CHAPTER I

INTRODUCTION

Morphology deals with the form and structure of plants. It is concerned with both gross, external features and minute, internal details. It includes a study of the development of plants throughout all their growth stages, called *ontogeny*, as well as their evolutionary development, or *phylogeny*, by means of which all existing plants have been derived from those of past ages. Morphology considers the interrelationships of the groups forming the larger units of classification, but does not deal with species, the study of which belongs to taxonomy. One of the main objectives of morphology is the determination, so far as possible, of lines of descent.

A sound knowledge of the structure and development of plants is a necessary foundation for successful specialization in any phase of botany, whether it be taxonomy, physiology, ecology, pathology, or genetics. A study of the lower plants is often neglected, since the higher ones are more familiar and, in general, more important. Many of the problems encountered in the higher plants, however, are more easily studied in the lower plants, whose structure and functions are much simpler. The logical procedure is to study simple plants before attempting to understand complex plants.

CLASSIFICATION OF PLANTS

For many years the system of classification most widely adopted by botanists has been one in which the plant kingdom is separated into four major divisions: Thallophyta, Bryophyta, Pteridophyta, and Spermatophyta. Each *division* comprises a number of *classes*. A class is made up of *orders*, an order of *families*, a family of *genera*, and a genus of *species*. Categories of intermediate rank are designated by the prefix *sub*.

At one time the two subkingdoms Cryptogamia and Phanerogamia were recognized, the former including the three lower divisions and the latter the fourth division. These names have fallen into disuse because they are inappropriate. *Cryptogam* means "fertilization concealed" and *phanerogam* means "fertilization evident." The names were given because stamens and pistils, the organs once thought to produce directly the cells which unite in fertilization, are present in seed plants but not in plants without seeds. After the true nature of fertilization was discovered, it was found to be actually more evident in the so-called cryptogams than in the phanerogams.

Often all plants above the level of the Thallophyta are grouped together as the Embryophyta, plants in which the zygote gives rise to an embryo that undergoes its early development within either an archegonium or an embryo sac. A less suitable name for these plants, but one sometimes used, is Cormophyta, meaning "plants with a stem." Many bryophytes have a stem, but it is not homologous with the stem of pteridophytes and spermatophytes. Sometimes the bryophytes and pteridophytes are combined into a single group, the Archegoniatae, a name that is not distinctive because archegonia are present in nearly all gymnosperms, which form the lower class of spermatophytes. A recent tendency is to place the pteridophytes and spermatophytes together under the name of Tracheophyta, which signifies that they are vascular plants.

Classification of Thallophyta. Some botanists disapprove of the term Thallophyta on the ground that it includes a heterogeneous assemblage of plants which are not closely related. This objection is more valid when the term is applied to one of the four divisions of the plant kingdom rather than to one of two subkingdoms; for the same objection could be raised against the term Embryophyta. A partial solution of the difficulty is to consider the Thallophyta as a subkingdom and to raise the algae and fungi to the rank of divisions, as follows:

A. Thallophyta
- I. Phycophyta (Algae)
- II. Mycophyta (Fungi)

B. Embryophyta (Cormophyta)
- I. Bryophyta
- II. Pteridophyta
- III. Spermatophyta

The thallophytes comprise a number of subordinate groups. These may either be considered as classes and assigned to the algae or the fungi, or may be distributed among a larger number of divisions. The first arrangement is a convenient one, but some of the groups classified as algae or fungi have little in common with the others. Furthermore, it makes the presence or absence of chlorophyll the basis for establishing the two divisions Phycophyta and Mycophyta, a distinction which cannot be maintained among the flagellates, where both green and colorless forms occur. The flagellates were formerly regarded as constituting a distinct class of thallophytes, but are now broken up into a number of separate groups.

Some of the groups commonly included among the algae and fungi are so distinctive that their separation seems justified. These include the

Cyanophyceae, Schizomycetes, Myxomycetes, Bacillariophyceae, and possibly some of the flagellate groups. The remaining classes of algae might then be retained in one division and the remaining classes of fungi in another, or some or all of these classes might be raised to the rank of divisions. Much difference of opinion exists as to which classes should be placed together.

