Chapter 5

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Eukaryotic Algae and Cyanobacteria

Steve L. Albrecht

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In any case, prokaryotic organisms held the earth as their exclusive domain during two-thirds to five-sixths of the history of life. With ample justice Schopf labels the Precambrian as the 'age of blue-green algae.'

Stephen Jay Gould

Soil algae occur in nearly all terrestrial environments. They are simple **photoautotrophic** organisms that lack tissue differentiation, but they vary greatly in morphology, physiology, reproduction, and habitat. Although considerable numbers of algae are present at the surface and within the subsurface layers of most soils, there is a general lack of awareness of their presence. Hence, the algae have been much less studied than nonphotosynthetic soil microorganisms. This lack of attention has fostered the impression that they are not an important component of the community of soil microorganisms, even though algae may be the only primary producers present in certain ecosystems.

The study of soil algae can be traced to the beginning of the nineteenth century. Beijerinck first reported the isolation of a soil alga in axenic culture in 1893, and in 1895 Graebner gave the first account of algae as ecological constituents of the soil (Chapman, 1941; Starks et al., 1981).

Classification

There are two major groups broadly defined as algae:

- **Eukaryotic algae** are part of the plant kingdom.
- **Prokaryotic cyanobacteria** (formerly known as blue-green algae) are part of the **Bacteria.**

Table 5–1 **Classes (and common names) for representative genera of the soil algae.**

Chlorophyceae Green	Bacillariophyceae Diatoms	Xanthophyceae Yellow-green	Cyanophyceae "Blue-green"	Euglenophyceae Euglenoids	Rhodophyceae Red
Ankistrodesmus	*Achnanthes*	*Botrydiopsis*	*Anabaena*	*Euglena*	*Cyanidium*
Characium	*Amphora*	*Botrydium*	*Calothrix*	*Peranema*	*Porphyridium*
Chlorella	*Caloneis*	*Bumilleria*	*Gleocapsa*		
Chlorococcum	*Cymbella*	*Bumilleriopsis*	*Lyngbya*		
Hormidium	*Fragilaria*	*Geobotrys*	*Microcoleus*		
Protococcus	*Hantzschia*	*Heterothrix*	*Nostoc*		
Stichococcus	*Navicula*	*Pleurochloris*	*Phormidium*		
Ulothrix	*Stauroneis*	*Vaucheria*	*Stigonema*		

Table 5–2 **Characteristics commonly used to classify algae.**

Class	Pigments	Storage products	Flagellation
Chlorophyceae	Chlorophyll a and b, α- and β-carotene, astaxanthin, lutein, neoxanthin, siphonein, siphonoxanthin, violaxanthin, zeaxanthin	Starch, oils	1, 2, 4 to many, equal apical or subapical insertion
Xanthophyceae	Chlorophyll a and c, β-carotene, lutein, neoxanthin	Chrysolaminarin, lipids	2, (equal or unequal) apical
Cyanophyceae	Chlorophyll a, β-carotene, antheraxanthin, aphanicin, allophycocyanin, aphanizophyll, flavacin, lutenin, myxoxanthin, myxoxanthophyll, oscilloxanthin, phycocyanin, phycoerythrin, zeaxanthin	Cyanophycean starch (the amylopectin portion of starch), proteins	Absent
Bacillariophyceae	Chlorphyll a and c, β-carotene, lutein, diadinoxanthin, fucoxanthin	Chrysolaminarin, oils	1 apical on sperm
Euglenophyceae	Chlorophyll a and b, β-carotene, antheraxanthin, astaxanthin, lutein, neoxanthin	Paramylon, oil	1, (usually) 2, or 3
Rhodophyceae	Chlorophyll a and d, α- and β- carotene, lutenin, taraxanthin, allophycoyanin, phycocyanin, phycoerythrin	Floridean starch, oils	Absent

Adapted from Alexopoulos and Bold (1969)

For convenience, many authors include the **edaphic** (soil dwelling) cyanobacteria as part of the soil algae, a convention that will be followed in this chapter. The most common soil algae are the cyanobacteria (class Cyanophyceae), the green algae (class Chlorophyceae), the diatoms (class Bacillariophyceae), and yellow-green algae (class Xanthophyceae). Euglenoids (class Euglenophyceae) and red algae (class Rhodophyceae) occur less frequently. Several representative genera are presented in Table 5–1 and illustrated in Figure 5–1.

