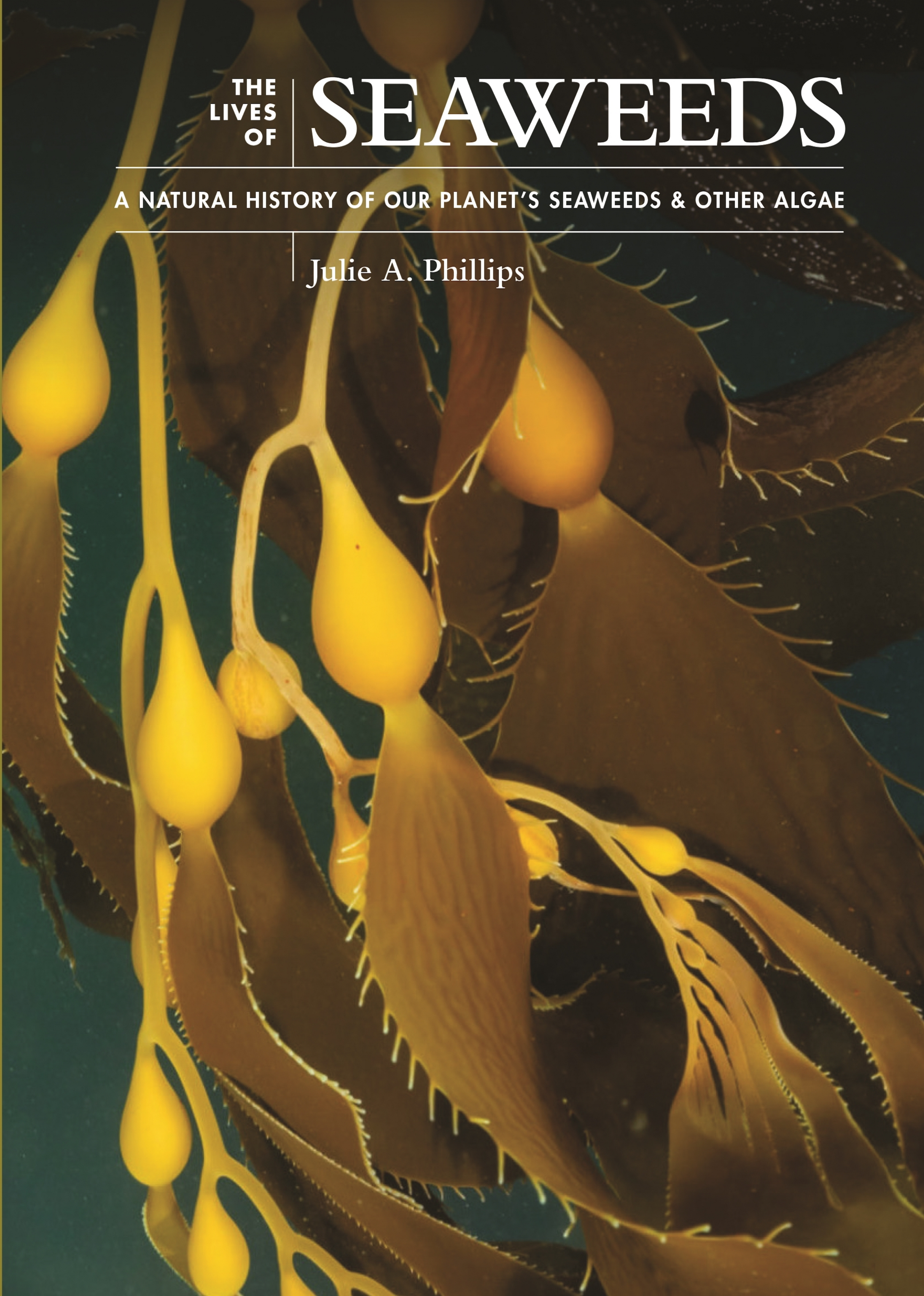


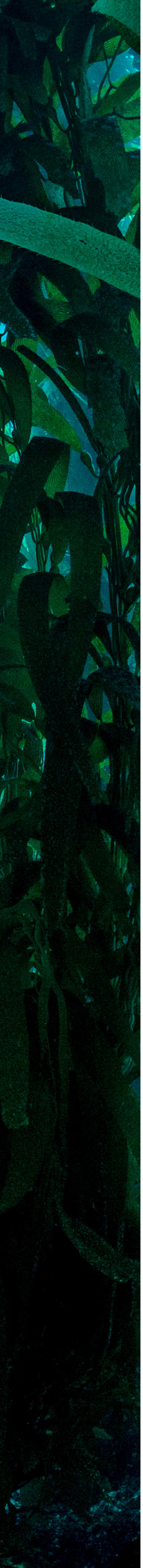
THE LIVES OF SEAWEEDS

A NATURAL HISTORY OF OUR PLANET'S SEAWEEDS & OTHER ALGAE

Julie A. Phillips

THE LIVES OF

SEAWEEDS



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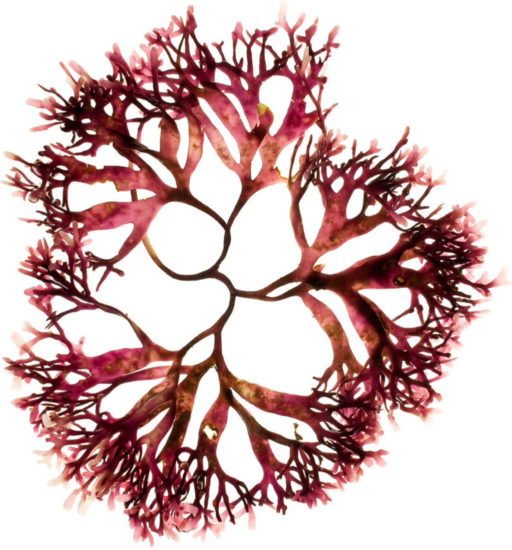

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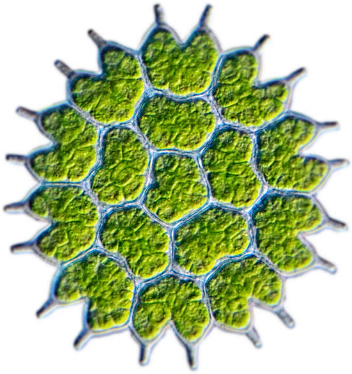

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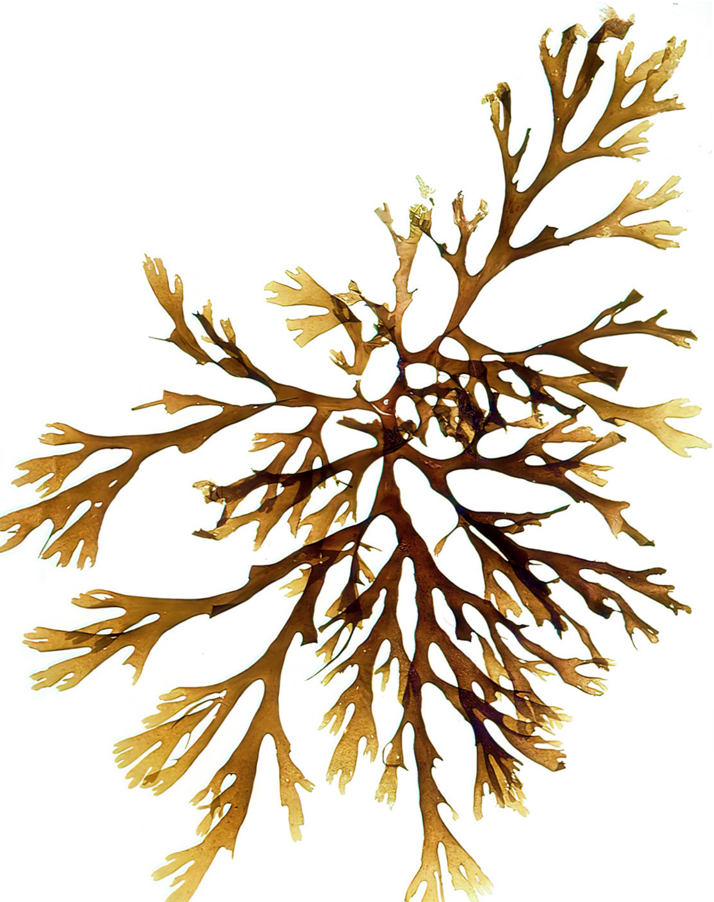


The algal world

Loved by the Japanese, seaweeds have long been integrated into their cuisine, Shinto religion, and literature. Ladies of Victorian England made beautiful, pressed seaweed pictures and albums. Delicious sushi rolls with their nori seaweed wraps are a twenty-first-century global culinary obsession. The Red Sea and Sargasso Sea are named after algae. Seaweeds and other algae have a multitude of uses as food, in industry, and in medicine. Since time immemorial, algae have enriched the lives of humans, but these endlessly fascinating organisms also play a pivotal role globally in sustaining life on Earth.