Two different arrangements for classifying the thallophytes are as follows:

A. THALLOPHYTA

I. Phycophyta[1]	I. Schizophyta
1. Cyanophyceae	1. Cyanophyceae
2. Xanthophyceae	2. Schizomycetes
3. Bacillariophyceae	II. Myxomycophyta (Myxomycetes)
4. Chlorophyceae	III. Bacillariophyta (Diatomeae)
5. Charophyceae	IV. Euphycophyta (Euphyceae)[1]
6. Phaeophyceae	1. Xanthophyceae
7. Rhodophyceae	2. Chlorophyceae
II. Mycophyta	3. Charophyceae
1. Schizomycetes	4. Phaeophyceae
2. Myxomycetes	5. Rhodophyceae
3. Phycomycetes	V. Eumycophyta (Eumycetes)
4. Ascomycetes	1. Phycomycetes
5. Basidiomycetes	2. Ascomycetes
	3. Basidiomycetes

[1] Several other classes, consisting almost entirely of flagellates, are generally recognized. These are the Euglenophyceae, Chrysophyceae, Cryptophyceae, and Dinophyceae.

The elevation of a great number of classes to the rank of divisions, thus making each coordinate with the bryophytes, pteridophytes, and spermatophytes (or even with the tracheophytes, if the last two are combined), tends to conceal relationships and gives a prominent place to small, obscure groups. Moreover, when the names of all the divisions are given the termination *phyta*, in order to make them consistent throughout the plant kingdom, many lose their distinctive meanings, and we find the various groups of algae called Chlorophyta (green plants), Phaeophyta (brown plants), Rhodophyta (red plants), etc.

Classification of Embryophyta. The position of the Bryophyta as a division of the plant kingdom seems secure. Those botanists who classify the higher plants on the basis of vascular anatomy discard the names Pteridophyta and Spermatophyta and designate all vascular plants as Tracheophyta. They point out that a marked tendency toward seed formation was present in several extinct groups of pteridophytes, and that the most primitive group of seed plants, the extinct Cycadofilicales, were very fern-like. The Tracheophyta, constituting a division, are separated into four classes, the Psilopsida, Lycopsida, Sphenopsida, and Pteropsida. The first three correspond to established classes of pteridophytes under the older classification, while the Pteropsida include the ferns (Filicinae), gymnosperms, and angiosperms.

The presence of leaf gaps in the vascular cylinder is thought to indicate a closer relationship between the ferns and seed plants than exists between the ferns and other pteridophytes. However, the basis used in distinguishing the ferns from the gymnosperms and angiosperms, when the three are grouped together as Pteropsida, is the same as when the ferns are placed in the Pteridophyta and the other two groups in the Spermatophyta. Furthermore, if the existing classes of pteridophytes represent collateral lines of descent from the psilophytes of the Devonian, a view widely accepted, their relationship to one another can better be expressed by including them in a division of their own. Certainly no greater degree of relationship is expressed by placing them in a division that also includes the gymnosperms and angiosperms.

The two different schemes of classifying the embryophytes are as follows:

B. Embryophyta

I. Bryophyta	I. Bryophyta
1. Hepaticae	1. Hepaticae
2. Musci	2. Musci
II. Pteridophyta	II Tracheophyta
1. Psilophytinae	1. Psilopsida
2. Lycopodiinae	2. Lycopsida
3. Equisetinae	3. Sphenopsida
4. Filicinae	4. Pteropsida
III. Spermatophyta	*a.* Filicinae
1. Gymnospermae	*b.* Gymnospermae
2. Angiospermae	*c.* Angiospermae

PLANT LIFE OF THE PAST[1]

The plants of today are the modified descendants of other plants that have lived on the earth throughout the course of geologic history. They are the products of a process of evolution that has been in operation since life first began. Our knowledge of the plants of the past has come from a study of fossil remains found embedded in the layers of rock that form the earth's crust. These remains constitute a direct record of the changes undergone by plants down through the ages. This record, incomplete as it is, helps us to follow the course of evolution and to understand the relationships that occur among the various existing plant groups.

