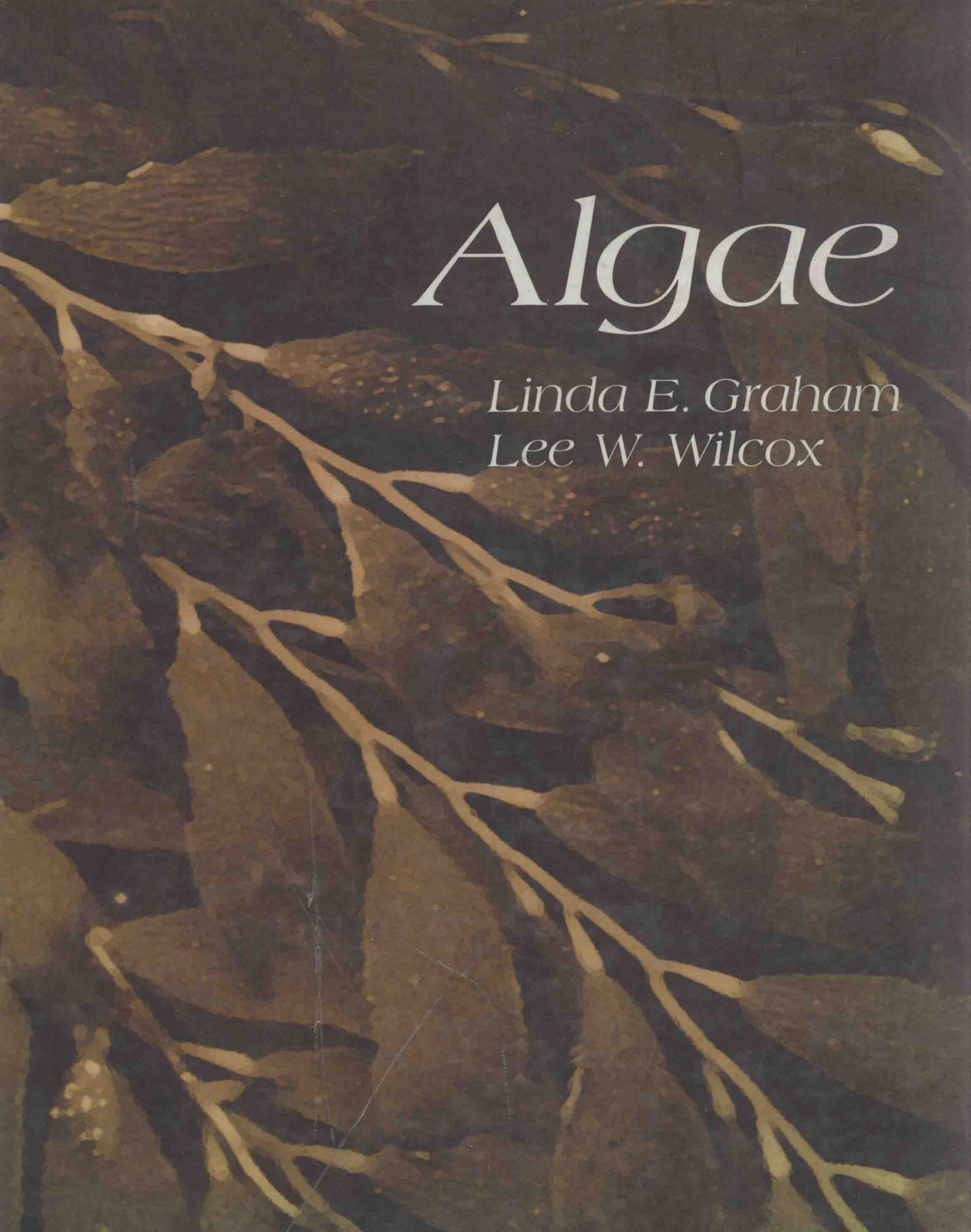
# Algae

Linda E. Graham
Lee W. Wilcox



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# Preface

This book is designed for use by undergraduate and graduate students in courses on the algae and aquatic ecology, as well as by researchers and professionals in the fields of aquatic ecology and technological applications of algae. This text includes extensive photographic illustrations and provides detailed descriptions of representative algal genera. Professor Paul Silva, University of California-Berkeley, graciously researched the etymologies of the generic names of these representative forms that are included with the descriptions. Terms defined in the glossary appear in boldface in the text.