Since prehistoric times, coastal people worldwide have foraged along their seashores harvesting seaweeds for food. Nowadays, the nutritious seaweeds are still eaten in many countries, more so in Japan, China, and Korea than in Norway, Britain, the United States, and Canada. Seaweeds have health benefits far beyond their macronutrient content, with some containing 10 to 100 times more minerals and vitamins per unit dry weight than terrestrial plants and animal-derived foods. Furthermore, dietary studies have reported significantly fewer obesity and diet-related diseases in Japan where seaweeds are regularly consumed, suggesting a strong link between seaweed consumption and good health.

Not only do the Japanese eat a larger quantity of seaweeds than other nationalities, they also ingeniously use them to enhance the flavors of other foods. Dashi stock, made from the fish, bonito, and the kelp, konbu, provides the sensational fifth (after sweet, sour, salt, and bitter) taste of umami, the “deliciousness” that underpins the famous Kyoto cuisine.

Several seaweed species are important in Shinto ceremonies and festivals, offered as food to the kami (gods). It is a Shinto belief that shaking, touching, and eating the brown seaweed *Sargassum* cleanses and purifies the human body. Interestingly, modern science has found that *Sargassum* and some other large brown seaweeds contain many bioactive chemical compounds that have potential health benefits owing to their antioxidant, anticancer, antibacterial, and anti-inflammatory properties.

The high regard the Japanese have for seaweeds is also apparent in their literature, in which seaweeds are used as metaphors to express feelings of love, compassion, truth, and sensuality. Even the famous *Tale of Genji*, written by the noblewoman Murasaki Shikibu in early eleventh-century Kyoto, possibly the first novel in world literature, has a romantic poem that mentions seaweed:

The world of the fisher folk
Might I hear it from afar?
The beach at Suma,
Seaweed-salt droplets fell,
For who, if not you . . .?

→ Title pages in Victorian-era seaweed albums were often decorated with a poem and a frame of artistically arranged seaweeds. During pressing and drying, the mucilage in their cell walls glued the seaweeds onto the paper sheets.

FLOWERS OF THE SEA.

CALL us not weeds, we are Flowers of the Sea,
For lovely, and bright, and gay-tinted are we;
And quite independent of culture or showers;
Then call us not weeds, we are Ocean's Gay Flowers.


2.
5.
3.
4.
6.
7.

SEAWEEDS AND OTHER ALGAE

Visible to the unaided eye, seaweeds, also called marine macroalgae, are the familiar macroscopic algae that inhabit rocky seashores. Less well known are the pondweeds, the macroalgae of freshwater lakes, rivers, ponds, and streams. Seaweeds and pondweeds are lumped together by their habitat, but actually they belong to five different evolutionary lineages partially distinguished by the dominant pigment that colors the alga blue-green (phylum Cyanobacteria), red (phylum Rhodophyta), green (phylum Chlorophyta, phylum Charophyta), or brown (class Phaeophyceae).

The body of a macroalga (seaweed and pondweed) is called the thallus; it has a simple structure. In most macroalgal species, one part of the thallus resembles the rest, as is evident in the netlike thallus of the red seaweed *Claudea elegans*. Notable exceptions are some large brown seaweed species that have rootlike, stemlike, and leaflike structures composed of similar types of tissues. Macroalgae do not have true roots, stems, and leaves. These structures evolved in the land plants as adaptations to life on land and are composed of highly differentiated tissue types, which are involved in transporting water (xylem) and sugars (phloem) around the plant, providing structural support, and reducing water loss.

Seaweeds and pondweeds exhibit an amazing diversity in form, ranging from small, barely visible filaments and crusts on rocks to the largest of the giant leathery kelps 164 ft (50 m) long.

In addition to the macroalgae, there are far greater numbers of microscopic, unicellular algal species, often referred to as "microalgae." These species, which belong to several different evolutionary lines (lineages), are well represented in diverse habitats, most notably in the hidden invisible world of the phytoplankton, floating or swimming in the sea, and in inland waters. Even three phyla with many macroalgal species also contain microalgae. Numerous microalgal species are recorded for the green algae (phylum Chlorophyta and Charophyta) and the phylum Cyanobacteria, compared to the relatively small numbers for the Rhodophyta.

← This nineteenth-century hand-colored lithograph illustrates the exquisite netlike red seaweed *Claudea elegans*, which curls gracefully near its tips and whose reproductive structures (2–7) form within the net.

→ The firm hollow sac of the green bubble weed (*Dictyosphaeria cavernosa*) is formed of one layer of large cells clearly visible to the unaided eye.

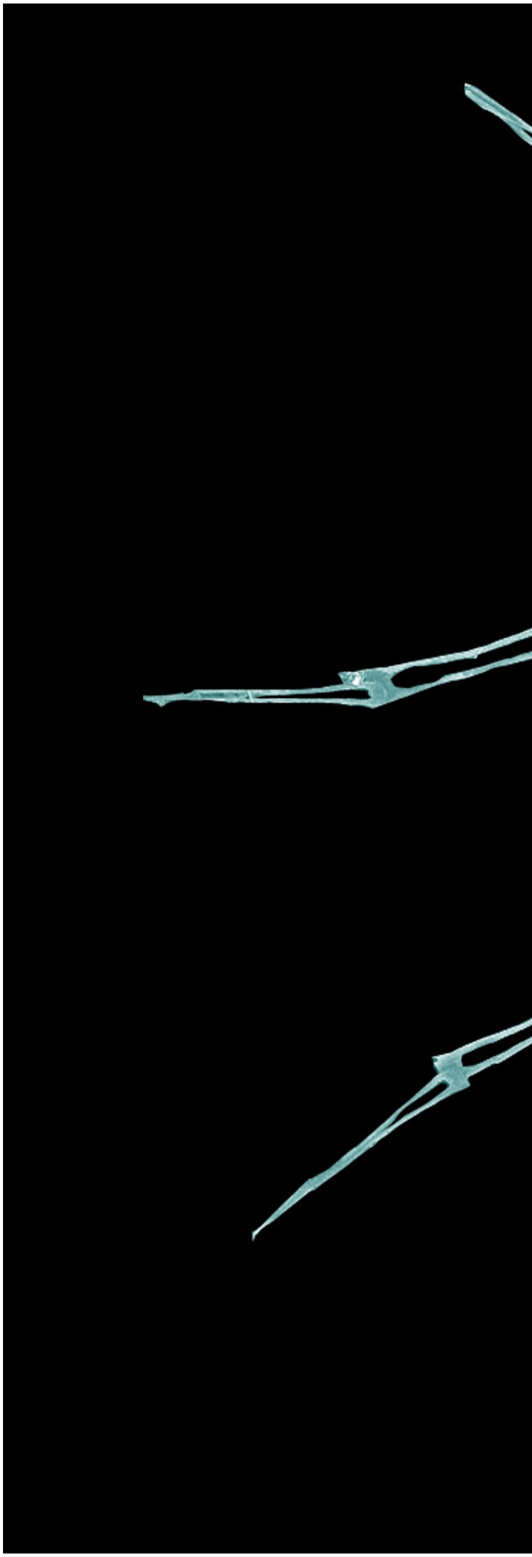
WHAT IS AN ALGA?