It is not known how or when life arose on the earth. It is not even known in what form it arose, although much evidence indicates that the first living things were extremely simple and from them forms more and

[1] This subject is presented in much greater detail in Arthur W. Haupt, An Introduction to Botany, 3d ed., Chap. XXII, New York, 1956.

more complex have been evolved. Some groups have made more progress than others. That is why existing groups are at different levels of development. Along with the tendency toward ever-increasing complexity, much retrogression has occurred and, as a result, some modern groups are more or less degenerate.

Paleobotany, the study of fossil plants, has made great progress because methods have been developed making it possible to study thin sections of petrified material under the microscope. Many of these sections show such an amazing wealth of structural detail that almost as much can be learned from them as from sections of living plants. Unlike petrifactions, fossils in the form of casts or impressions, made when some part of a plant falls into soft earth that later hardens into stone, show no internal structure but preserve many external features. Most fossils are of this kind.

Geologic time, whose total duration is about 2 billion years, is divided into five great eras. The Archeozoic era came first. Then followed, in order, the Proterozoic, Paleozoic, Mesozoic, and Cenozoic eras. Each era is divided into periods. The Archeozoic and Proterozoic, with an estimated duration of 800 million and 650 million years, respectively, comprise nearly three-fourths of all geologic time. Most of the evidence for the existence of life during these two great eras is indirect, consisting of extensive deposits of graphite, limestone, and iron ores, substances that are formed, at least to some extent, by organisms. The earliest plants may have been similar to certain existing bacteria and blue-green algae.

The fossil record of nonwoody plants is very fragmentary. Because of their soft and perishable nature, few have left any direct evidence of their existence. Remains are more numerous of such algae as diatoms, which have siliceous shells, and of lime-secreting seaweeds. Bryophytes have been poorly preserved and their remains are scanty. Vascular plants, on the other hand, are represented by an abundance of well-preserved fossil material, and much is known of the geologic history of many groups.

The fossil record really begins with the Paleozoic era, since so little is known of the life of the Archeozoic and Proterozoic. The periods into which the Paleozoic, Mesozoic, and Cenozoic eras are divided are given in the table on page 6. The figures in the time scale denote millions of years.

Fossil algae furnish the only record of plant life during the Cambrian and Ordovician, and the diversity of types which have been found indicates that all four of the great algal groups were represented in both periods. Silurian deposits have yielded remains of the oldest known land plants, the psilophytes, but these are scanty. During the Devonian so much progress was made, that not only were many kinds of primitive land plants in existence, but even such highly developed forms as large lycopods, ferns, and primitive gymnosperms were abundant.

The Carboniferous was characterized by a wonderful display of plant life. Tree lycopods and horsetails, as well as fern-like and other primitive gymnosperms, formed a most luxuriant growth surpassing even the

Time scale	Periods	Eras
0	Recent	Cenozoic
1	Quaternary	
60	Tertiary	
100	Upper Cretaceous	Mesozoic
125	Lower Cretaceous	
160	Jurassic	
195	Triassic	
220	Permian	Paleozoic
255	Upper Carboniferous	
305	Lower Carboniferous	
355	Devonian	
395	Silurian	
480	Ordovician	
550	Cambrian	

densest tropical jungles of today. The accumulated remains of the plants that lived in the vast Carboniferous swamp forests have formed our most extensive coal deposits.

The plant life of the Mesozoic, except during the Upper Cretaceous, was dominated by the gymnosperms, these being of much more advanced types than had lived during the Paleozoic. Nearly all the large pteridophytes of the late Paleozoic, as well as the primitive gymnosperms, became extinct early in the Mesozoic. A striking feature of the Cretaceous was the rise of the angiosperms, as a result of which they came to dominate the vegetation of the entire earth, a position they have maintained ever since. With the rise of the angiosperms, the gymnosperms have become a subordinate group.

