycocyanin allophycocyanin β-carotene xanthophylls	starch	some cellulosic
Euglenophyta	chlorophyll *a, b* β-carotene, other carotenes and xanthophylls	paramylon	proteinaceous pellicle beneath plasma membrane
Cryptophyta	chlorophyll *a, c* phycocyanin phycoerythrin α, β-carotene xanthophylls	starch	proteinaceous periplast beneath plasma membrane
Haptophyta	chlorophyll *a, c* β-carotene xanthophylls	chrysolaminaran	$CaCO_3$ scales common
Dinophyta	chlorophyll *a, c* β-carotene xanthophylls	starch	cellulosic plates in vesicles beneath plasma membrane
Ochrophyta (diatoms, chrysophytes, brown algae, etc.)	chlorophyll *a, c* β-carotene xanthophylls	chrysolaminaran, lipids	some naked; some with silica/organic scales; cellulose, alginates in some
eustigmatophytes	chlorophyll *a* β-carotene xanthophylls	chrysolaminaran	present, but unknown composition
Rhodophyta	chlorophyll *a* phycocyanin phycoerythrin allophycocyanin α, β-carotene xanthophylls	floridean starch	cellulose, sulfated polysaccharides; some calcified
Chlorophyta	chlorophyll *a, b* β-carotene, other carotenes and xanthophylls	starch	wall of cellulose/other polymers; scales on some; some naked; some calcified

the transfer of genetic function from one cellular compartment to another, such that the molecular biology of organelles has been dramatically influenced by endosymbiosis. Among the algae occurrence of multiple endosymbiotic events has generated particularly diverse cellular anatomies. Endosymbiosis has been a major force in the origin of the various algal groups and has been such a recurrent theme in algal evolution that it will be explored in much greater detail in Chapter 7 and subsequent chapters.

As previously mentioned and illustrated by Figure 1–16, the organisms known as algae do not fall within a single group linked by a common ancestor, so we cannot give the set of all organisms considered to be algae a formal name within the rules of biological nomenclature. There can be no relationship-based kingdom or phylum (division) that at the same time includes all of the algae and excludes organisms such as trypanosomes, oomycetes, ciliates and opalinids—organisms not generally considered to be algae. So, in contrast to monophyletic groups (such as the Kingdoms Fungi, Plantae, and Animalia), there are no defining features for the algae as a whole. However, sets of characteristics do define each of the algal phyla (pp. 19–21, Table 1–1).

Variations in Algal Nutrition—Relevance to Defining the Algae

As an alternative to a phylogenetic definition for the algae, we might attempt to define this group of organisms in terms of their ecologically important functions, most notably photosynthesis and **carbon fixation**—the transformation of dissolved inorganic carbon, such as carbon dioxide or bicarbonate ion, into an organic form. Therefore presence of chlorophyll—specifically chlorophyll *a*, which occurs in all photosynthetic algae—might be considered as a criterion for algae. Unfortunately, possession of chlorophyll and associated accessory pigments, along with the ability to perform photosynthesis, does not characterize all of the organisms that are considered to be algae. This has become particularly obvious in light of modern systematic investigations coupled with recent findings in studies of algal nutrition. Most algal groups contain colorless members that are devoid of chlorophyll or plastids but which are indisputably related to pigmented forms. Moreover, most major algal groups do not consist exclusively of obligate **photoautotrophs**. In other words, they have members that do not depend entirely upon the photosynthetic apparatus and the availability of light to produce organic carbon from CO_2.

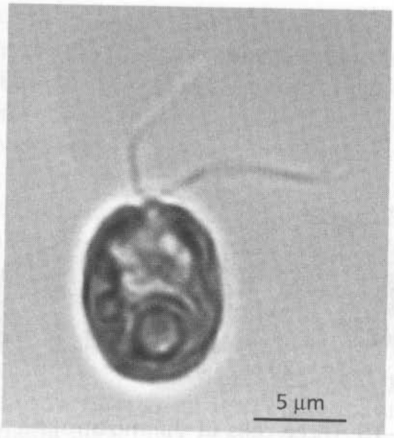


Figure 1–17 The motile unicellular green alga, *Chlamydomonas reinhardtii*. A number of *Chlamydomonas*-like flagellates can use acetate as a carbon source.

The majority of algal groups contain **heterotrophic** species that obtain organic carbon from the external environment either by ingesting particles by a process known as **phagotrophy**, or through uptake of dissolved organic compounds, an ability termed **osmotrophy**. Many kinds of pigmented algae, including multicellular forms, are able to supplement photosynthesis with import of sugars, acetate, or other small organic compounds using cell membrane-based transport proteins similar to those found in osmotrophic protozoa and bacteria. Examples of osmotrophs include the acetate flagellates—relatives of the green alga *Chlamydomonas* that can use acetate as their sole source of carbon and energy (Fig. 1–17). Some algae, referred to as **auxotrophs**, are incapable of synthesizing certain essential vitamins and hence must import them. Only three vitamins are known to be required by auxotrophic algae—biotin, thiamine, and cobalamin (B_{12}).