This book covers freshwater, marine, and terrestrial forms. For the student this provides the widest possible background, and thus greater flexibility in research options and when entering the job market. Our wide ecological treatment allows discussion of some important algal transmigrations. Furthermore, considerations of algal biodiversity and evolutionary topics also require coverage of forms that occupy a wide range of algal habitats.

Distinctive features of this book include a series of five introductory chapters designed to stimulate student interest and to provide an overview of the importance of algae. A survey of algal habitats, general characteristics, nutritional variation, and life-history types constitutes Chapter 1. Chapter 2 is focused on the roles of algae in global biogeochemistry and algal influences on present and past climates and atmospheric chemistry. Chapter 3, which considers biotic associations involving algae, includes discussion of herbivory interactions, algal food quality, predatory algae, pathogens of algae, algae as pathogens, and herbivory- and pathogen-defense adaptations. A chapter on technological applications (Chapter 4) includes discussion of algae grown for use as food and in the production of industrially useful materials, mariculture of economically useful algae, and applications of algae in effluent treatment and space technologies. We have, in Chapter 5, provided a primer on modern approaches to algal systematics, including coverage of major molecular systematic techniques and procedures commonly used to evaluate the significance of phylogenies. Already essential in studies of algal evolution, molecular phylogenetics will increasingly be added to the repertoire of algal ecologists. Operating under the assumption that students may be familiar with major algal groups but not with generic names, we have routinely coupled descriptive modifiers with generic names of algae in the five introductory chapters.

Another distinctive feature of this text is a chapter (Chapter 7) on the topic of endosymbiosis—an extremely widespread and ecologically important natural phenomenon that is the mechanism by which the eukaryotic algal groups arose. We believe knowledge of this subject to be essential for understanding differences in physiological and ecological behavior among protist groups. Chapter 7 provides an introduction to the eukaryotic algae. A core group of 15 chapters (Chapters 6 and 8–21) focuses on one or more groups of related algae. Each chapter includes group-specific structural, physiological, evolutionary, and ecological information. This book concludes with two chapters that provide brief synthetic treatments of phytoplankton ecology (Chapter 22), contributed by Dr. James Graham, and periphyton and seaweed ecology (Chapter 23).

Throughout this book we have included examples of new findings and approaches in algal molecular biology. Many instances of recently discovered algal forms are provided to demonstrate that algal biodiversity is incompletely known and that unknown forms await discovery by the curious and prepared investigator. We have provided somewhat more detail regarding the ultrastructure of flagellar apparatuses of algae than is found in many introductory texts, because such information is often essential (as are pigment and molecular sequence data) for the detection and classification of new forms. There is also an emphasis on algae of extreme habitats, in view of recent widespread interest in exotic biodiversity and its possible relevance to extraterrestrial biology (exobiology or astrobiology).

We have not provided taxonomic keys to the algal genera described due to space constraints and because we believe that the correlative use of more comprehensive, locally relevant taxonomic keys is a better alternative. Further, we have provided class, order, and family classifications only when these are supported by both classical and molecular data. References are provided to classification systems currently in use for the major groups, but we have avoided detailing those that have as yet not been tested by application of molecular phylogenetic methods. Colloquial names referring to members of phyla (divisions) are given the suffix "phyte" and members of classes, "phycean."

We have arranged algal groups in order of their phylogenetic divergence (antiquity), as inferred primarily from nuclear SSU rDNA gene sequences. The red algae are a possible exception, their phylogenetic position being currently controversial. We have placed the chapter on red algae between chapters covering brown and marine green algae for the convenience of users in coastal regions where brown, red, and green algae often co-occur. Each chapter is designed to stand alone—the content not depending on that found in other chapters (except Chapter 1)—so that Chapters 2 through 23 may be read in any order.

We have tried to incorporate both very recent and older classic references to research literature from around the world, but have been unable to provide a comprehensive review of the literature due to space limits. Further, we have attempted to reference work accomplished by investigators throughout the world, though few works in languages other than English are cited. Although there is much useful information on algae available on the internet, we have chosen not to include website addresses because of their volatility. We have commonly placed literature citations at the end of a series of relevant sentences to facilitate uninterrupted flow of thought. We would be pleased to receive recommendations of critical literature citations that might be added to a later edition.

Numerous phycologists from around the world graciously contributed original photographs to this project. Contributors are cited in the figure captions. As a token of our appreciation for the use of these images as well as the use of line art, we pledge a substantial contribution arising from book royalties to the International Phycological Congress for use by students for travel to congress meetings.

