third edition

A Biology of the Algae

Philip Sze

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Georgetown University

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About the cover: Enlarged branch tips of the intertidal brown alga, *Fucus spiralis,* containing the reproductive structures.

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A Biology of the Algae

PREFACE

The need for a third edition of *Biology of the Algae* is gratifying and, I hope, reflects the continuing desire to introduce undergraduate students to this fascinating group of organisms. As in the earlier editions, my overall goal is to provide an overview of the algae that emphasizes their morphologic, evolutionary, and ecologic diversity. The book can serve either as the primary text for a one-term course on the algae, in which the instructor will want to expand on topics of interest with supplementary readings, or as a text for a course that includes the algae as well as other topics, such as an algae-fungi course or an aquatic botany course. I have assumed that the reader is familiar with basic concepts covered in a standard introductory biology course.

Organization

Text organization is the same as in previous editions. Chapter 1 is a general introduction to the algae that emphasizes the aspects of their diversity to be considered in more detail in subsequent chapters. Chapters 2 through 6 cover the different groups of algae, distinguishing among divisions and classes and using representative genera to show morphologic variation. Chapters 7 through 9 describe the roles of algae in different ecosystems. Research on many aspects of algal biology has been prolific since the second edition. A challenge of the revision process was selecting new material for inclusion while trying to keep the text to approximately the same length.

Molecular comparisons using specific genes or ribosomal RNA are an exciting new tool for evaluating relationships among algal groups. I have added a short section on molecular phylogeny to chapter 1, focusing on the use of RNA in the small subunit of ribosomes and raising some interesting questions about how closely the different algal divisions are related. In subsequent chapters, I have indicated where this molecular evidence agrees or disagrees with relationships indicated by the more traditional approaches to classification, which are based on structure and pigmentation.

I treat the evolution of algal photosynthetic systems as a one- or two-step process. The basic system in eukaryotic algae is derived from cyanobacteria either directly as a primary endosymbiotic event, as seen in the green and red algae, or indirectly as a secondary symbiotic event, in which the chloroplasts of some groups are derived from another eukaryotic alga. In the final section in chapter 2 on the cyanobacteria, I introduce the origin of the chloroplasts of eukaryotic algae.

I have made some fairly significant changes from the second edition in the treatment of several groups of algae. Molecular evidence does not support either the separation of the prochlorophytes from the cyanobacteria in chapter 2 or a role for the prochlorophytes as ancestors of green algal chloroplasts. In chapter 3, division of green algae into four classes (Prasinophyceae, Chlorophyceae, Ulvophyceae, Charophyceae) seems warranted based on ultrastructural differences, especially basal body orientation, and molecular comparisons. In chapter 4, the division Chromophyta contains algae with chlorophyll *c* and heterokontous flagellation, which includes the brown algae (Phaeophyceae) but excludes the haptophytes. The haptophytes (or prymnesiophytes), which were treated as a class of the Chrysophyta in the second edition, have been moved to chapter 5 as a separate division and their coverage expanded, reflecting recognition of their importance in the oceans. In chapter 5, I use division Dinophyta for the dinoflagellates instead of division Pyrrophyta and have added a brief section on *Chlorarachnion.*

The material on algal ecology in the last three chapters, especially information on coastal phytoplankton and the Antarctic region, has been updated. In chapter 7, I added a general introduction to primary production and in chapter 9 replaced the introductory listing of environmental factors affecting benthic algae with a short section on regulation of ecologic cycles of macroalgae.

Each chapter concludes with a short summary and a list of general references, which should serve as guides to the published literature. An appendix at the end of the text lists references that describe methods for studying algae and guides for algal identification. Key terms in the text are defined in the end-of-book glossary.

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Students in my courses at Georgetown University and at the Shoals Marine Laboratory have provided the inspiration for *Biology of the Algae*, and have also served as a "testing ground" for its contents. I am also indebted to everyone who has taken the time to send comments, and owe special thanks to the publications and authors who have allowed me to reproduce their illustrations. As reviewers, the following people provided valuable suggestions for the preparation of this edition:

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1

Introduction to Algal Characteristics and Diversity

Living cells appeared on earth over 3.5 billion years ago. These first cells lacked a well-defined nucleus and other complex cellular compartments, and obtained energy as either heterotrophs, consuming organic material from the surrounding seawater, or as autotrophs, using inorganic material. Autotrophs included chemosynthetic forms, similar to bacteria found today near geothermal vents in the deep seas, and photosynthetic forms, similar to present-day sulfur bacteria using a single photosystem in photosynthesis.