A variety of other **flagellates**—motile, single-celled or colonial algae distinguished by possession of one or more flagella per cell—accomplish phagotrophy through intricate cellular feeding apparatuses similar to those of protozoa. Some dinoflagellates, euglenoids, and chrysophyceans are renowned for their ability to ingest whole planktonic cells (as well as smaller particulate organic materials). For example, the chrysophycean *Poterioochromonas malhamenhis* can graze algal prey two to three times its diameter (Zhang, et al.,

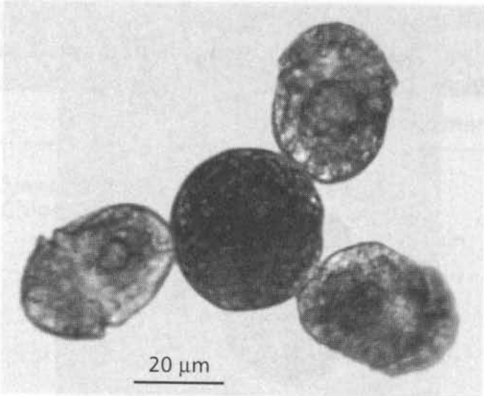


Figure 1–18 Three cells of the mixotrophic dinoflagellate, *Amphidinium cryophilum*, feeding upon another dinoflagellate. (Photograph by L. Wilcox and G. Wedemayer)

1996). Dinoflagellates so commonly exhibit phagotrophy that Jacobson and Anderson (1996) concluded that dinoflagellates are "overwhelmingly and fundamentally a phagotrophic lineage."

Numerous algae exhibit a mixed mode of nutrition; that is, photosynthesis in addition to osmotrophy and/or phagotrophy—an ability termed **mixotrophy**. In the literature the term mixotrophy has sometimes been applied exclusively to pigmented phagotrophic algae, in which case the multicellular green, red, and brown algae would be said to lack mixotrophic representatives. However in this text we will follow the definition of mixotrophy used in a major limnology text (Cole, 1994) because of its functional and ecological relevance—mixotrophy is the ability of chlorophyll-containing algae to utilize "both organic and inorganic carbon sources." Such a definition includes both phagotrophy and osmotrophy, and inasmuch as there is considerable evidence that osmotrophy occurs in multicellular green, red, and brown algae, mixotrophy can be said to characterize at least some members of all major algal groups. An example of a mixotrophic alga is the dinoflagellate *Amphidinium cryophilum*, a cold-water organism that is active during winter beneath ice and snow cover (Fig. 1–18). Observations suggest that when light levels are adequate, it actively photosynthesizes; under low light levels it feeds upon other dinoflagellates (Wedemayer, et al., 1982). An example of mixotrophy in a nonflagellate alga is the uptake of dissolved amino acids by rhizoids of the green seaweed *Caulerpa* (Chisholm, et al., 1996) (Fig. 1–19). Mixotrophic algae may modulate their different nutritional modes as the environment changes, sometimes functioning primarily as photoautotrophs (producers)—by "turning up" expression of the photosynthetic apparatus—and at other times as heterotrophs (consumers). Mixotrophs do not always behave as might be expected, however: some increase grazing rates as light levels decrease, while others decrease grazing under the same conditions (Jones, 1997). The mechanisms by which nutritional mode is regulated and the ecological significance of nutritional modulation by algae are not adequately understood at present and are potentially fertile areas for future research.

The widespread occurrence of mixotrophy among algae reflects the involvement of endosymbiosis in the evolutionary history of particular algal groups. Mixotrophs have retained feeding mechanisms originally present in host cells, despite their having gained photosynthetic capabilities through the acquisition of autotrophic endosymbionts (Tuchman, 1996). The frequent occurrence of mixotrophy among algae suggests that it is highly adaptive in aquatic habitats and therefore needs to be considered when making assessments of algal abundance and function in natural systems. Instantaneous and highly integrative ecosystem-level measures of algal abundance such as chlorophyll *a* levels, or water-sample measures of activity such as conversion of radiolabeled inorganic carbon to cellular organic compounds, can provide useful estimates of algal function under well-defined conditions. However because many algae are so nutritionally versatile, and since colorless members of the algae are not uncommon, such measures can generate an incomplete picture of **primary productivity** (conversion of carbon dioxide to organics) and **remineralization** (conversion of organic compounds to inorganic molecules). Mixotrophic algae acting as autotrophs at one time may undergo rapid transition to heterotrophy; instantaneous measures would not detect such shifts. In view of algal nutritional versatility, the accuracy of a commonly used estimator of algal productivity—particle size coupled with pigment composition—will vary depending upon the taxonomic composition of algal communities (Tang, 1996). Using this approach, productivity would be underestimated if algae were supplementing the carbon fixed through photosynthesis with that obtained through osmotrophy or phagotrophy.

The foregoing overview of algal diversity and nutritional variability leads to the concept of algae as a heterogeneous aggregation of remotely related

Figure 1–19 *Caulerpa*, a green seaweed capable of auto- and osmotrophy. The form of this macroalgal species is quite similar to that of certain gorgonian corals. (Photograph courtesy Ronald J. Stephenson)

groups that have several ecophysiological attributes in common: (1) most are photosynthetic oxygenic producers of organic compounds; (2) most are aquatic, occurring in oceans, lakes, ponds, wetlands, rivers, and streams; and (3) most are smaller and less complex than land plants. Exceptions to the first two of these generalities have been noted—there are heterotrophic and mixotrophic algae, and algae may occur in nonaquatic habitats. We need now to address the features of algae that separate them from plants.