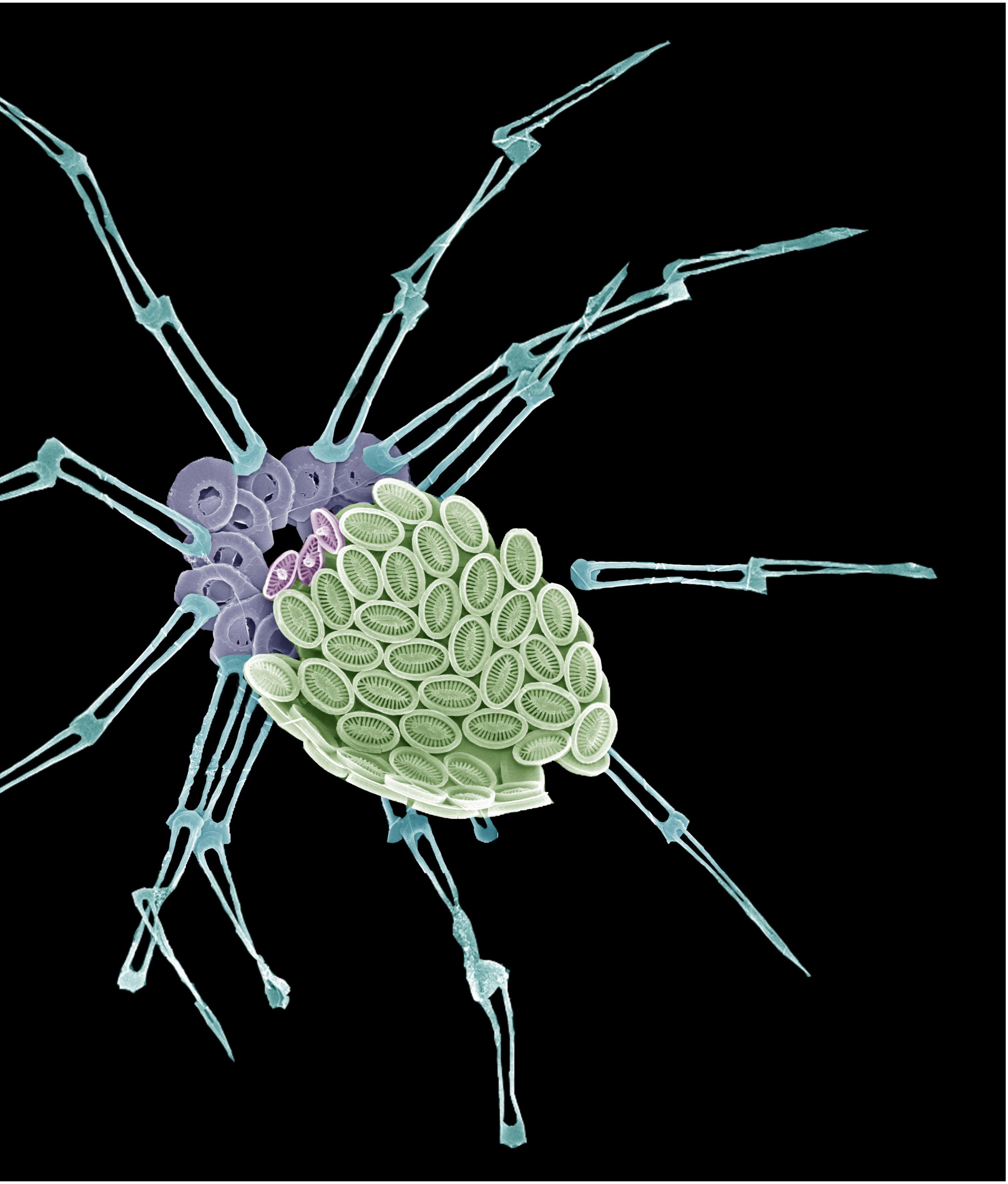
The scientists who study algae are called phycologists. They are aware of the difficulties in defining the most megadiverse group of living organisms on Earth, well illustrated by the bizarre animallike unicellular alga *Michaelsarsia elegans*, whose tiny cell is covered by five different types of calcareous scales. For over two centuries, the algae had been defined as photosynthetic organisms that evolved in aquatic environments and, in the case of the macroalgae, never developed the roots, stems, leaves, and flowers that equipped the land plants for life in terrestrial environments. This definition, which is now known to have limited evolutionary significance, was reinforced by the two kingdom classification scheme that operated prior to the 1960s. In this scheme, the animals were assigned to the kingdom Animalia and all other living organisms (the land plants, algae, fungi, and bacteria) to the kingdom Plantae. It is now acknowledged that many algal groups are not closely related to the land plants or fungi.

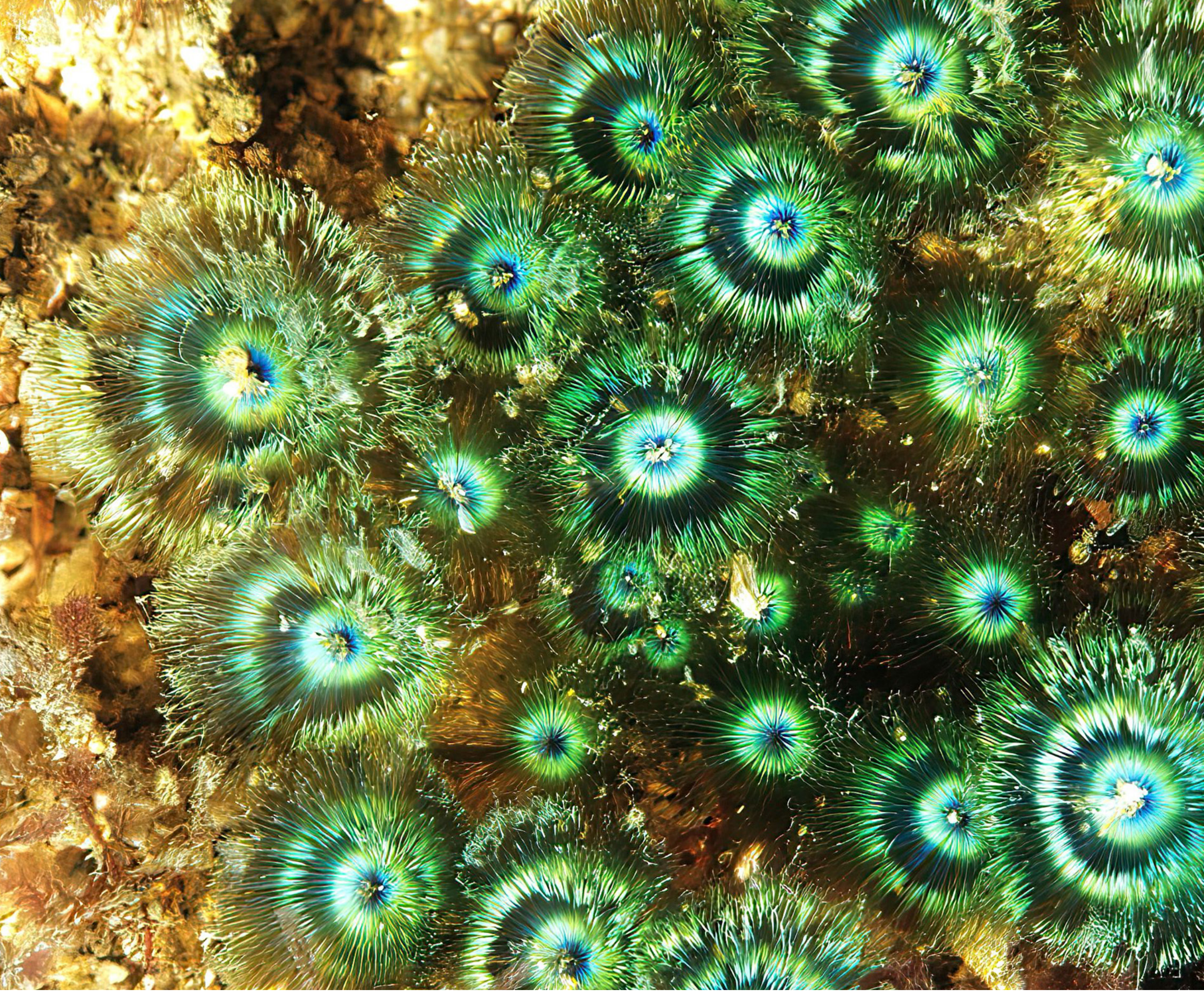
By contrast, the land plants (the mosses, ferns, gymnosperms, and flowering plants) are genetically related to each other, a monophyletic group that originated from a common ancestor—a freshwater green alga. It is possible to trace the evolution of the land plants from a freshwater green algal ancestor through the mosses, ferns, and gymnosperms to the flowering plants, fulfilling the requirement that biological classification must be based on the evolutionary history of the organisms.