Cyanobacteria, the first algae, appeared over 3 billion years ago. They introduced photosynthesis with two photosystems, in which water is split and oxygen is given off as a by-product. This oxygen release profoundly affected the earth. Accumulation of oxygen in the atmosphere led to formation of an ozone layer, which protected against high-energy ultraviolet radiation, and to development of aerobic respiration in living cells to break down organic material more effectively. Under these new conditions, another type of cell, with a nucleus and complex cellular compartments (organelles), evolved about 1.5 billion years ago. Among these early eukaryotic cells were the ancestors of today's eukaryotic algae. Today, algae continue to be important producers of oxygen and organic material in ocean and freshwater environments, while other algae have adapted to living on land or in symbiotic associations with other organisms.

Algae have evolved into a diverse group of photosynthetic organisms, ranging in size from microscopic single cells to complex, multicellular seaweeds many meters long. Their cellular structures, their cell arrangements to form multicellular bodies or thalli, and their pigments for photosynthesis vary greatly. Algae span the range of structural complexity from bacteria to plants. Both algae and land plants have photosynthetic systems based on chlorophyll *a*, but algae lack plants' complex reproductive structures. In development, algae do not form embryos within protective coverings the parents produce. Also, algal reproductive structures do not have sterile cells—all cells are potentially fertile. None are formed exclusively to provide protection or nutrition during development. The algae also include a few "colorless" or nonphotosynthetic species that are closely related to photosynthetic species.

Traditionally, the study of algae, called **phycology** (less correctly, algology), has dealt with photosynthetic organisms that are not bryophytes or vascular plants. With the recognition that we can no longer divide living organisms into "plants" and "animals," a five-kingdom system has become popular. In this system, the eukaryotic algae are placed in the kingdom Protista, which also includes fungal protists and protozoa, and the prokaryotic algae in the kingdom Monera with

Table 1.1 ***Divisions (=Phyla) and Classes of Algae***

Prokaryotic Algae
Division Cyanophyta (cyanobacteria or blue-green algae)
Class Cyanophyceae (includes prochlorophytes)
Eukaryotic Algae
Chloroplasts Surrounded by Two Membranes
Division Rhodophyta (red algae)
Class Rhodophyceae
Division Chlorophyta (green algae)
Class Prasinophyceae
Class Chlorophyceae
Class Ulvophyceae
Class Charophyceae
Chloroplasts Surrounded by More Than Two Membranes
Division Chromophyta (=Chrysophyta)
Class Chrysophyceae (golden brown algae)
Class Synurophyceae
Class Tribophyceae (=Xanthophyceae) (yellow-green algae)
Class Eustigmatophyceae
Class Raphidophyceae (=Chloromonadophyceae)
Class Bacillariophyceae (=Diatomophyceae) (diatoms)
Class Phaeophyceae (=Fucophyceae) (brown algae)
Division Haptophyta
Class Prymnesiophyceae (=Haptophyceae)
Division Dinophyta (=Pyrrophyta) (dinoflagellates)
Class Dinophyceae
Division Cryptophyta (cryptomonads)
Class Cryptophyceae
Division Euglenophyta
Class Euglenophyceae
[Division Chorarachniophyta
Class Chlorarachniophyceae]

Table 1.2 ***Levels of Classification***

	***Ulva lactuca* L.**	***Laminaria saccharina* (L.) Lamouroux**	**Suffix**
Division	Chlorophyta	Chromophyta	-phyta
Class	Ulvophyceae	Phaeophyceae	-phyceae
Order	Ulvales	Laminariales	-ales
Family	Ulvaceae	Laminariaceae	-aceae
Genus	*Ulva*	*Laminaria*	(variable)
Species	*Ulva lactuca*	*Laminaria saccharina*	(variable)

eubacteria. Recent molecular evidence suggests that the ancestors of different groups of eukaryotic algae may have acquired photosynthetic systems from different sources and thus are less closely related to each other than to other groups of protists. This indicates that the algae represent a number of independent evolutionary lines and thus are not one well-defined taxonomic group. This text classifies the algae into eight major divisions (or phyla) with seventeen classes (table 1.1). These divisions, and even some classes within divisions, exhibit great diversity. We will examine differences among algae with special attention to the following features:

1. Light-harvesting pigments for photosynthesis
2. Polysaccharide reserve
3. Cellular organization
4. Molecular phylogeny
5. Morphology
6. Ecology

Variation in these characteristics separates algae at different taxonomic levels. (Table 1.2 reviews the major taxonomic levels.)