Distinguishing Algae from Plants

Algae are often conceptually and systematically linked to the land plants because they include at least some forms—such as seaweeds—that look much like plants, and as with plants, are commonly sessile (attached or rooted in place), oxygenic (oxygen-producing) photosynthesizers. In contrast, fungi, though sessile, are invariably heterotrophic. Also, although fungi possess cell walls, theirs (composed of chitin) are biochemically distinct from those of plants and algae. While some animals may contain symbiotic algal cells, animals (metazoa) can be distinguished from algae and other protists in that all are multicellular and obligately heterotrophic.

Photosynthetic algae and plants typically require sunlight as well as similar types and amounts of inorganic nutrients such as carbon dioxide, phosphorus, and fixed nitrogen. Since both groups store food in the form of organic carbon compounds, they are vulnerable to herbivorous predators and parasitic microorganisms such as viruses, bacteria, and fungi. Photosynthetic algae and plants must also contend with taller photosynthetic competitors and epiphytes, both of which reduce light available for photosynthesis. Therefore similarities exist in the means by which plants and algae obtain sunlight and in the uptake of inorganic nutrients at the cell membrane, as well as in the defense strategies they employ, such as production of anti-herbivory, allelopathic, or antimicrobial compounds.

Many seaweeds are very plantlike in appearance, having root, stem, and leaf analogs in the form of anchoring holdfasts, stipes, and blades. Certain kelps are noted for their internal phloemlike conducting tissues. However, as the phylogeny illustrated by Figure 1–16 suggests, brown, red, and even green seaweeds are only remotely related to land plants. Kelps, for example, are much more closely related to smaller brown seaweeds, their unicellular cousins among the golden algae, and heterotrophic pseudofungi such as oomycetes, than to land plants. Thus similarities in macroscopic structure between seaweeds and land plants are due to **parallel evolution.**

In modern classification schemes based upon molecular phylogenetic systematics, the plant kingdom (Kingdom Plantae) includes only the **embryophytes** (land plants), which comprise the bryophytes and vascular plants (Fig. 1–16). Even the most plantlike seaweeds are classified in the Kingdom Protista (Raven, et al., 1999). Embryophytes, though sharing many features with green algae (such as photosynthetic pigments and storage products), nevertheless are characterized by a suite of characters not found among the green algae. These include a multicellular, diploid embryo stage that is developmentally and nutritionally dependent on parental gametophyte tissues for at least some time during early development. This feature is the source of the term embryophyte (Margulis and Schwartz, 1988). Other unique and defining features (**autapomorphies**) of embryophytes include tissue-generating apical meristems and preprophase microtubule bands in cells preparing to divide—features absent from the closest green algal relatives of embryophytes (Graham, 1996). Thus there are phylogenetic reasons for distinguishing algae from land plants.

A Definition for the Algae

In summary, we can say that algae are (with numerous exceptions) aquatic organisms that (with frequent exceptions) are photosynthetic, oxygenic autotrophs that are (except for the kelps) typically smaller and less structurally complex than land plants. This rather inelegant definition allows us to include the cyanobacteria (chloroxybacteria), which, although **prokaryotic**, resemble some members of other (eukaryotic) algal groups in terms of overall structure and ecosystem function. Cyanobacteria are distinguished from other bacteria mainly by their possession of the biochemical apparatus necessary for oxygen production (some other bacteria are photosynthetic but do not generate molecular oxygen). In addition to cyanobacteria, the algae consist of several groups of remotely related protists, many members of which have acquired plastids through endosymbiosis. Although it is possible to clearly distinguish algae from plants, animals, and fungi, they cannot, as a whole, be separated from the rest of the protists.

General Characteristics of Algae

As should now be apparent, it is difficult to make broad statements about the ancient and diverse assemblage of organisms referred to as algae. Attempts to list the salient features of a particular algal group is likewise difficult, since for virtually every characteristic considered there are at least some exceptions. In the next portion of this chapter we shall nevertheless attempt to outline some general characteristics of the major algal groups, including pigment composition, types of storage products, and the nature of the cell covering. We will also introduce some of the common types of algal growth forms in addition to the basic modes of sexual and asexual reproduction in algae. In Chapters 6 and 8–21 we will cover these topics in more detail with respect to individual algal groups and consider some of the exceptions to the generalizations made here, which often provide unique insights into the creative ways algae have adapted to diverse habitats and selective pressures.

Range of Morphological Diversity in Algae

A great deal of variation exists in the morphology of the algal **thallus** (the algal body), the most commonly encountered forms of which are described briefly in the following paragraphs and illustrated in Figure 1–20.

Unicells and colonies

Many algae occur as solitary cells (unicells) while others may be made up of several to many individual cells held together loosely or in a highly organized fashion. Some unicellular algae are nonmotile, while others possess one (or more) of the various means of locomotion found among the algae. As mentioned earlier, some algae have locomotory structures known as flagella. Such flagellates can be either unicellular or colonial. A **colony** is an assemblage of individual cells in which there may be either a variable number of cells or a predictable number and arrangement of cells that remain constant throughout the life of the individual. A colony of the latter type is referred to as a **coenobium**. Depending on the organism, cells in coenobia may be either flagellated or nonmotile.

Filaments

A common growth form among the algae is the **filament**, where daughter cells remain attached to each other following cell division forming a chain of cells. Filaments may be unbranched or branched and may be **uniseriate** (a single series of cells) or **multiseriate** (pluriseriate), where a few to many individual filaments fuse together to form a larger, more complex structure. Linear colonies, formed by some diatoms, for example, can be distinguished from true filaments by the fact that cells of the former each possess their own individual walls, whereas adjacent cells of true filaments share a wall.