We are also grateful to Kandis Elliot, UW-Madison Department of Botany artist, who provided technical advice; the staff at Prentice Hall, particularly our editor, Teresa Ryu, and production editor, Kim Dellas; the UW-Madison Biology Library staff; and Professors Jane Gray, University of Oregon, and Ron Hoham, Colgate University, who provided reviews of limited material at our request. The following people were commissioned by Prentice Hall to review one or more book chapters, and we are very appreciative of their helpful efforts:

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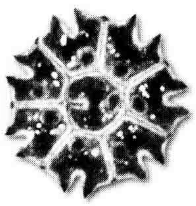
# Brief Contents

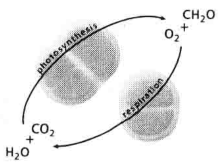
# Contents





## 1 Introduction to the Algae—Occurrence, Relationships, Nutrition, Definition, General Features 1





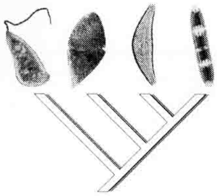

## 2 The Roles of Algae in Biogeochemistry 22



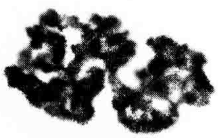
## 3 Algae in Biotic Associations 40



## 4 Technological Applications of Algae 64

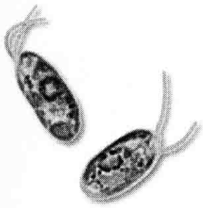




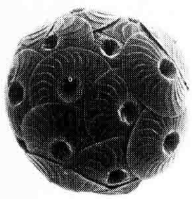




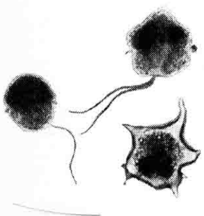




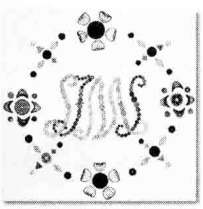


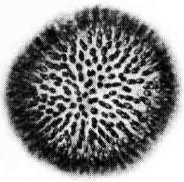




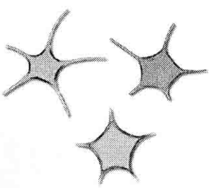


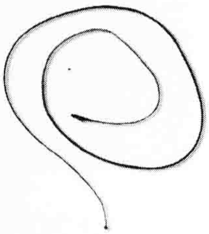




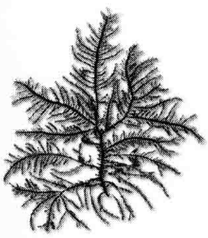




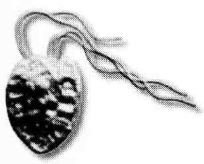


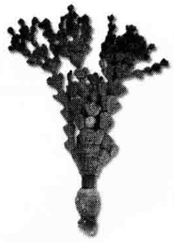




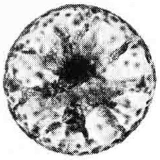




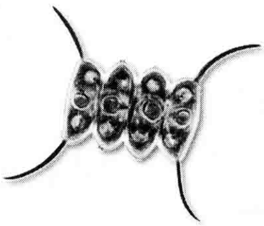




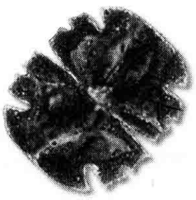




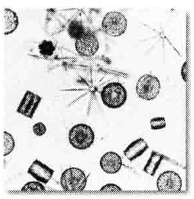






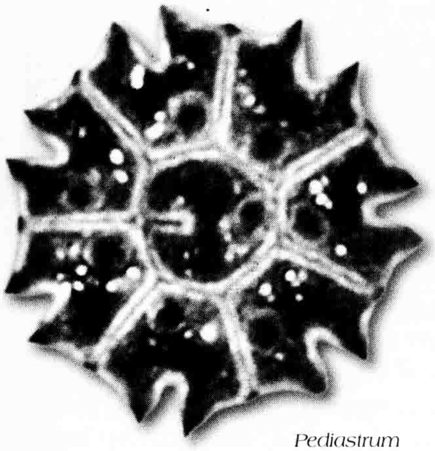






## 23 Macroalgal and Periphyton Ecology 603

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.)