Diversity of Photosynthetic Pigments

For photosynthesis, pigments absorb light, which is converted into chemical energy in ATP (adenosine triphosphate) and NADP (nicotinamide adenine dinucleotide phosphate), which are used to synthesize organic compounds from carbon dioxide. Usable light for photosynthesis is in the 400–700 nanometer range of the electromagnetic spectrum, referred to as **photosynthetically active radiation** (PAR). Individual pigments selectively absorb certain wavelengths of PAR. The principal pigment in all algae is chlorophyll *a*, but accessory pigments absorb other wavelengths of PAR and transfer the light energy to chlorophyll *a*.

Photosynthetic pigments associate with proteins in the thylakoid membranes of a cell to form light-harvesting complexes or photosystems (phycobiliproteins are on thylakoid surfaces in cyanobacteria and red algae). Each photosystem consists of several hundred pigments funneling energy into a reaction center consisting of a special chlorophyll-*a*–protein unit. Two types of photosystems operate together to reduce NADP and to convert ADP (adenosine diphosphate) to ATP (fig. 1.1). Photosystem I is composed primarily of chlorophyll *a*, while photosystem II contains chlorophyll *a* and several accessory pigments. Algae may respond to their light environment by increasing or decreasing their overall pigment content (number and/or size of photosystems), changing the composition of accessory pigments (chromatic adaptation), varying the ratio of photosystem I to photosystem II, and adjusting the relative flow of electrons in photosystem I and photosystem II (Chow, Melis, and Anderson 1990).

The Calvin cycle is the principle pathway for the formation of organic compounds from carbon dioxide. Here, the energy and reducing potential of NADP and ATP are used to synthesize sugars, usually represented as glucose molecules. The glucose may be oxidized immediately for energy, combined in short polysaccharides for transport, or stored in long chain polysaccharides.

Reaction center activities and the Calvin cycle are similar in all algae, but algae show considerable diversity in their accessory pigments. Table 1.3 summarizes principal photosynthetic pigments in the different algal divisions. Photosynthetic pigments are divided into three classes: **chlorophylls, carotenoids,** and **phycobilins.** In addition to chlorophyll *a*, many algal groups have another form of

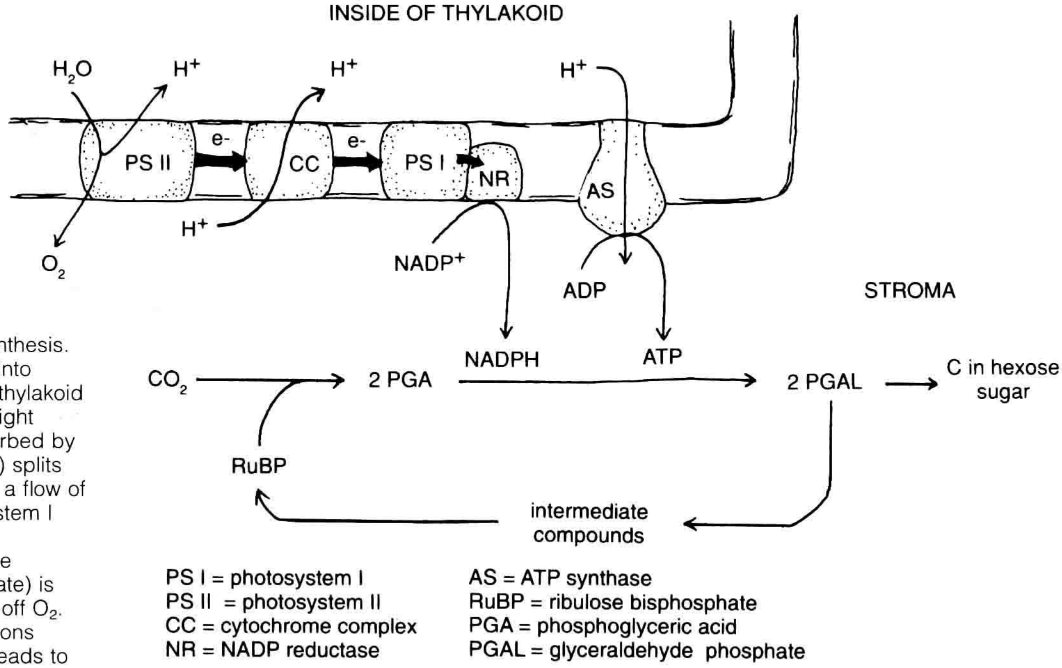

Figure 1.1
Summary of photosynthesis. Pigments organized into photosystems in the thylakoid membranes absorb light energy. Energy absorbed by photosystem II (PS II) splits water and generates a flow of electrons to photosystem I (PSI), where NADP (nicotinamide adenine dinucleotide phosphate) is reduced. PS II gives off O_2. Accumulation of H^+ ions inside the thylakoid leads to the synthesis of ATP (adenosine triphosphate) when the H^+ ions recross the membrane. The Calvin cycle occurs in the stroma of a chloroplast. Carbon dioxide combines with ribulose bisphosphate (RuBP) to produce phosphoglyceric acid (PGA). Ultimately, some of the carbon atoms in PGA are used to synthesize sugar (glucose), and other carbon atoms regenerate RuBP. ATP and NADP are used in the process.