Coenocytic or siphonaceous forms

Less common are algae with a **coenocytic** or **siphonous** growth habit. Such organisms basically consist of one large multinucleate cell, without cross walls.

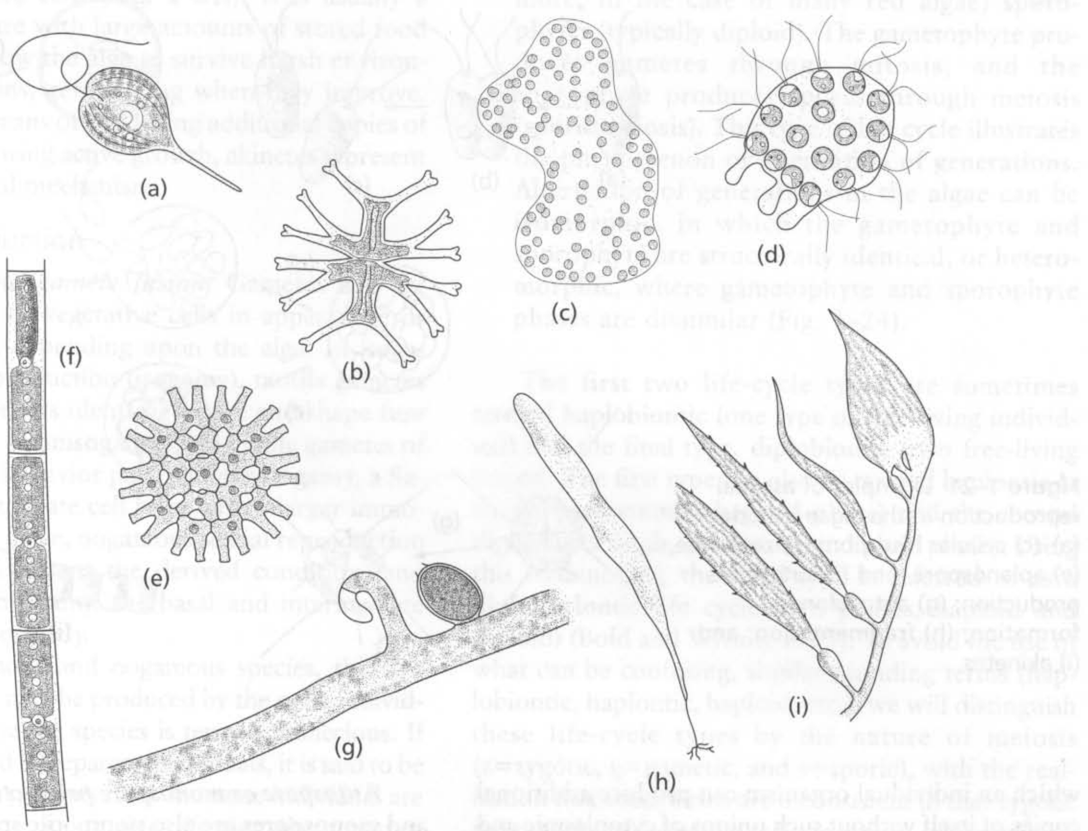


Figure 1–20 Algal growth habits include motile (a—the euglenoid *Phacus*) and nonmotile (b—the green alga *Micrasterias*) unicells; non-coenobic colonies or aggregations (c—the cyanobacterium *Microcystis*); motile (d—the green *Platydorina*); and nonmotile (e—the green *Pediastrum*) coenobia; filaments (f—the green *Mougeotia*); siphonous (g—the tribophycean *Vaucheria*); pseudoparenchymatous multicellular types (h—the green *Monostroma*); and parenchymatous forms (i—the brown kelp *Macrocystis*). (h: After Bold and Wynne, 1985)

Parenchymatous and pseudoparenchymatous algae

Parenchyma is a term used to describe plant (or algal) tissue that is composed of relatively undifferentiated, isodiametric cells generated by a meristem. It results from cell divisions occurring in three directions, which gives rise to a three-dimensional form. Pseudoparenchymatous algae have thalli that superficially resemble parenchyma, but which are actually composed of appressed filaments or amorphous cell aggregates. Evolutionarily, parenchymatous growth habits are thought to represent the most highly derived state, with pseudoparenchymatous forms representing an intermediate condition between filamentous and parenchymatous conditions. Parenchymatous and pseudoparenchymatous algae assume a wide range of shapes (sheets, tubes, stem- and leaf-like arrangements, etc.) and sizes (microscopic to lengths of 50 m or greater).