During the 1960s, a few biologists were fervently challenging the validity of the two-kingdom classification scheme. Fortuitously, two new techniques, electron microscopy (or ultrastructural) and DNA molecular studies, began generating exciting and new irrefutable evidence, ultimately proving two decades later that the algae had evolved from different ancestors and therefore are polyphyletic. From the 1960s to the 1990s, several new classification schemes were proposed, but most were subsequently found to have marked shortcomings until one, finalized in 1998 and widely accepted since, recognized six kingdoms of life for the planet.

→ False-colored electron microscope image of the golden-brown alga *Michaelsarsia elegans*.



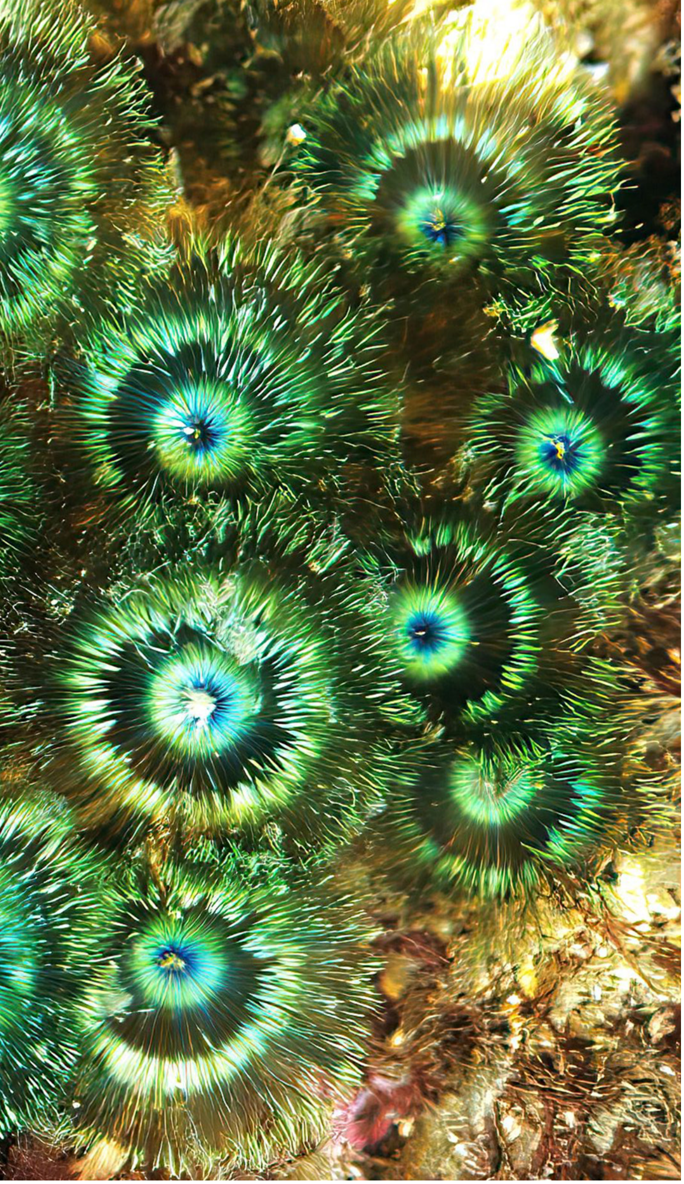




FOUR OF SIX KINGDOMS

The new classification scheme radically changed the higher (kingdom to class) levels of classification of the algae, assigning algal species to four of the six kingdoms. The blue-green algae are actually blue-green bacteria, the only algal phylum classified in the kingdom Bacteria. The red algae (Rhodophyta) and green algae (Chlorophyta and Charophyta) are plants and are assigned to the kingdom Plantae; the euglenoids, a group of unicellular green microalgae, to the kingdom Protozoa; and the brown algae (Phaeophyceae) and many microalgal groups to the exclusively algal kingdom Chromista. Brown seaweeds that include the spectacular *Tomaculopsis herbertian*a are the most familiar members of the kingdom Chromista. Only the kingdoms Animalia and Fungi lack algal species.

The classification of the algae is rigorous, based on several independent lines of evidence derived from morphological, biochemical (pigment composition, storage carbohydrate, and cell wall composition), ultrastructural (structure of the cell wall, motile cells), and, since the 1990s, DNA sequence data. Morphological and anatomical characters are observed with the light microscope at magnifications to 1,000



← The brown seaweed *Tomaculopsis herbertiana* is spectacularly iridescent. Each tuft of radiating hairlike filaments emits gorgeous hues of brilliant blue and green.

times and ultrastructural characters with the electron microscope at magnifications to 100,000 times.

The number of algal species currently existing on Earth remains unknown. An inventory lists 32,260 of an estimated 43,918 described algal species, a number that many phycologists believe is far from complete. They consider that the known algal species will increase by a factor of four to eight once poorly known geographical regions and habitats are surveyed and after cryptic species, defined as several morphologically similar species masquerading as one, are identified by DNA sequencing studies.

WHAT ARE PHOTOTROPHS, HETEROTROPHS, AND MIXOTROPHS?

Living organisms are often described by their mode of nutrition as phototrophs, heterotrophs, or mixotrophs. Long characterized as photosynthetic organisms, the majority of algal species are indeed phototrophs, defined as deriving their nutrition from photosynthesis: a process that produces the organic compound glucose by directly capturing the sun's energy. The growth of phototrophs is largely limited by temperature and the availability of light and the nutrients nitrogen and phosphorus.

However, not all algae are phototrophs. Some algal species are heterotrophs. They are incapable of photosynthesis and derive their energy from consuming organic compounds or other living organisms. Still other algal species are mixotrophs, capable of both phototrophic and heterotrophic modes of nutrition, the balance between these modes also varying. Some mixotrophs switch to absorbing organic matter when the light is too low for photosynthesis, while others need to both eat other organisms and photosynthesize to survive.

The algae are unique in having species classified in four of the six kingdoms of life. Algal species exhibit a great diversity in form, from the weird to the wonderfully beautiful. They live in almost every habitat on Earth, from the stable and favorable subtidal habitats in shallow seas to inhospitable acidic hot springs. Various algal species drive the global biogeochemical cycles that make the planet habitable. This book provides a snapshot of the exciting megadiverse world of the algae.

EVOLUTION

Billions of years of algal evolution

How phycologists unraveled the amazing evolutionary history of the organisms traditionally assigned to the algae is a remarkable story. The evolution of the algae—and indeed all plants—began around 3.5 billion years ago, when cyanobacteria (formerly called blue-green algae) were among the first living organisms on Earth.