Table 1.3 ***Photosynthetic Pigments and Carbohydrate Reserves***

Division	Principal Photosynthetic Pigments	Carbohydrate Reserve
Cyanophyta	Chlorophyll *a*; phycocyanobilin, phycoerythrobilin	Starch (α-1,4-linked glucan)
Rhodophyta	Chlorophyll *a*; phycoerythrobilin	Starch
Chlorophyta	Chlorophylls *a*, *b*	Starch
Chromophyta	Chlorophylls *a*, c_1, c_2; fucoxanthin	Chrysolaminarin or laminarin (β-1,3-linked glucan)
Haptophyta	Chlorophylls *a*, c_1, c_2; fucoxanthin	Chrysolaminarin (β-1,3-linked glucan)
Dinophyta	Chlorophylls *a*, c_2; peridinin (some chlorophylls *a*, c_1, c_2; fucoxanthin)	Starch
Cryptophyta	Chlorophylls *a*, c_2; phycocyanobilin or phycoerythrobilin	Starch
Euglenophyta	Chlorophylls *a*, *b*	Paramylon (β-1,3-linked glucan)

chlorophyll, either chlorophyll *b* or chlorophyll *c* (fig. 1.2). Chlorophyll *c* may be present in two or sometimes three slightly different forms, designated c_1, c_2, and c_3. While chlorophylls are green pigments, carotenoids are brown, yellow, or red. Although approximately sixty carotenoids occur in algae (Rowan 1989), the major carotenoids participating in photosynthesis are fucoxanthin, peridinin, siphonaxanthin, and possibly β-carotene (fig. 1.3). Most algae have β-carotene, but usually, it has secondary importance. In some green algae, siphonaxanthin may

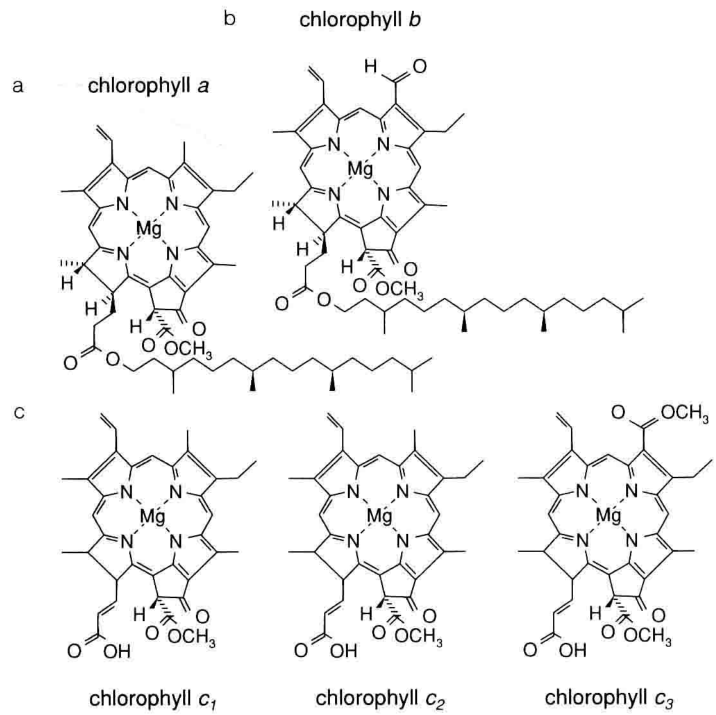

Figure 1.2
Chlorophylls. (*a*) Chlorophyll *a* (*b*) Chlorophyll *b*. (*c*) Forms of chlorophyll *c*. (*a–c* from Egeland et al. 1995, courtesy *Journal of Phycology*.)