Algal Reproduction

Algae reproduce by a variety of means, both sexual and asexual. In sexual reproduction, **plasmogamy**—fusion of haploid reproductive cells (**gametes**)—is followed by **karyogamy** (nuclear fusion), to form a diploid zygote. The homologous chromosomes contributed by each of the two gametes pair and at some point are partitioned into haploid cells through the process of meiosis. Asexual reproduction is a means by

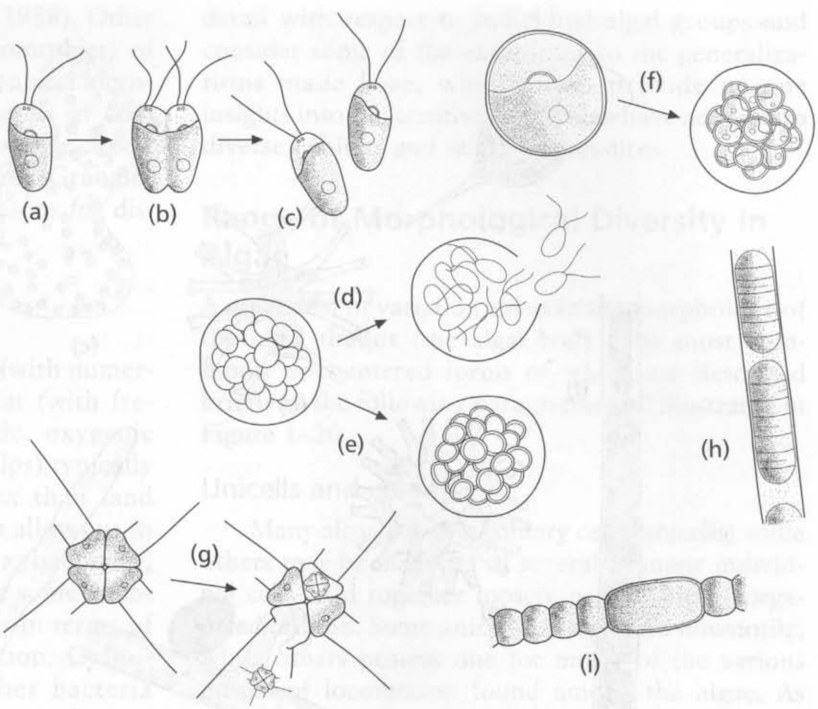


Figure 1–21 Examples of asexual reproduction in the algae include (a)–(c) cellular bisection; (d) zoospore, (e) aplanospore, and (f) autospore production; (g) autocolony formation; (h) fragmentation; and (i) akinetes.

which an individual organism can produce additional copies of itself without such unions of cytoplasmic and nuclear materials or meiosis.

Asexual reproduction

A number of the more common processes and structures involved in asexual reproduction in the algae are introduced here and illustrated in Figure 1–21. Additional discussion is found in Chapters 6 and 8–21.

Cellular bisection. In many unicellular algae reproduction is simply by longitudinal or transverse cell division (Fig. 1–21a, b, c). In multicellular algae (or colonies with indeterminate numbers of cells), this process would lead to growth of the individual, i.e., an increase in the size and the number of its cells. In unicells cell division leads to population growth.

Zoospore and aplanospore formation. **Zoospores** are flagellate reproductive cells that may be produced within vegetative cells or in specialized cells, depending on the organism (Fig. 1–21d). Zoospores contain all of the components necessary to form a new individual. Sometimes, rather than forming flagella, the spores begin their development before being released from the parental cell or sporangium (Fig. 1–21e). These nonmotile spores (which possess the ontogenetic possibility of developing into zoospores) are termed **aplanospores**.

Autospore or monospore production. **Autospores** and **monospores** are also nonmotile spores, but unlike aplanospores, lack the capacity to develop into zoospores. They typically look like miniature versions of the parental cell in which they form (Fig. 1–21f). In green algae, such cells are known as autospores; they are termed monospores in red algae.

Autocolony formation. In coenobia, each cell goes through a consistent number of successive divisions giving rise to a miniature version—an **autocolony**—of the original coenobium (Fig. 1–21g). Depending on the organism, autocolonies may be formed from nonmotile or motile cells that arrange themselves in a pattern identical to that of the parental cells.

Fragmentation. Some multicellular and noncoenobic colonial algae give rise to new individuals through **fragmentation** (Fig. 1–21h). In colonies and some filamentous species this can be a simple, more or less random process whereby an individual breaks into two or more pieces, each of which can continue to grow. In other algae the process is more specialized, with, for example, predictably occurring weak links in filaments or elaborate budlike propagules in some multicellular algae.

Akinetes. An **akinete** is a specialized cell that develops a thickened cell wall and is enlarged, compared to typical vegetative cells (Fig. 1–21i). It is usually a resistant structure with large amounts of stored food reserves that allow the alga to survive harsh environmental conditions, germinating when they improve. Rather than a means of producing additional copies of the individual during active growth, akinetes represent a type of survival mechanism.

Sexual reproduction

Gametes and gamete fusion. Gametes may be nearly identical to vegetative cells in appearance or vastly different, depending upon the alga. In isogamous sexual reproduction (**isogamy**), motile gametes that are more or less identical in size and shape fuse with each other. In **anisogamy**, two motile gametes of different size or behavior pair, while in **oogamy**, a flagellate or nonflagellate cell fuses with a larger immobile egg. Among algae, oogamous sexual reproduction is thought to represent the derived condition, and isogamy and anisogamy, the basal and intermediate conditions, respectively.

In anisogamous and oogamous species, the two types of gametes may be produced by the same individual, in which case the species is termed **monecious.** If they are produced by separate individuals, it is said to be **dioecious.** When gametes from the same individual are able to fuse and produce viable offspring, the organism is termed **homothallic** (self-fertile). If such gametes are incompatible, then two individuals of different genetic makeup are required for successful mating, and the organism is termed **heterothallic** (self-sterile).