CHAPTER II

THALLOPHYTA: ALGAE

The thallophytes comprise a large and diverse assemblage of simple plants forming the lowest division of the plant kingdom. They number about 88,000 species. The plant body may be unicellular but, where multicellular, as is generally the case, it is a *thallus*—a body without differentiation into true vegetative organs, such as characterize the higher plants. This distinction is not absolute, however, as some of the marine algae have parts that superficially resemble true vegetative organs, while some of the bryophytes have thallus bodies. A more tenable distinction is based on the structure of the reproductive organs. The sporangia of thallophytes, with only a few exceptions, are unicellular; those of the higher plants are always multicellular. The gametangia of thallophytes are prevailingly unicellular but, where multicellular, have no outer layer of sterile cells (except in the Charophyceae). In the thallophytes the zygote does not produce an embryo within the female sex organ, as it does in all the higher groups.

The Thallophyta include two main series, the algae (Phycophyta) and the fungi (Mycophyta), the former with 18,000 species and the latter with 70,000. The algae, having chlorophyll, are able to make food by photosynthesis and so are independent (*autotrophic*) plants. The fungi, lacking chlorophyll, must obtain their food from an external source and so are dependent (*heterotrophic*) plants. This distinction, being physiological, is a convenient one but does not necessarily express relationship; thus it may be without phylogenetic significance. For this reason the various classes of algae and fungi are often regarded as separate and more or less coordinate groups of thallophytes rather than as members of two different series.

Algae live in both fresh and salt water, while a few grow on moist soil, wet rocks, tree trunks, or in other terrestrial habitats. They include the pond scums, kelps and other seaweeds, and a host of less familiar forms. Many are microscopic, but some kelps reach a large size. Because of their perishable nature, algae have left few reliable records of their existence during geologic times. Most of those preserved as fossils are lime-secreting seaweeds and forms with siliceous shells (diatoms). As here presented, the algae are distributed among 10 main classes, the Cyanophyceae, Euglenophyceae, Chrysophyceae, Dinophyceae, Xanthophyceae, Bacillariophyceae, Chlorophyceae, Charophyceae, Phaeophyceae, and Rhodophyceae.

1. CYANOPHYCEAE

The Cyanophyceae,[1] or blue-green algae, are the simplest and lowest group of green plants. They are characterized by having, in addition to chlorophyll and carotinoids, a blue pigment, *phycocyanin*, the combination resulting in a blue-green color. Some of the Cyanophyceae, however, also possess a red pigment, *phycoerythrin*, the presence of which, in varying amounts, produces shades of red, brown, or purple. The Red Sea is said to have received its name from a floating species, *Trichodesmium erythraeum*, which is red and sometimes occurs in such abundance as to color the water. The Cyanophyceae are unicellular plants, the cells being nearly always grouped to form colonies of various kinds. About 1,500 species are known.

The Cyanophyceae comprise two orders: (1) the Coccogonales, whose cells are either solitary or arranged in nonfilamentous colonies; and (2) the Hormogonales, whose cells are in filamentous colonies. Some of the genera belonging to the Coccogonales are *Chroococcus, Gloeocapsa, Merismopedia, Coelosphaerium*, and *Chamaesiphon*. The main genera of the Hormogonales include *Oscillatoria, Lyngbya, Nostoc, Anabaena, Rivularia, Gloeotrichia, Tolypothrix, Scytonema*, and *Stigonema*.

Distribution and Habitat. Blue-green algae are found in all parts of the world where plants can grow. Most of them live in fresh water, some occur on moist earth, rocks, and trees, while others live in the ocean. They commonly form scums, slimy mats, or gelatinous lumps. They are especially prevalent in stagnant water, where large quantities of organic matter accumulate. Some live in hot springs at temperatures as high as 75°C. Many forms extract calcium and magnesium from the water and cause minerals, which are often brightly colored, to be deposited on rocks in the vicinity. Some species of *Nostoc* and *Anabaena* live as endophytes in the intercellular cavities of other plants, as in the thallus of *Anthoceros*, the leaves of *Azolla*, and the roots of cycads. Some blue-green algae enter into the formation of lichens.