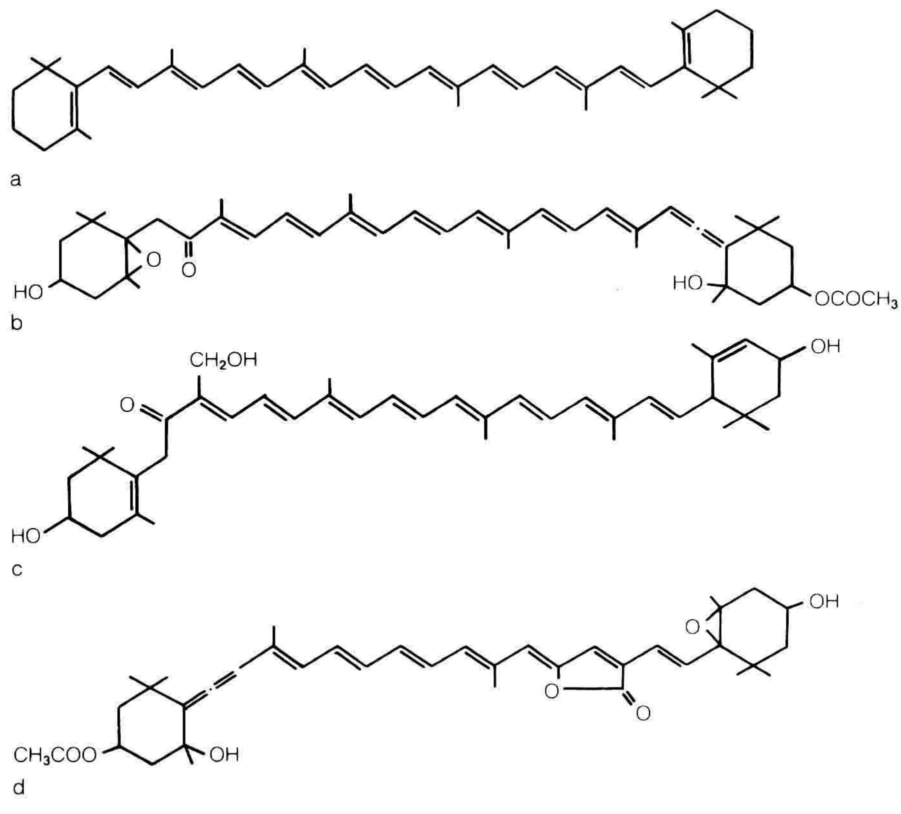

Figure 1.3
Carotenoids. (*a*) β-carotene. (*b*) Fucoxanthin. (*c*) Siphonaxanthin. (*d*) Peridinin.

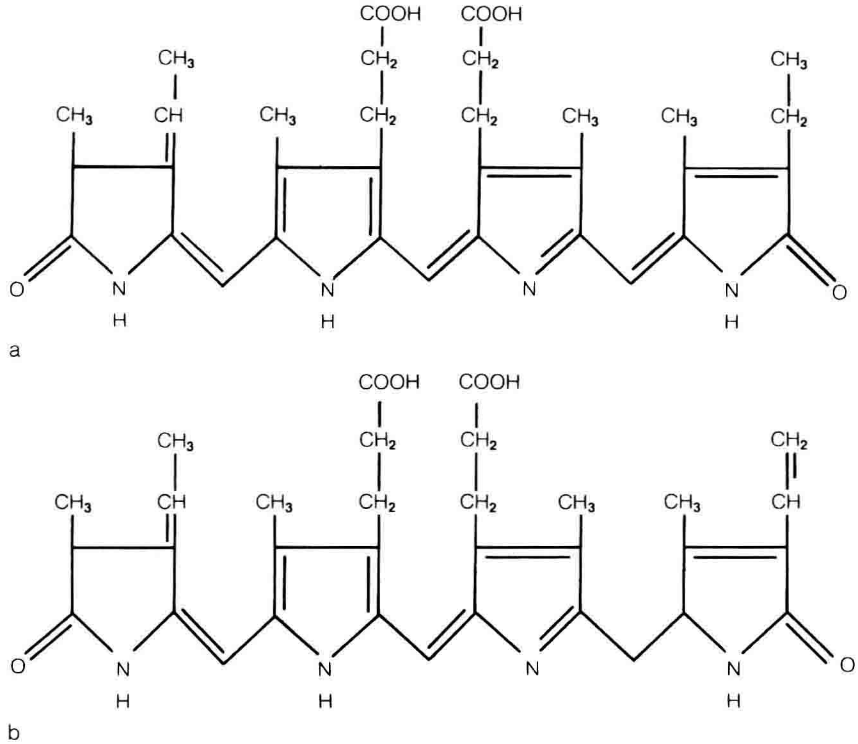

Figure 1.4
Phycobilins.
(*a*) Phycocyanobilin.
(*b*) Phycoerythrobilin.

be an adaptation for absorbing light in relatively deep water. Fucoxanthin occurs in some algae with chlorophyll *c*, while peridinin is present in many dinoflagellates. Functions of other carotenoids are poorly understood, but some are important for photoprotection, as discussed later in this section. Three divisions of algae have phycobiliproteins. Each phycobiliprotein consists of several pigment molecules, called phycobilins, tightly bound to a protein. The phycobilins include the red pigment phycoerythrobilin and the blue pigment phycocyanobilin (fig. 1.4).