Early classification schemes relied heavily on the presence of specific photosynthetic and accessory pigments. Current systems of classification additionally incorporate information about cell-wall constituents, cellular organization, flagellation, and molecular biology (Table 5–2). Much algal taxonomy, especially that of the Chlorophyceae, remains uncertain. The systematics of soil algae have been reviewed

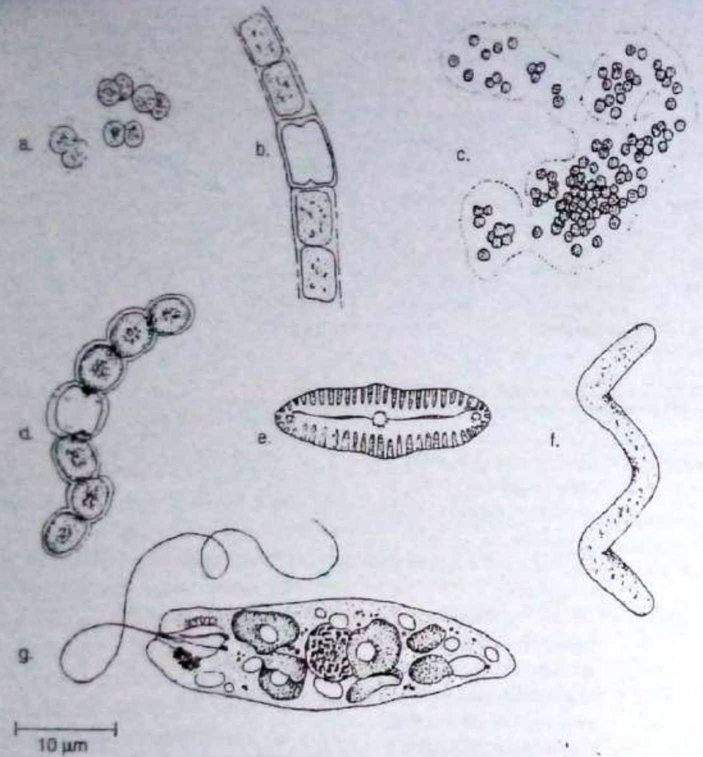

Figure 5–1 Some representative soil cyanobacteria (a–d and f) and eukaryotic algae (e and g). (a) *Gleocapsa*, (b) *Anabaena*, (c) *Microcystis*, (d) *Nostoc*, (e) *Pinnularia*, (f) *Spirulina*, (g) *Euglena*. *Original drawing by Kim Luoma*

by Metting (1981), and a recent two-volume survey by Christensen (1980, 1994) provides comprehensive coverage of algal systematics.

Major Groups Found in Soil

Cyanobacteria

The cyanobacteria are widely distributed. In addition to soil, the terrestrial species may also be found on plants, rocks, and even animals. All species belonging to this group are unicellular or filamentous; cells frequently remain together, surrounded by a gelatinous material. At the subcellular level, the cyanobacteria are morphologically and physiologically similar to bacteria. Their cell walls show some chemical similarity to those of bacteria. As would be expected, cyanobacterial DNA is not separated from the rest of the cytoplasm by a nuclear membrane; hence there is no distinct nucleus. However, many species may have a relatively dense