THE ARCHEAN LANDSCAPE

Imagine being transported back 3.5 billion years in time into the landscape of the Archean eon. Having originated 1 billion years earlier, Earth was a harsh environment that was inhospitable to life as we know it today. Water was abundant and had formed the oceans. There was a significant amount of volcanic activity and the atmosphere was composed mostly of nitrogen and carbon dioxide, with little or no oxygen. At this time, bacteria that used substances other than oxygen for respiration were the only life on the planet capable of surviving in the low-oxygen environment.

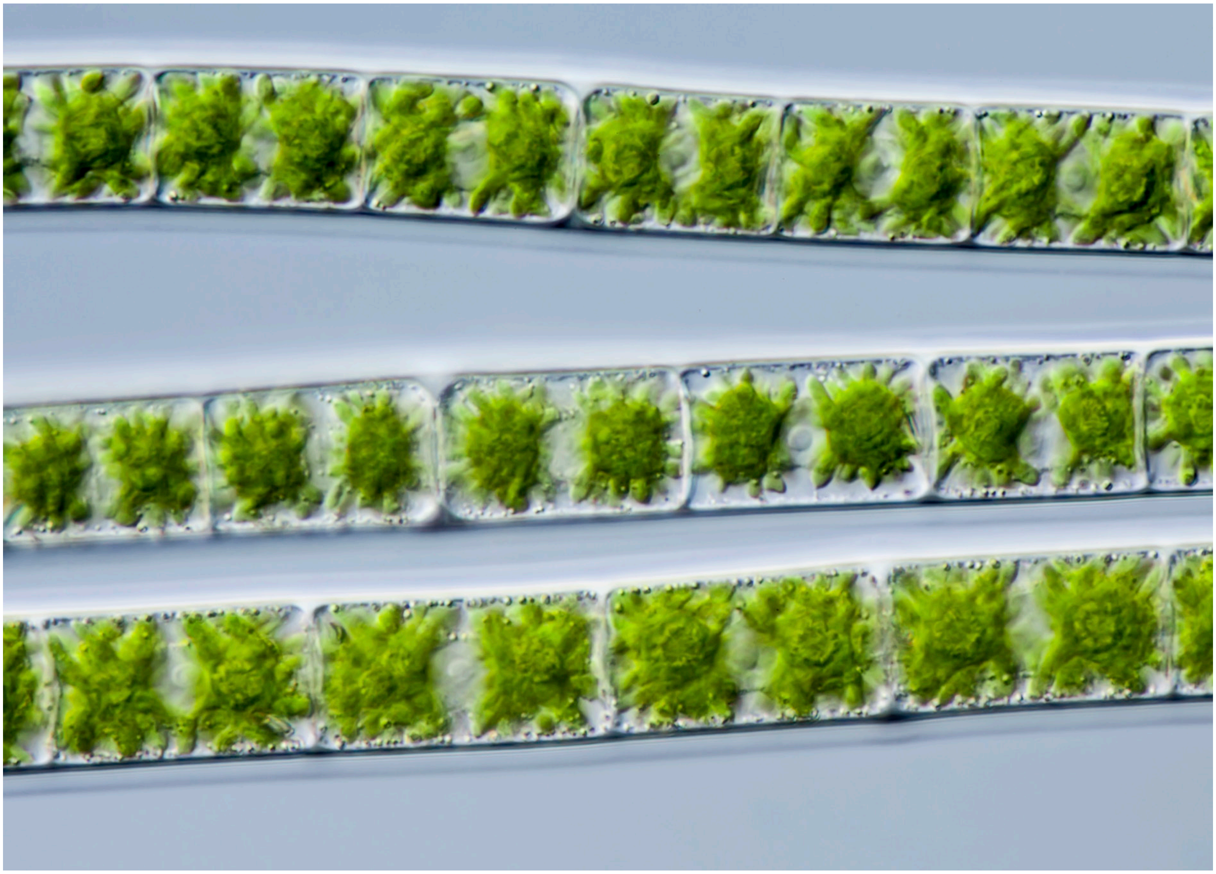
In this primeval soup, one type of bacteria—the cyanobacteria—would have a profound effect on the evolution of life. Cyanobacteria are responsible both for releasing oxygen into the early atmosphere and for the evolution of all organisms on Earth that possess plastids. Plastids are membrane-bound structures (organelles) found in the cytoplasm of the majority of algal and plant cells and, importantly, are the site of photosynthesis. Uniquely positioned as the first oxygenic photosynthetic organisms on Earth, the cyanobacteria synthesized glucose and liberated oxygen into the atmosphere as the by-product. Around 2 billion years ago, cyanobacterial photosynthesis had expelled so much oxygen into the atmosphere that it could support the evolution of nonbacterial life. It might sound like the premise of a science fiction movie, but around this time a colorless cell engulfed and took a cyanobacterial cell into its cytoplasm, where it became a plastid. By acquiring a plastid, the colorless cell was transformed into the first plant cell on Earth that

subsequently gave rise to three algal lineages. This was not a one-off occurrence; it happened again, many times over, some as recently as 250 million years ago. On these occasions, colorless cells engulfed and enslaved either a red or a green algal cell, which became the plastids for six more algal lineages. It is amazing to think that plastids not only played a pivotal role in the evolution of life on Earth, but through photosynthesis have driven a range of important natural processes and helped shape the global economy.

↑ The first life-form on Earth, the moundlike stromatolites evolved in Earth's inhospitable aquatic environments in the Archean eon 3.5 billion years ago.

Symbiotic theory of algal evolution

Different types of plant plastids have long been recognized. The well-known chloroplasts of the land plants are different to the red plastids of the red algae, the brown plastids of the brown algae, and the colorless plastids of plant roots and plant parasites. However, the full extent of plastid diversity and the pivotal role that plastids played in algal evolution has only been realized in the last five decades.



SYMBIOSIS

As early as the 1880s and again in the early 1900s, some botanists proposed the radical theory that plastids had originated by symbiosis, a situation in which two different organisms live together in close association. In this symbiosis, a cyanobacterium (as a plastid) lives inside a colorless cell; both the cyanobacterium and the cell benefit from the association. The cyanobacterium receives protection, carbon dioxide, and nutrients (nitrogen and phosphorus) from the cell, which, in turn, receives the products of photosynthesis (glucose and oxygen) from the cyanobacterium.

Their symbiotic theory would take 100 years to prove. The early evolution of the algae had taken place inside cells and could only be investigated from the late 1950s after the invention of electron microscopy and DNA techniques. Over the following decades, these new techniques began accumulating evidence piece by piece that documented the differing structure and the genetic relationships of algal plastids.

Plastids have long fascinated botanists. Between 1846 and 1885 they reported the astounding observations that the plastids of various algal species proliferated by dividing into two (the same pattern of cell division—binary fission—that characterizes the bacteria), rather than dividing when their cell divided by mitosis. Botanists also suggested that plastids were passed from generation to generation through the female gamete. This information led the German ecologist A.F.W. Schimper to surmise in his 1883 paper that plastids and their host cells were somewhat symbiotic, and that green plants may have originated through the "unification of a colorless organism with one uniformly tinged with chlorophyll."

In 1905, Constantin Mereschkowsky, a Russian botanist from a small German university, proposed that plant cells acquired their plastids when a photosynthetic bacterium was engulfed by an animal cell, giving rise to the three main branches in the plant kingdom: the red, green, and brown algae. Mereschkowsky not only compared plastids to "little green slaves" that harnessed sunlight to provide their hosts with energy, but also identified other aspects of the symbiosis. He observed that the plastids were transmitted from generation to generation, continued to function in cells whose nucleus had been removed, lived in the cells of animals such as *Amoeba* and *Hydra*, and resembled the lower forms of cyanobacteria. These were astute observations, made at a time when laboratory equipment was primitive and more than 25 years before the vast differences between bacterial and nonbacterial cells were first proposed. However, while Mereschkowsky's symbiotic theory was initially accepted, after World War I it was dismissed as being based on wild speculation. Relegated to a fringe hypothesis, it was largely neglected for decades to come.