The Cyanophyceae living in hot springs thrive under conditions that

[1] Sometimes called Schizophyceae or Myxophyceae. Schizophyceae means "splitting algae"; Myxophyceae means "slime algae." These names are used by some botanists in preference to Cyanophyceae, which means "blue algae," because not all the members are blue-green. But it is also true that some of them lack the slippery feel. As long as we retain the names Chlorophyceae, Phaeophyceae, and Rhodophyceae for other algal groups, we might as well retain the name Cyanophyceae for the sake of uniformity, especially since some of the Chlorophyceae are not green, some of the Phaeophyceae are not brown, and some of the Rhodophyceae are not red. The things most desired in a name are that it shall express the most prominent feature of the group and that it shall be consistent with the names of coordinate groups.

would be fatal to almost all other forms of life. For this reason, because of their simplicity in cellular organization, and because they are autotrophic, members of this group may have lived on the earth before conditions were favorable for the existence of other organisms, with the possible exception of bacteria. Their great antiquity is indicated by the presence, in rocks of Proterozoic age, of what seem to be fossil Cyanophyceae, as well as numerous calcareous deposits resembling those made by blue-green algae now living in hot springs. There is more certain

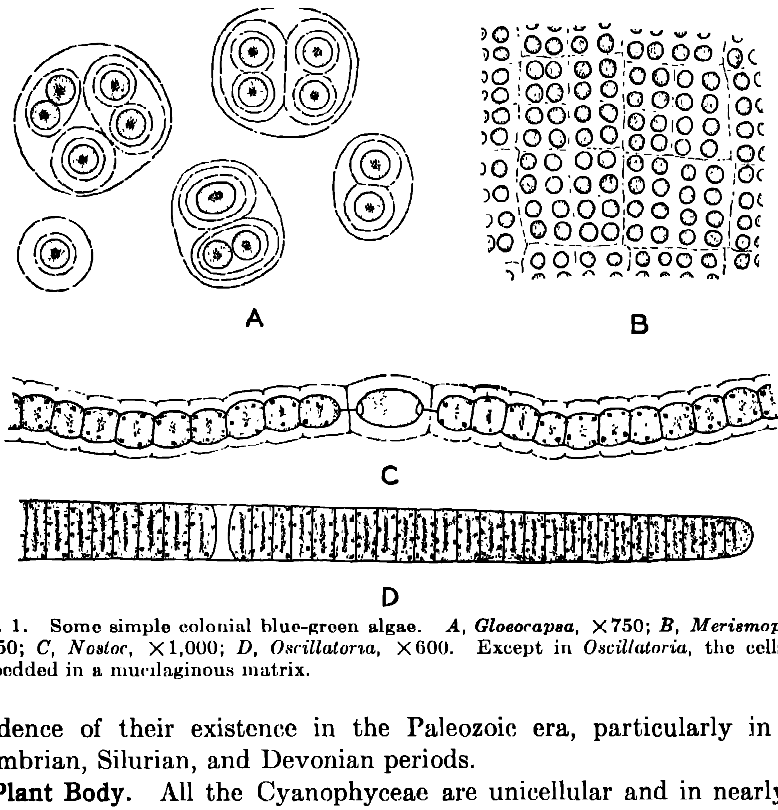

FIG. 1. Some simple colonial blue-green algae. *A*, *Gloeocapsa*, ×750; *B*, *Merismopedia*, ×750; *C*, *Nostoc*, ×1,000; *D*, *Oscillatoria*, ×600. Except in *Oscillatoria*, the cells are embedded in a mucilaginous matrix.

evidence of their existence in the Paleozoic era, particularly in the Cambrian, Silurian, and Devonian periods.

Plant Body. All the Cyanophyceae are unicellular and in nearly all of them the cells are organized to form colonies (Fig. 1). None has a truly multicellular body, although this condition is approached by the higher members of the group. In some species of *Chroococcus* the cells are solitary, while in *Gloeocapsa* they form small irregular colonies loosely held together in a gelatinous matrix. In *Merismopedia* the colonies are plate-like, the cells being arranged in regular rows. In *Coelosphaerium* the colonies are globular and hollow, in *Nostoc* they resemble a string of beads, while in *Oscillatoria* they form a compact filament. The filamentous type of colony is most common.