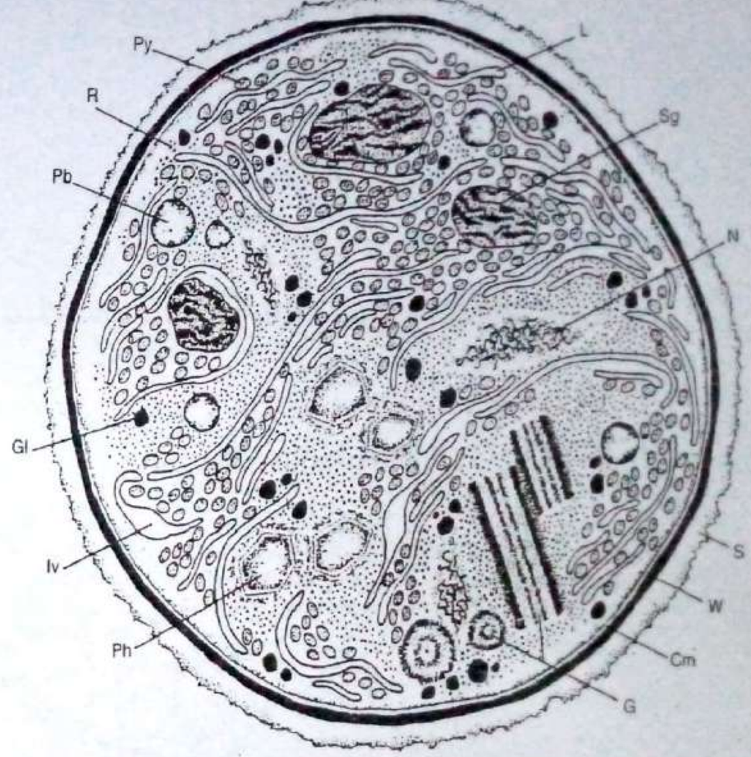

Figure 5–2 Diagram of a cross section of a cell of a cyanobacterium: G = gas vesicles, Gl = glycogen granules, Iv = intralamellar vesicle, L = lamellae, N = nucleoplasm, Pb = polyphosphate body, Ph = polyhedral body, Cm = cytoplasmic membrane, Py = phycobilisomes, R = ribosomes, S = sheath, Sg = structured (cyanophycin) granule, W = wall. *Adapted from Pankratz and Bowen, 1963. Used with permission. Figure redrawn by Kim Luoma.*

mass of material called the *central body*. Cyanobacteria do not have chloroplasts; their photosynthetic pigments are usually associated with membranous layers called **lamellae** and appear uniformly distributed throughout the cytoplasm (Fig. 5–2). The cyanobacteria contain **chlorophyll** a, but not chlorophyll b; however, the dominant pigment is the blue-colored phycocyanin. The storage product in cyanobacteria is starchlike but somewhat different from that of higher plants. Some species store food reserves as oils. Reproduction is by simple cell division without mitosis. The cyanobacteria produce several different types of immobile spores. They are usually found within a filament or trichome, arising from a vegetative cell. They form a thick wall after being filled with food reserves. Many filamentous species can form sporelike cells called **heterocysts**, which are involved in N_2 fixation.

Green Algae

In contrast to the cyanobacteria, considerable cellular organization exists in the eukaryotic green algae. Their organization and physiology closely resemble that of higher plants. In general, the cell walls of eukaryotic algae are similar to those of higher plants; their DNA is localized within minutely perforated nuclear membranes, and the photosynthetic apparatus, including the pigments, is contained in chloroplasts. Green algae possess chlorophyll a as the predominant pigment. In addition to the nucleus, eukaryotic cells may also contain organelles, including vacuoles, flagella, Golgi bodies, and mitochondria.

Diatoms and Yellow-Green Algae

Diatoms live in fresh and salt water and in the soil. Terrestrial diatoms are generally smaller than aquatic species, and most are capable of movement. The diatoms are usually unicellular but may occur in filamentous colonies or as branched or unusual clusters. The cell wall or **frustule** (Fig. 5–3) is composed of two slightly overlapping valves. The cytoplasm contains a single nucleus and