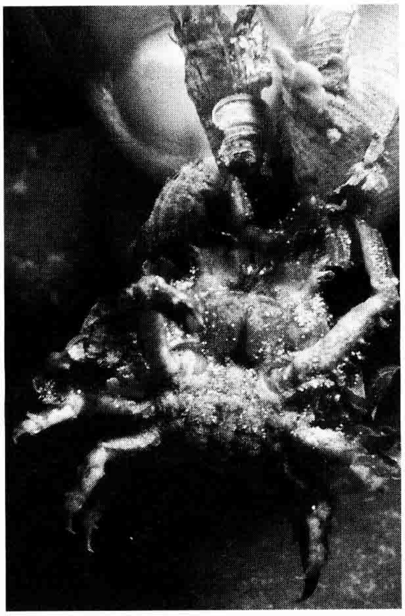


Figure 1–3 A small decorator crab with various attached algae.

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)

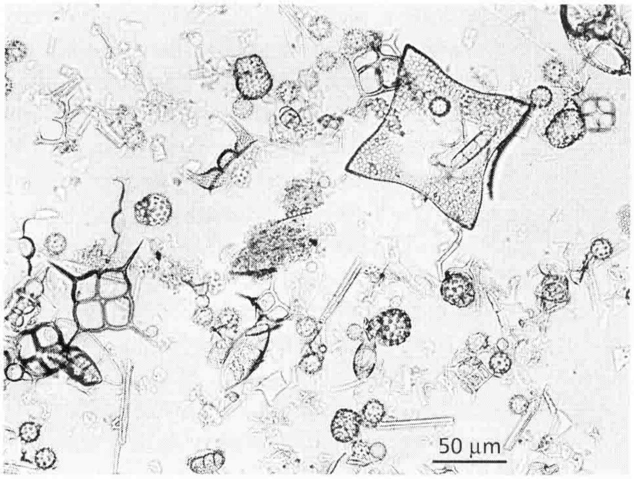



**Figure 1–5** Sedimented phytoplankton from the late Cretaceous and early Cenozoic Arctic Ocean, including silicoflagellate and diatom remains. (Specimen courtesy D. Clark)

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.

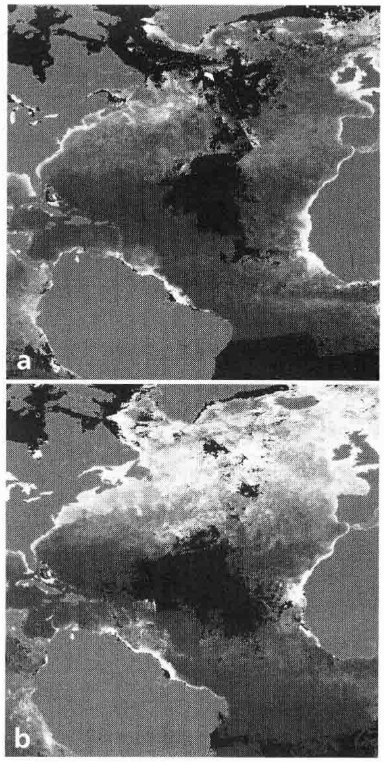



**Figure 1–6** Two NASA satellite images of the North Atlantic taken in (a) winter and (b) spring. Brighter areas represent higher concentrations of chlorophyll and, hence, phytoplankton. Totally black areas are regions for which data were not collected.

## 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

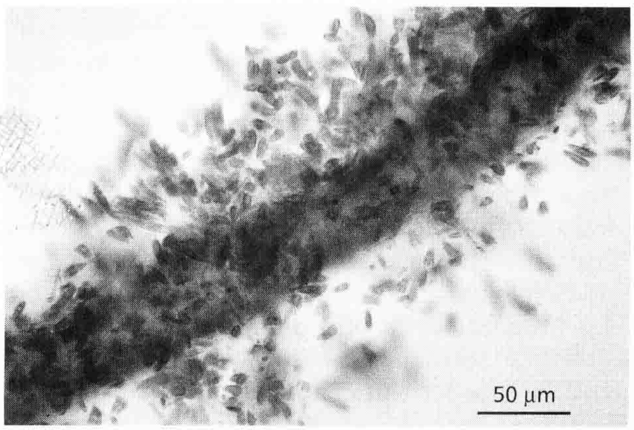



**Figure 1–7** A specimen of the freshwater green alga *Oedogonium* with large numbers of epiphytic diatoms.