Life-history types. Algae exhibit an amazing diversity of life histories. The three principal types are illustrated in Figures 1–22, 1–23, and 1–24, and summarized here. The primary differences between them include the point where meiosis occurs and the type of cells it produces, and whether or not there is more than one free-living stage present in the life cycle. Characteristics of the three types are:

1. The major portion (vegetative phase) of the life cycle is spent in the haploid state, with meiosis taking place upon germination of the zygote (**zygotic meiosis**) (Fig. 1–22).

2. The vegetative phase is diploid, with meiosis giving rise to the haploid gametes (**gametic meiosis**) (Fig. 1–23).

3. Two or three multicellular phases occur—the **gametophyte** (typically haploid) and one (or more, in the case of many red algae) **sporophytes** (typically diploid). The gametophyte produces gametes through mitosis, and the sporophyte produces spores through meiosis (**sporic meiosis**). This type of life cycle illustrates the phenomenon of **alternation of generations.** Alternation of generations in the algae can be **isomorphic**, in which the gametophyte and sporophyte are structurally identical, or **heteromorphic**, where gametophyte and sporophyte phases are dissimilar (Fig. 1–24).

The first two life-cycle types are sometimes termed **haplobiontic** (one type of free-living individual) and the final type, **diplobiontic** (two free-living stages). The first type can also be termed **haplontic** (a single, predominant haploid phase) and the second **diplontic** (a single, predominant diploid phase). Using this terminology, the third type is referred to as a **diplohaplontic** life cycle (two phases, haploid and diploid) (Bold and Wynne, 1985). To avoid the use of what can be confusing, similar-sounding terms (haplobiontic, haplontic, haploid, etc.), we will distinguish these life-cycle types by the nature of meiosis (z=zygotic, g=gametic, and s=sporic), with the realization that these terms are inconsistent in that zygotic refers to the place where meiosis occurs, while gametic and sporic refer to the nature of the meiotic products. We have included an icon in each of the life-cycle diagrams in this text to indicate its type.

The third type of life cycle also typifies the land plants (sporic, alternation of generations, diplobiontic, diplohaplontic). Careful comparison of alternation of generations in the algae reveals fundamental differences among different algal groups, as well as critical differences from the life cycle of land plants. It is quite clear that this type of life cycle has evolved multiple times. Therefore the possession of this life-history pattern by plants and a particular algal group should not be taken as evidence of a close relationship between the two. In fact, as we shall see in Chapters 17 and 21, the evidence is compelling that the green algal progenitors of land plants lacked alternation of generations and that origin of this trait in plants coincided with the evolution of the multicellular plant embryo.

A final comment on algal reproduction is that in some algae, one or both gametes may develop into haploid individuals if they do not happen to fuse with another gamete to form a zygote. This phenomenon is referred to as **parthenogenesis.**

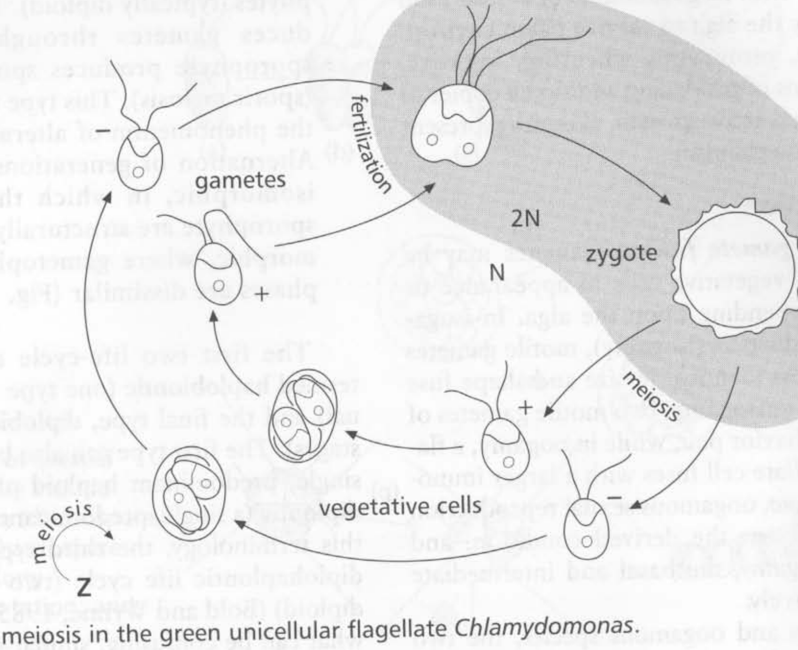


Figure 1–22 Zygotic meiosis in the green unicellular flagellate *Chlamydomonas.*

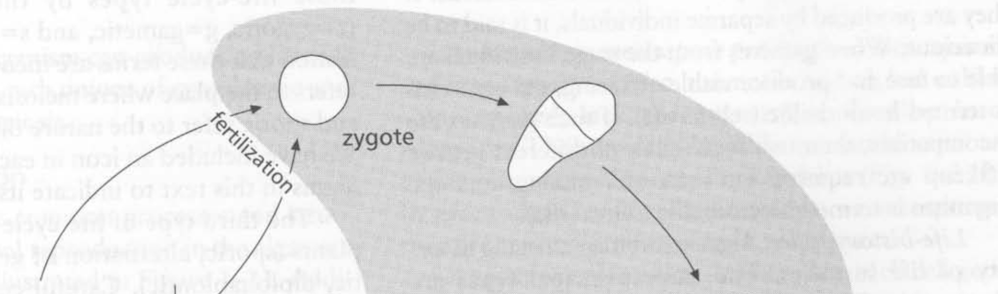


Figure 1–23 Gametic meiosis in a monecious species of the brown rockweed *Fucus*.