The dominant photosynthetic pigments often give algae a distinct color and their common names (see table 1.1). However, observed color is not always a reliable indicator of taxonomic position. For instance, not all members of the Rhodophyta (red algae) have an obvious red color; many are tan, dark brown, or another color (compare plates 6*b* and 7*b*).

Exposure to high levels of light may inhibit photosynthesis and even damage the photosynthetic system. To reduce such adverse effects, some carotenoids function in photoprotection by screening the chloroplasts, by deactivating highly reactive forms of oxygen before cellular damage occurs (superoxide dismutase is also important in this role), or by absorbing and dissipating excess energy (Demmig-Adams and Adams 1992). Screening pigments are dispersed in the cytoplasm (Hagen, Braune, and Björn 1994). Energy dissipation involves carotenoids in the photosynthetic photosystems that are part of the "xanthophyll cycle" (Demmig-Adams 1990; Frank et al. 1994). In response to high levels of light, these carotenoids remove excess energy by the following conversion: violaxanthin → antheraxanthin → zeaxanthin. Zeaxanthin is reconverted to violaxanthin when light becomes limiting. Similarly, in some chromophytes, dinoflagellates, and haptophytes, the conversion of diadinoxanthin to diatoxanthin removes excess energy (Olaizola, Bienfang, and Ziemann 1992).

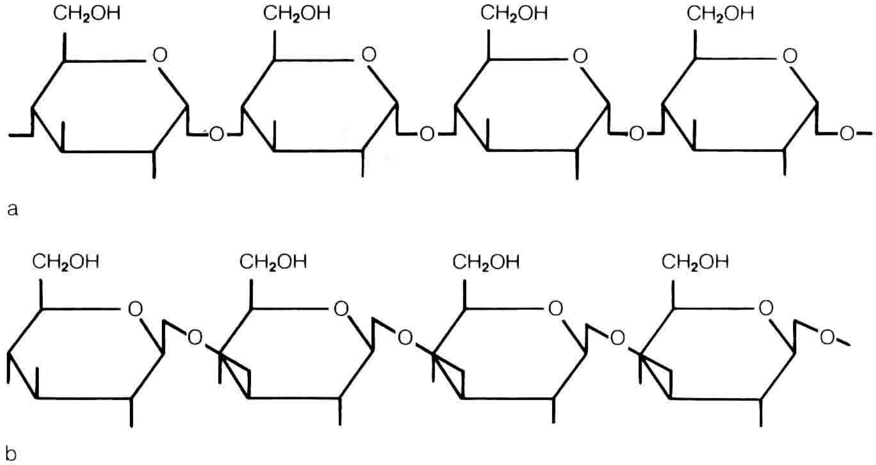

Figure 1.5
Carbohydrate reserves are polymers of glucose with different linkages between units. (*a*) Starches with α-1,4-linked glucose units. (*b*) Laminarin, chrysolaminarin, and paramylon with β-1,3-linked glucose units.

Reserve Carbohydrates

The glucose molecules the Calvin cycle produces may join in long chains (glucans) for storage. Algae have two types of these polysaccharide reserves, depending on how the glucose units link (fig. 1.5). The various forms of **starch** are α-1,4-linked glucans. The β-1,3-linked glucans include **chrysolaminarin** (=leucosin), **laminarin,** and **paramylon.** In both types, side branches may arise from the six-carbon, and the degree of branching and the length of chains vary. The carbohydrate reserve is characteristic for different algal divisions (table 1.3).

Diversity of Cellular Organization

Prokaryotic and eukaryotic forms are included among the algae. All prokaryotic algae belong to the cyanobacteria and lack a nuclear region surrounded by a nuclear envelope and complex organelles, such as chloroplasts, mitochondria, Golgi bodies, and endoplasmic reticula. Prokaryotic algae resemble other eubacteria in their walls, ribosomes, and chromosome structure, but differ from other photosynthetic bacteria by having two photosystems and producing oxygen. The chlorophylls (and carotenoids) of cyanobacteria are on internal membranes of flattened vesicles called **thylakoids,** while phycobiliproteins occur in granular structures called **phycobilisomes** on the outer surfaces of thylakoid membranes.