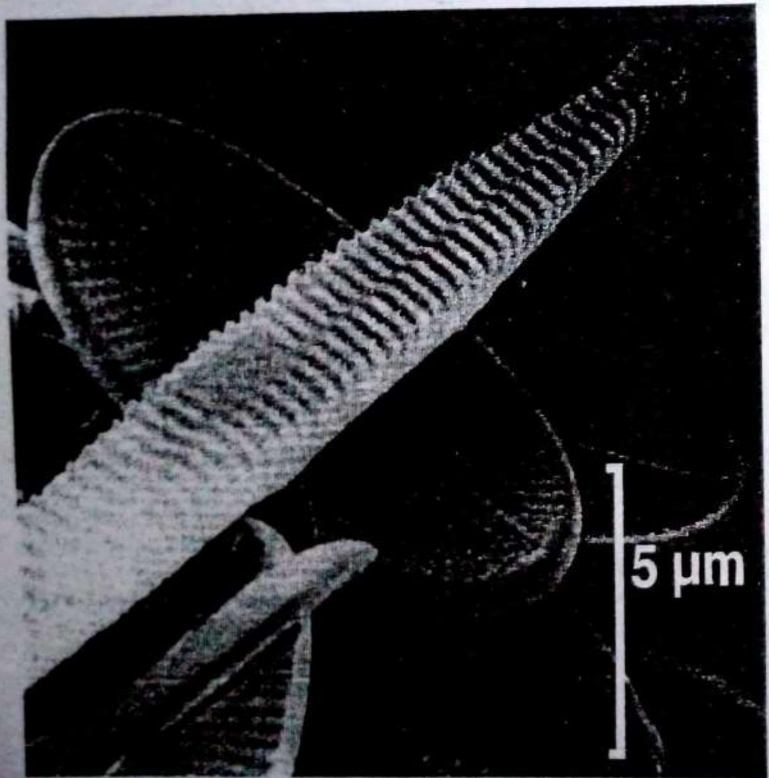

Figure 5–3 Photomicrograph of diatom cell walls, also called frustules. *From the Soil Science Society of America, Division S–3 slide set. Used with permission.*

one to many plastids. The chloroplasts contain chlorophyll a and c. Giving the cells their characteristic color that can vary from green or yellow to golden-brown is the major carotenoid, golden-brown fucoxanthin (Fig. 5–4a). The normal method of reproduction is asexual by division of one cell into two. The storage product in the diatoms is chrysolaminarin, a β-1,3 linked glucan. Diatoms form resting spores with thick, ornamented walls. In addition, they can form resting cells, distinct from the spores, that are morphologically similar to vegetative cells but lack a protective layer.

Yellow-green algae can be motile, with separate forward-directed and posteriorly-directed flagella. Their chloroplasts contain chlorophyll a but lack fucoxanthin; other carotenoid pigments provide the characteristic yellow-green coloration of this group. The cell walls of the yellow-green algae are usually composed of cellulose and consist of two overlapping halves. The principal storage product is probably a β-1,3 linked glucan, but research suggests that lipids are also important for food storage. Members of this class usually multiply asexually by fragmentation and motile or nonmotile spores. Sexual reproduction has been found in *Botrydium* and *Vaucheria*. They have the ability to form resting spores.

Morphology and Reproduction

Soil algae are simple, undifferentiated organisms. As noted previously, they may occur as unicellular types or as cell aggregates, the latter ranging from filamentous to more complex colonial species (Fig. 5–1). Individual algal cells may also differ greatly in size and shape. The cyanobacteria are similar in size to other prokaryotes and commonly have cellular volumes ranging from 5 to 50 μm^3, although volumes from 0.1 to 5,000 μm^3 are known. The unicellular eukaryotic algae are somewhat larger and have a normal range of 5,000 to 15,000 μm^3, with extremes of 5 to 100,000 μm^3. Rudimentary colonies are formed when several generations of cells remain attached after cell division. Other groupings may take the form of branched or unbranched filaments called **trichomes**. Although these organisms are considered simple, they possess great diversity. For example, the euglenoids, a small group often classified as animals rather than plants, lack a cell wall and may ingest food through a gullet. Conversely, the genus *Botrydium* has a balloon-shaped aerial thallus and a mass of branched rhizoids.

Many soil algae are able to form spores. These spores are a means of carrying the species over periods of unfavorable environmental conditions rather than a means of reproduction. They can be formed either sexually or asexually. Some species may form thick-walled resting stages, which are usually morphologically specialized structures. However, formation of resting spores may involve primarily physiological changes, including decreased metabolic activity or the production of protective mucilage.

Algae demonstrate as much variation in reproduction as they do in morphology; vegetative, asexual, and sexual processes are all present. Reproduction in the eukaryotic algae is more varied than in the other groups. Practically all the green algae include some form of sexual reproduction. Reproduction in the