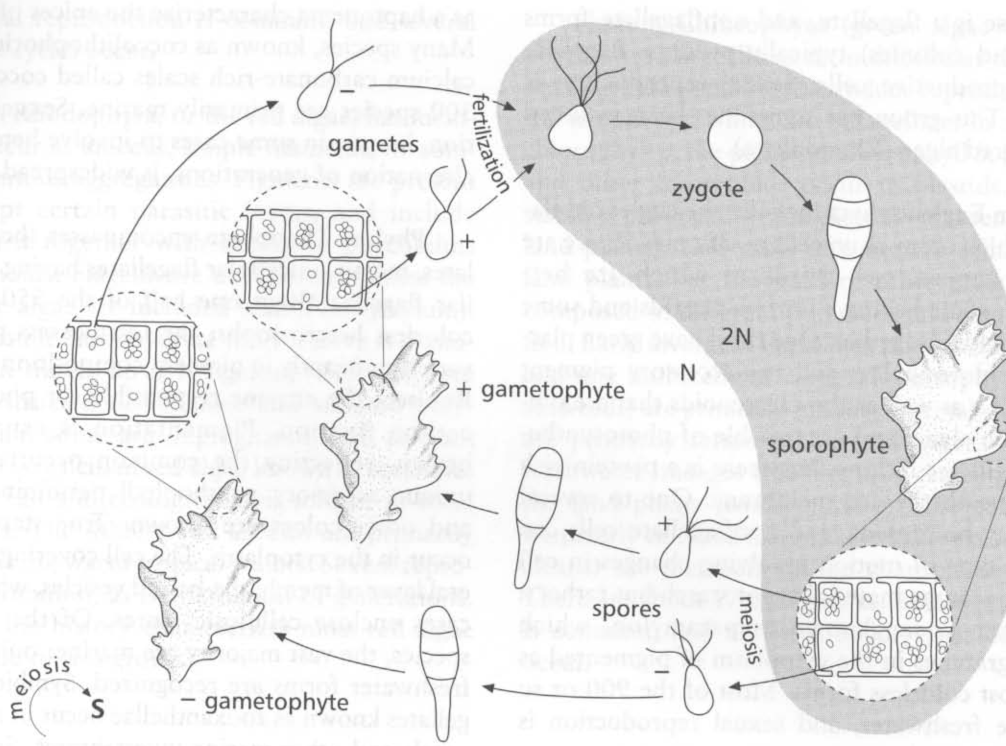


Figure 1–24 Sporic meiosis in the green alga *Ulva*. Note that there are two free-living multicellular stages, one haploid and one diploid (alternation of generations).

Biochemical and Structural Features of Algae

A number of characteristics have been traditionally used in distinguishing among the major algal groups. Prominent among these are the types of photosynthetic pigments, nature of the cell covering, and the type(s) of storage reserves present. More extensive discussion of each of these topics will be given in Chapters 6 and 8–21. We have, however, included a brief summary of these features in Table 1–1, as a reference for subsequent chapters.

Summaries of the Nine Algal Phyla Treated in This Book

Phylum Cyanobacteria (chloroxybacteria, blue-green algae) is a well-defined group of eubacteria. Cyanobacteria include unicellular and filamentous forms, some having specialized cells. Uniquely among bacteria, cyanobacteria produce oxygen as a by-product of photosynthesis. Chlorophyll *a* and accessory and protective pigments—phycobilins and carotenoids—are present, associated with membranous thylakoids. Some members of the group—the prochlorophytes—also possess chlorophyll *b*. The photosynthetic storage products include an α-1,4-glucan known as cyanophytan starch. Among autotrophs, cyanobacterial cells are unique in being prokaryotic in organization, hence typical eukaryotic flagella and organelles (chloroplasts, mitochondria, and nuclei) are lacking. Cyanobacteria are common and diverse in both freshwaters and the sea. Given the difficulties in applying species concepts to prokaryotes, the number of species has been difficult to determine. Sexual reproduction of the typical eukaryotic type, involving gamete fusion, is not present.

Phylum Glaucophyta (the glaucophytes) includes several eukaryotes having blue-green plastids (known as cyanelles or cyanellae) that differ from other plastids and resemble cyanobacteria in several ways, including the possession of a thin peptidoglycan wall. The cyanelles/plastids possess chlorophyll *a* and phycobilins, as well as carotenoids. Granules of true starch (an α-1,4-glucan) are produced in the cytoplasm. There are about nine genera, all freshwater. At least one of these is a flagellate, and nonflagellate forms (unicells and colonies) typically produce flagellate asexual reproductive cells. Sexual reproduction is unknown. This group has sometimes been included within the red algae (Rhodophyta).

Phylum Euglenophyta includes the euglenoid flagellates, which occur as unicells or colonies. There are about 40 genera, two thirds of which are heterotrophic, some having colorless plastids and some lacking plastids altogether. One third have green plastids with chlorophyll *a* and the accessory pigment chlorophyll *b* as well as the carotenoids that are typical of green algae, and are capable of photosynthesis. Cell walls are lacking, but there is a protein-rich pellicle beneath the cell membrane. One to several flagella may be present, and nonflagellate cells can undergo a type of motion involving changes in cell shape. The storage material is not starch but rather a β-1,3-linked glucan known as paramylon, which occurs as granules in the cytoplasm of pigmented as well as most colorless forms. Most of the 900 or so species are freshwater, and sexual reproduction is not known.