The other divisions of algae are eukaryotic. Let us consider two hypothetical eukaryotic cells representing primitive and advanced conditions. Primitive eukaryotic algae were probably flagellated (except in Rhodophyta). Figure 1.6*a* is a diagram of a hypothetical primitive phytoflagellate. The beating of two anterior flagella propels the cell through the water. Each flagellum arises from basal bodies and has an axoneme of microtubules in a 9+2 arrangement (nine peripheral pairs and two central microtubules). Sliding of the peripheral pairs of microtubules relative to each other causes flagella to flex. The primitive algal cell lacks a wall but may have a covering of platelike **scales** composed of complex polysaccharides. Scales formed in Golgi vesicles within the cell are deposited on the cell membrane's outer surface, sometimes in overlapping layers (see fig. 4.5*a*). Scales form a protective covering about the cell and represent an intermediate condition between a cell without any external covering and a cell enclosed by a wall.

A conspicuous structure within the hypothetical primitive alga is a single, large chloroplast. It is surrounded by an envelope composed of two closely associated membranes and contains flattened sacs called **thylakoids** (similar to cyanobacterial thylakoids). Photosynthetic pigments are in thylakoid membranes. The chloroplast

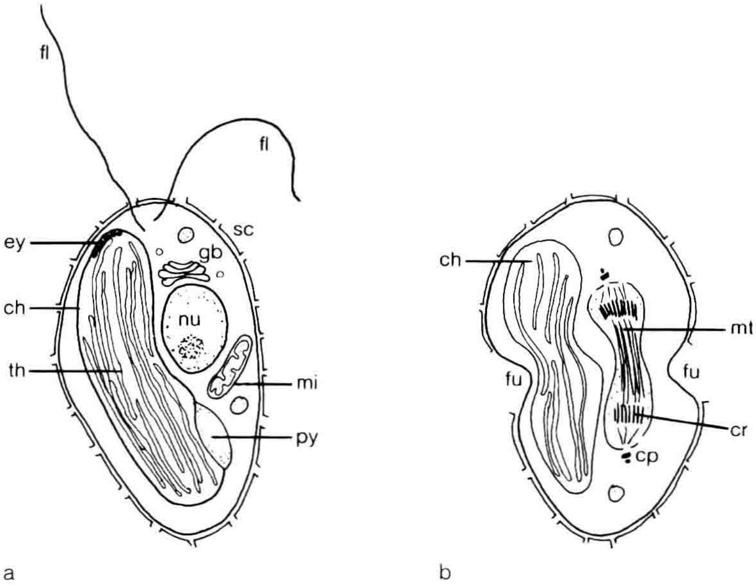

Figure 1.6
Flagellated cell representing a primitive eukaryotic cell. (*a*) Structures of vegetative cell. (*b*) Asexual reproduction involving mitosis with a persistent nuclear envelope and cell division by furrowing. ch = chloroplast; cp = centriole pair; cr = chromosomes; ey = eyespot; fl = flagellum; fu = furrow; gb = Golgi body; mi = mitochondrion; mt = spindle of microtubules; nu = nucleus; py = pyrenoid; sc = scale; th = thylakoid

may contain a distinct region called the **pyrenoid,** whose principal component is the enzyme ribulose bisphosphate carboxylase, which catalyzes the incorporation of carbon dioxide into organic compounds in the Calvin cycle. A pyrenoid also may contain other proteins (Okada 1992). In some algae, carbohydrate reserves accumulate on the pyrenoid. An eyespot, consisting of several layers of carotenoid granules, also may be part of the chloroplast. Most flagellated algae swim toward the sunlight at the water surface and thus show a positive phototaxis. The eyespot helps sense the direction of light but is not the actual photoreceptor, which is either part of the cell membrane or a swelling near the base of one flagellum. The eyespot blocks light from some directions and reflects light from other directions onto the receptor. A chloroplast also contains ribosomes and DNA (Coleman 1985).

Other cellular structures present in the cytosol include mitochondria, Golgi bodies, endoplasmic reticulum, various types of vesicles, ribosomes, and cytoskeletal components. Some eukaryotic algae have mitochondria with flattened cristae, while others have tubular cristae (see table 1.6). In the cell's center is a large nucleus surrounded by a nuclear envelope composed of two membranes and containing chromosomes composed of DNA and proteins. The nucleus may have a distinct nucleolus. Freshwater flagellates often have contractile vacuoles near the bases of their flagella. These organelles regulate the cell's fluid content by slowly filling with excess liquid and expelling it through pores, and also may function in secretion and uptake of material into the cell. Some algal groups store their carbohydrate reserve in cytoplasmic vesicles rather than in the chloroplast. The cell's cytoskeleton is associated with the basal bodies and controls cell shape, position of organelles, movements of materials within the cell, formation of the cell covering, and various aspects of cell division. It consists of connecting fibers between the basal bodies, a fibrous root extending from the basal bodies toward the nucleus, and bundles of microtubules radiating around the cell periphery (see fig. 1.10).