← Microscopic plastids, including the star-shaped chloroplasts in cells of the freshwater green alga *Zygnema*, have played a central role in algal evolution.

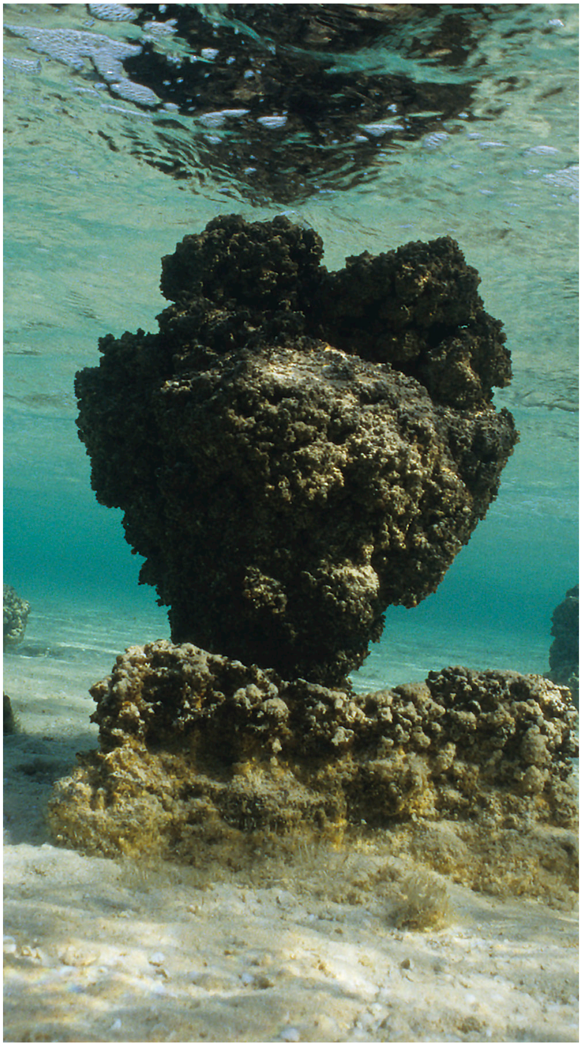
Cyanobacteria and stromatolites

The important role that cyanobacteria played in the evolution of early life on Earth has been preserved in the fossil record. The ancient cyanobacteria that inhabited shallow marine environments grew in mats, forming layered microbial communities called stromatolites. The 3.5-billion-year-old stromatolites found in the Archean rocks in Western Australia's Pilbara region—the oldest identifiable fossils on Earth—are crucial to our understanding of the origins of life on the planet.

LIVING FOSSILS

Although they were rare in the Archean eon, stromatolites became more abundant when shallow marine environments expanded around 2.5 billion years ago. About 850 million years ago, they became the dominant life form on Earth, peaking in abundance before experiencing a sharp decline some 570 million years ago but persisting until the present. Modern stromatolites are constructed by cyanobacteria as well as other more recently evolved algae. Today, these living fossils can be found in the United States, the Bahamas, the Persian Gulf, the Red Sea, and Australia. However, their distribution is often restricted to extreme environments that are similar to those of the Archean eon, such as the thermal springs of Yellowstone National Park, the hypersaline Great Salt Lake in the United States, and Hamelin Pool in Australia's Shark Bay, where the toxic salinity is around twice that of seawater.

Cemented to the underlying rock platform, stromatolites are dark-green, stony, domed mounds that reach around 2 ft (60 cm) in height—some project above the water's surface, while others grow fully submerged. These organo-sedimentary structures are formed when the gluelike mucilage produced by the mat-forming cyanobacteria and the other algae living in the spongy upper surface (the organic



component) trap, bind, and deposit sediment. The cyanobacteria and other algae glide on the mucilage and migrate toward the light, always remaining on the sunlit upper surface of the stromatolite in order to photosynthesize, and to avoid burial by the deposited sediment. Most stromatolites grow extremely slowly. In Hamelin Pool, those with a growth rate of less than 0.04 inches (1 mm) per year have taken hundreds of years to achieve their maximum height of 2 ft (60 cm).

↑ The stromatolite in hypersaline Hamelin Pool, Shark Bay, Western Australia, is not an inanimate rock but a living structure with a soft and spongy upper surface.

↖ The ultimate living fossil, strange moundlike stromatolites have been made by the cyanobacterial inhabitants of aquatic environments for the last 3.5 billion years.

Prokaryotes and eukaryotes

The Cyanobacteria are similar to other algae in their biochemistry and physiology. All algal groups are defined in part by the possession of the green pigment, chlorophyll *a*, and the capacity for photosynthesis. Cyanobacteria are the only bacteria with these characteristics. Furthermore, the Cyanobacteria and the red algae share other biochemical and physiological characteristics including blue-green and red photosynthetic pigments.

STRUCTURAL DIFFERENCES

Despite these similarities between the Cyanobacteria and the red algae, profound differences in the cell structure exist between bacteria—including cyanobacteria—and all nonbacterial life (chromists, plants, animals, and fungi). The differences are far greater than those that exist between plant and animal cells: bacteria are prokaryotes, whereas all other living species are eukaryotes.

PROKARYOTIC CELLS

Prokaryotic cells have a simple level of organization. There are no membrane-bound structures inside the cell. There is no nucleus, only strands of DNA. The cyanobacteria do not have plastids, only many thylakoid membranes—the sites for photosynthesis—on which are situated spherical or disklike structures containing the photosynthetic pigments.

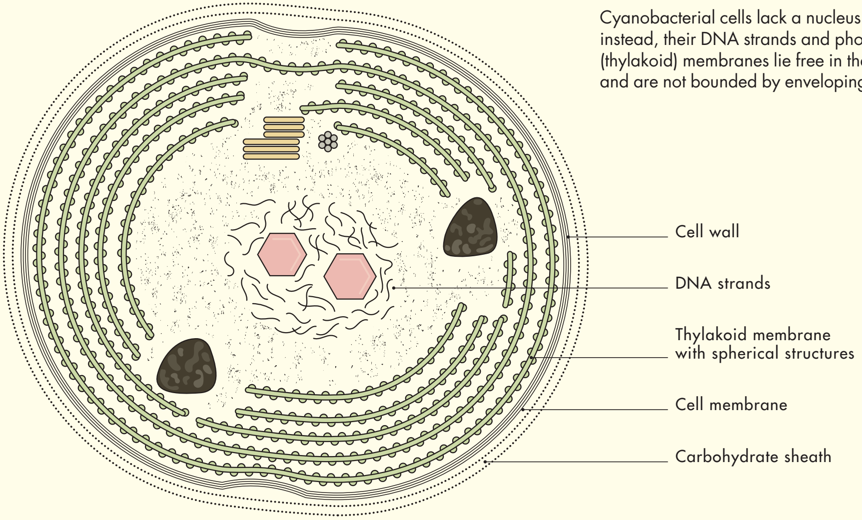
The cyanobacterial cell wall consists of outer and inner membranes that are separated by a carbohydrate and protein middle layer. There is no sexual reproduction. Instead, prokaryotic cells divide into two equal halves through the process of binary fission (a typically bacterial method of cell division).