Phylum Cryptophyta contains the unicellular cryptomonad flagellates, with 12–23 genera. A few are colorless, but most possess variously colored plastids with chlorophyll *a*. Chlorophyll *c*, carotenoids, and phycobilins constitute the accessory pigments. Alloxanthin is a xanthophyll that is unique to cryptomonads. There is not a typical cell wall. Rather, rigid proteinaceous plates of various shapes occur beneath the cell membrane. Cells can be recognized by their typical flattened asymmetrical shape and the two anterior, slightly unequal flagella. The storage carbohydrate is starch, located in a space between plastid membranes. There are about 100 freshwater species and about 100 marine species. There is some evidence for sexual reproduction.

Phylum Haptophyta (haptophytes or prymnesiophytes) comprises unicellular flagellates or nonflagellate unicells or colonies that have flagellate life-history stages. The photosynthetic pigments include chlorophyll *a*, and accessory and photoprotective pigments including chlorophyll *c* and carotenoids such as fucoxanthin. Species vary in the form of chlorophyll *c* and presence or absence and form of fucoxanthin. There is a β-1,3-glucan storage material. Two flagella and a nearby structure known as a haptonema characterize the apices of flagellates. Many species, known as **coccolithophorids**, produce calcium carbonate-rich scales called **coccoliths**. The 300 species are primarily marine. Sexual reproduction, known in some cases to involve heteromorphic alternation of generations, is widespread.

Phylum Dinophyta encompasses the dinoflagellates, mostly unicellular flagellates having two dissimilar flagella. About one half of the 550 genera are colorless heterotrophs; the rest possess plastids that vary significantly in pigment composition and type of **Rubisco**, the enzyme responsible for photosynthetic carbon fixation. Pigmentation is usually golden brown, reflecting the common occurrence of the unique accessory xanthophyll peridinin, but green and other colors are known. True starch granules occur in the cytoplasm. The cell covering is a peripheral layer of membrane-bound vesicles, which in many cases enclose cellulosic plates. Of the 2000–4000 species, the vast majority are marine; only about 220 freshwater forms are recognized. Symbiotic dinoflagellates known as zooxanthellae occur in reef-forming corals and other marine invertebrates. Sexual reproduction is known.

Phylum Ochrophyta (also known as chromophytes) includes diatoms, raphidophyceans, chrysophyceans, synurophyceans, eustigmatophyceans, pelagophyceans, silicoflagellates, pedinellids, tribophyceans, phaeophyceans (brown algae), and some other groups. Members range in size from microscopic unicells to giant kelps having considerable tissue differentiation. Chlorophyll *a* is present in most ochrophytes, but some colorless heterotrophic forms also occur. In the pigmented forms, dominant accessory and photoprotective pigments may include chlorophyll *c* and carotenoids such as fucoxanthin or vaucheriaxanthin. The food reserve is cytoplasmic lipid droplets and/or a soluble carbohydrate—the β-1,3-glucan chrysolaminaran or laminaran—which occurs in cytoplasmic vacuoles. There are usually two heteromorphic flagella, one bearing many distinctive three-piece hairs known as mastigonemes. Cell coverings vary widely and include silica scales and enclosures as well as cellulose cell walls. There are more than 250 genera and 10,000 species of extant diatoms alone. Some groups of the Ochrophyta are primarily freshwater, some are primarily marine, and some, such as diatoms, are common in both fresh and salt water. The brown algae known as the giant kelps are the largest of all the algae. Sexual reproduction is common, and several types of life cycles occur.

Phylum Rhodophyta, or the red algae, has members that occur as unicells, simple filaments, or complex filamentous aggregations. Pigments are present in all except certain parasitic forms, and include chlorophyll *a* together with accessory phycobilins and carotenoids. Flagella are not present (unless the glaucophyte algae are included within this phylum). The cytoplasmic carbohydrate food reserve is granular floridean starch, an α-1,4-glucan. Cell walls are loosely constructed of cellulose and sulfated polygalactans, and some are impregnated with calcium carbonate. The calcified red algae known as corallines are widespread and ecologically significant in coral reef systems. The 4000–6000 species are primarily marine, favoring warm tropical waters. Sexual reproduction is common, as is alternation of generations. A triphasic life history characterizes most red algae and is unique to this group.

Phylum Chlorophyta (green algae or chlorophytes) have unicellular or multicellular thalli. Some are flagellates, and others produce reproductive cells, the majority of which are biflagellate. In addition to chlorophyll *a*, the pigments chlorophyll *b*, β-carotene, and other carotenoids occur in plastids. Uniquely, starch is produced within plastids of green algae (and land plants). Cell walls of some are cellulosic as in land plants, but the walls of other green algae are composed of different polymers, and some are calcified. Early divergent flagellates (the prasinophyceans) and one multicellular clade (the ulvophycean green seaweeds) are primarily marine, whereas other groups are primarily terrestrial or freshwater. One of the freshwater lineages (the charophyceans) gave rise to the land plants (embryophytes). The common and frequently calcified macrophyte stoneworts (the charaleans) are members of the charophycean lineage. There are about 17,000 species. Sexual reproduction is common, and all three major types of life cycle occur.