Mitosis and cell division are associated with cellular reproduction. In a primitive alga, the nuclear envelope remains intact, enclosing the mitotic spindle (closed spindle), and centrioles are organizing centers for the microtubules composing the spindle (fig. 1.6*b*). In more advanced algae, the nuclear envelope breaks down, resulting in an open spindle. Other organelles, including the chloroplast,

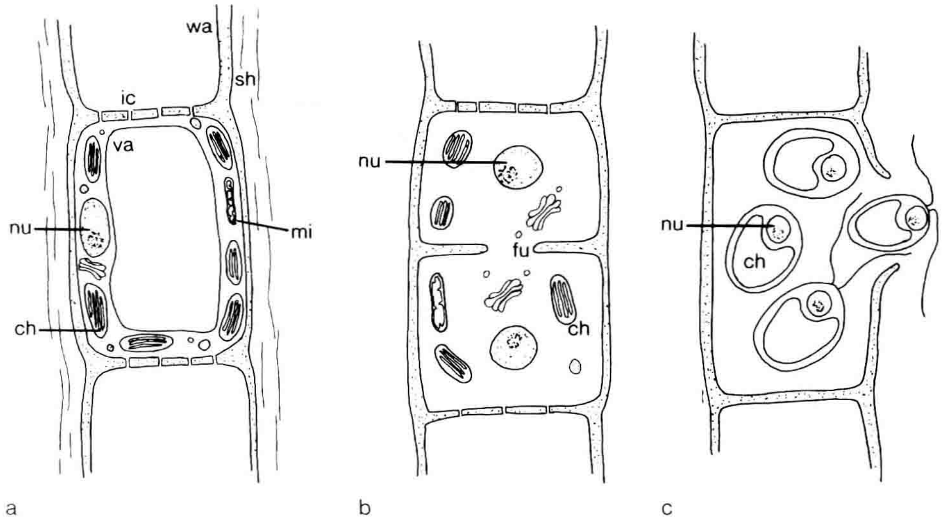

Figure 1.7
Cell of a filament.
(*a*) Structures of a vegetative cell. (*b*) Vegetative cell division adding a new cell to the thallus. (*c*) Formation of flagellated reproductive cells.
ch = chloroplast;
fu = furrow; ic = intercellular connection;
mi = mitochondrion;
nu = nucleus; sh = sheath;
va = vacuole; wa = wall.

divide with the nucleus. As mitosis is completed, the cell divides at its equator by **furrowing**—ingrowth of the cell membrane under the control of a contractile ring of actin. Stressful environmental conditions may cause a cell to discard its flagella, form a thick wall, and become a dormant **cyst.** When external conditions are favorable again, the cell becomes metabolically active.

More advanced, multicellular algae are colonies, filaments, blades, or cylinders. The body of an alga is its **thallus.** A filament, with its cells arranged in a linear series, is representative of an advanced alga (fig. 1.7*a*). Filaments appear threadlike and may be branched or unbranched. Each cell is surrounded by a wall and lacks flagella, basal bodies, and an eyespot. Adjacent cells in a filament share a common end wall. Intercellular connections through these end walls may create cytoplasmic continuity between cells. A cell wall consists of a framework of polysaccharide bundles or fibrils surrounded by a mucilaginous material composed primarily of other polysaccharides (mucopolysaccharides). Most algae form fibrils composed of cellulose, but in a few algae, xylans or mannans replace cellulose. Enzyme complexes (cellulose synthase) in the cell membrane control the polymerization of glucose units to form chains of cellulose and the organization of these chains into fibrils. The mucilaginous material filling the space between the fibrils consists of a variety of polysaccharides (sometimes divided into pectic substances and hemicelluloses); proteins also may be present. Mucilage may extend beyond the wall as a gelatinous sheath. Sheaths have a variety of functions, including holding cells together, attaching cells to the substrate, reducing water loss during exposure to air, facilitating nutrient uptake, and producing gliding movement. A sheath also may reduce an alga's susceptibility to epiphytes and herbivores. Mucilaginous polysaccharides are synthesized in Golgi bodies and transported to the cell membrane in vesicles. Some algae deposit a stony layer of calcium carbonate on their walls for protection.

Each cell in a filament has a large central vacuole containing a watery solution of inorganic and organic materials called the cell sap. The cytoplasm, confined to a thin layer adjacent to the wall, contains the nucleus, one or more chloroplasts, and other organelles, as in primitive phytoflagellates. The cytoskeleton consists of actin microfilaments and microtubules. Actin filaments near the cell membrane are involved with cytoplasmic streaming, movement of organelles, and furrowing during cell division. Microtubules composed of tubulin are associated with microtubu-