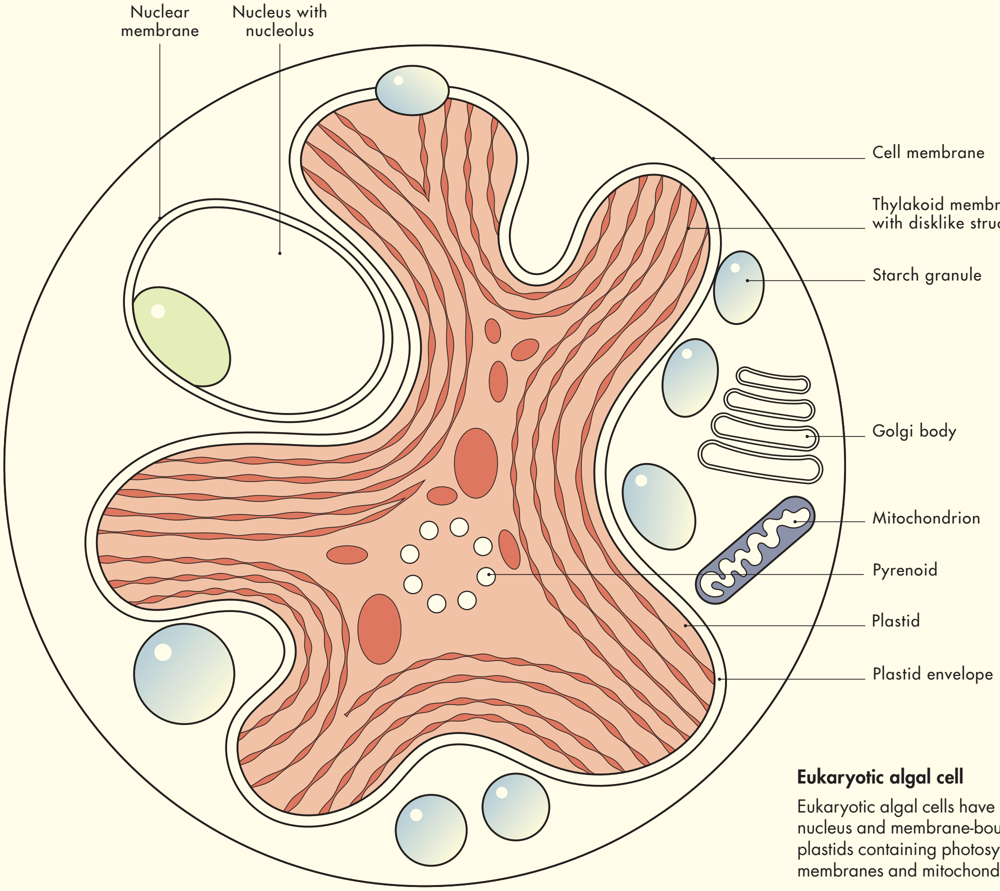
EUKARYOTIC ALGAE

In contrast, the eukaryotic cell has a higher level of organization, which is evident by the membrane-bound structures within it: the nucleus is bounded by two nuclear membranes (the nuclear envelope), the photosynthetic thylakoid membranes are organized into a plastid bounded by plastid membranes (the plastid envelope) and cellular respiration occurs in membrane-bound mitochondria. Unlike the nuclei and mitochondria, which are remarkably uniform structures, the structure of the plastid varies among the algal phyla. The number of membranes in the plastid envelope varies from two to four and the number of thylakoid membranes stacked in the plastid matrix generally varies from one to six. These characters are important in understanding the evolution of the algae. Cells divide by mitosis and produce gametes for sexual reproduction.

Prokaryotic cyanobacterial cell

Cyanobacterial cells lack a nucleus and plastids; instead, their DNA strands and photosynthetic (thylakoid) membranes lie free in the cytoplasm and are not bounded by enveloping membranes.



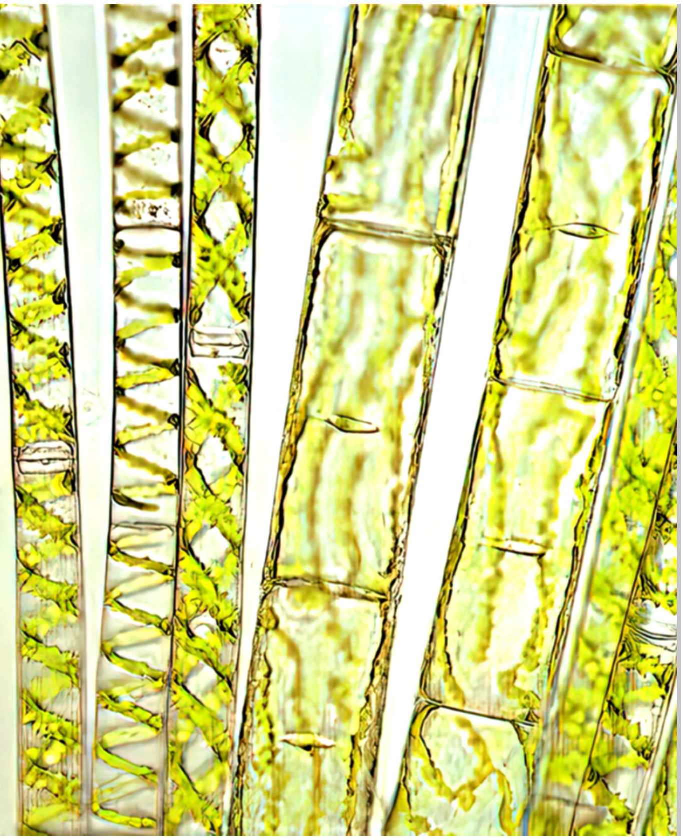


Eukaryotic algal cell

Eukaryotic algal cells have a membrane-bound nucleus and membrane-bound organelles, including plastids containing photosynthetic (thylakoid) membranes and mitochondria.

The symbiotic theory resurrected

The resurrection of the symbiotic theory was largely due to the efforts of the American biologist Lynn Margulis, of Boston University. Based on cytological, biochemical, and paleontological evidence, Margulis revitalized the proposal that plastids and mitochondria arose through symbiosis. Attracting much skepticism, her radical hypothesis was eventually published in 1967 (under the name Lynn Sagan), having been rejected by 15 scientific journals.



THE EVIDENCE

The symbiotic theory had remained out of favor until 1959, when DNA was discovered in the plastid of the green alga *Spirogyra*. Until then, DNA—the genetic material—was thought to only occur in the nucleus. This amazing discovery reignited interest in the symbiotic theory, although some biologists continued to challenge its validity.

More startling revelations followed. *Spirogyra* was only one of many algal and land plant species whose plastids were found to contain DNA. Then, in 1974, great excitement resonated throughout the botanical world when electron microscopy studies revealed the presence of a reduced nucleus in the plastid of a single-celled alga (a cryptophyte).

↗ In the 1960s, biologist Lynn Margulis (1938–2011) began championing, against much early opposition, the new radical theory of algal evolution.

← The 1959 discovery of DNA in the large, ribbonlike chloroplasts of the green alga *Spirogyra* reignited interest in the central role that plastids have played in the evolution of the algae.

The evidence supporting the symbiotic theory continued to accumulate particularly when DNA studies established that the plastid genes in the primitive red algal genus *Porphyra* were most closely related to the genes of the cyanobacteria. The mounting evidence suggested that the plastids of the algae and land plants had originated from a cyanobacterial cell.

THE SYMBIONTS

A huge research effort over the last five decades has established how algal cells acquired their plastids by endosymbiosis, the process by which one symbiont lives inside the other symbiont ("endo" means "inner"). The first plastids of algal cells were acquired when a colorless cell ingested a cyanobacterium that continued to live as an endosymbiont inside the host cell.

One cell ingesting another cell is a common method of feeding employed by unicellular organisms. In this process—known as phagocytosis—the cell membrane forms a pocketlike depression in which the food item is trapped. The membrane surrounding the food pinches off from the rest of the cell membrane, amazingly without disrupting the continuity of the cell surface, to form a membrane-bound food vacuole in the cell. Usually, the food item in the vacuole is digested. However, the endosymbionts that formed the first plastids escaped this fate.

MITOCHONDRIA

Mitochondria are the powerhouses of cells, the sites of metabolic processes including respiration. Mitochondria also originated by endosymbiosis. They were formed when a colorless cell engulfed an oxygen-consuming bacterium. Unlike the many different types of plastids, which were acquired on several occasions, the mitochondrion was acquired only once, given their relative uniform structure in the cells of animals, fungi, algae, and the land plants. This event pre-dated the acquisition of plastids by cells that subsequently gave rise to the algae and land plants.

The evolutionary saga begins

Around 1.5 billion years ago, a colorless cell was feeding when it ingested and enclosed a cyanobacterial cell in a membrane-bound vacuole in its cytoplasm. The cyanobacterial cell became a plastid that transformed the once colorless cell into an algal cell. This event—primary endosymbiosis—was the beginning of an evolutionary trajectory that would result in at least nine different algal lineages.

PRIMARY ENDOSYMBIOSIS

After its capture, the cyanobacterial cell became an endosymbiont that lived in its host's cell. Two cyanobacterial cell membranes envelope the endosymbiont, following the loss of the membrane produced by the colorless cell, to surround the ingested cyanobacterium. The endosymbiont was reduced significantly in size and a large number of its genes were transferred to the host's nucleus. These processes transformed the ingested cyanobacterium into a functional plastid, largely composed of photosynthetic thylakoid membranes. Remarkably, the plastid has been transferred from generation to generation in the host cell.

In primary endosymbiosis, the cell with its newly acquired plastid is the common ancestor to three algal lineages: blue-gray algae, red algae, and green algae. In these three lineages (and the land plants, which are descendants of the green algae), the two cyanobacterial membranes that bound the plastids is an important characteristic that places these organisms in the kingdom Plantae (see pages 32 and 278–279).

THE FIRST THREE ALGAL LINEAGES

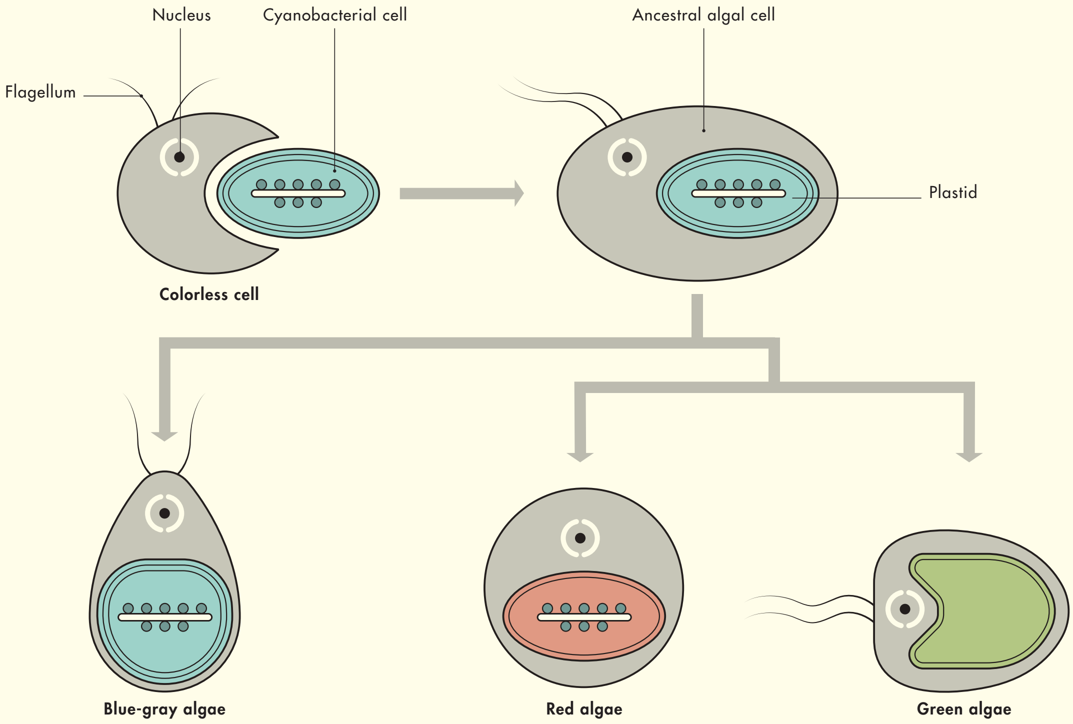
The phylum Glaucophyta (the blue-gray algae) is a group of approximately 15 species of freshwater unicellular flagellates and colonies that form the missing link in the transition between the primitive cyanobacterium and the plastid of the red and green algae. The plastid of the blue-gray algae is bounded by an intact cyanobacterial cell wall with the two membranes separated by the middle protein and carbohydrate layer. Like cyanobacteria and red algae, glaucophytes have blue-green and red phycobilin photosynthetic pigments located in spherical or discoid structures on the surfaces of the single thylakoid membranes.

The phylum Rhodophyta (the red algae) is a large group of predominantly marine macroalgae (seaweeds). Red algal plastids have lost the middle protein and carbohydrate layer that is typical of the cyanobacterial cell wall, but retain the cyanobacterial characteristics of the blue-green and red phycobilin photosynthetic pigments, located in the spherical or disklike structures on the surfaces of single thylakoid membranes.

The phylum Chlorophyta (the green algae) is a large group of unicellular, colonial, or macroscopic plants that live predominantly in freshwater and marine habitats—the green seaweeds are the best-known species. Green algal plastids have lost many of the cyanobacterial characters that are present in the blue-gray and red algae and are characterized by stacks of two to many thylakoid membranes as well as the presence of a new pigment, chlorophyll *b*.

Primary endosymbiosis

From the top left: a colorless cell ingested and retained a cyanobacterial cell, which became the plastid (symbiont) of the first algal cell (top right). The first algal cell was the ancestor of the first three algal lineages: blue-gray algae, red algae, and green algae.



More algal lineages

More than a billion years after the events that resulted in primary endosymbiosis, it happened again, many times, some as recently as 250 million years ago. In this second round of endosymbiosis, a colorless cell ingested and retained a red or a green algal cell that had previously acquired their plastids from a cyanobacterial cell. The ingested red or green algal cell became the plastids of the new algal lineages.

FOUR PLASTID MEMBRANES

Six major algal lineages are recognized to have arisen through secondary endosymbiosis, two of which—the euglenoids (phylum Euglenozoa) and the green spider algae (phylum Chlorarachniophyta)—are derived from a green algal cell, with the remaining four derived from a red algal cell (see pages 32 and 278–279).

Secondary plastids—those that arise during secondary endosymbiosis—are usually bounded by four membranes: the innermost three originated from the ingested cell and the fourth from the colorless cell. The innermost three membranes originated from the two membranes of the plastid envelope and the cell membrane of the ingested green or red alga. The fourth (outermost) membrane was produced by the colorless cell and bounded the vacuole that took the red or green alga into the colorless cell. However, there are always exceptions in biology: the plastids of the euglenoids and dinoflagellates have only three membranes, having lost the cell membrane of the ingested green or red alga.

CHLOROPHYLL *B* ALGAE

Since the mid 1800s, photosynthetic pigments have played a central role in classifying the algae. There are several different kinds of the green pigment chlorophyll, which differ from each other only in their molecular structure. Chlorophyll *b* is found only in the green algae and the lineages that evolved from the green algae: the euglenoids, green spider algae, and the land plants. The euglenoids (phylum Euglenozoa) are a group of unicellular green flagellates that are common in, and largely restricted to, freshwater habitats. There are 2,000 known species, around half of which possess a plastid. The other half are colorless cells that are incapable of photosynthesis and feed either by absorbing soluble organic compounds or by preying on other unicellular organisms. Euglenoid plastids contain chlorophyll *a* and *b*, are bounded by three membranes, and have stacks of three closely appressed thylakoids. Now classified in the phylum Euglenozoa, the parasites that cause African sleeping sickness in humans (trypanosomes) are closely related to euglenoids.