Although cilia are never present, many of the filamentous blue-green algae have the power of movement. If a mass of *Oscillatoria* growing on mud is placed in a flat dish, the filaments soon creep out in all directions. Under the microscope the filaments are seen to shift frequently their position laterally in the water. In performing these movements, the cause of which is unknown, the cells of the colony function as a unit, thus approaching a condition characteristic of multicellular plants—a cooperation of cells in the performance of their functions.

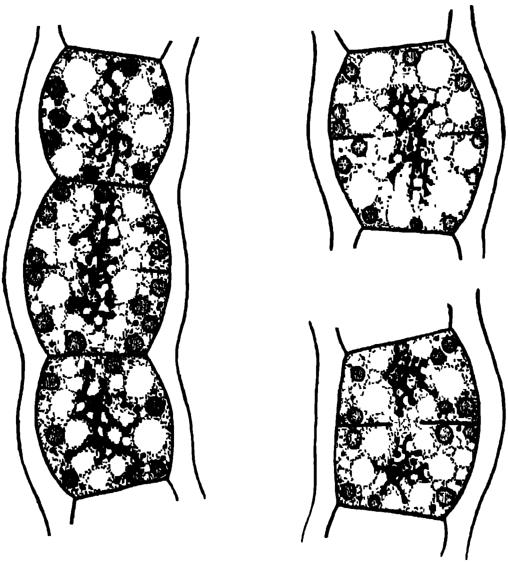

FIG. 2. Longitudinal sections through cells of *Anabaena circinalis*, some of which are dividing, ×2,750. The nuclear material is in the form of irregular masses. The spherical bodies are cyanophycin granules and represent reserve food. (*After Haupt.*)

Cell Structure. The Cyanophyceae are characterized by a very primitive cell structure. A thin cell wall, composed of cellulose and pectic compounds, seems always to be present. Generally it becomes mucilaginous and forms a matrix around the cell. The protoplast lacks the degree of organization seen in the higher plants. It consists of an outer colored portion, containing the blue and green pigments, and a central colorless portion. The latter, representing an incipient nucleus, contains a mass of scattered chromatin granules not surrounded by a membrane and without a nucleolus (Fig. 2). Plastids are not organized, the pigments being merely diffused throughout the peripheral region of the cell. Carbohydrate food is stored as glycogen, starch being absent. Reserve food often occurs also as minute oil droplets and as spherical bodies (cyanophycin granules) that are probably protein in nature.

These granules usually lie in the outer part of the cell, in many filamentous forms being commonly grouped along the cross walls.

Cell division is accomplished by a ring-like wall that develops from the outside toward the center, finally cutting the cell in half (Fig. 2). At the same time the chromatin separates into two approximately equal masses without the formation of chromosomes or other features of mitosis.

Reproduction. Because the Cyanophyceae are unicellular plants, cell division results in reproduction, a method called *fission.* The division of a cell to form two new individuals directly is the simplest method of reproduction in the plant kingdom. In most of the Cyanophyceae the cell walls break down to form abundant mucilage. Generally, as in *Gloeocapsa*, this holds together a group of cells derived from a single cell by repeated division, thus forming a colony (Fig. 1*A*). Here the mucilage surrounding the cells is in concentric layers; but in many other genera it is in a continuous mass made up of the confluent sheaths of the individual cells.

In some of the filamentous types, such as *Lyngbya*, a firm mucilaginous sheath is present around the whole colony, but in *Oscillatoria*, a related genus, the cell walls are more resistant and no sheath is formed (Fig. 1*D*). In both genera the cells are compactly arranged in the colony, each cell, except the terminal one, being shortly cylindrical. That their shape results from mutual pressure is shown by the fact that the free surface of the end cell is convex. This is also true of cells adjacent to a dead cell in the filament.

The type of colony produced depends on the way in which the cells divide. In a filament all the divisions occur in one plane. Where the cells divide in two planes, a plate or a hollow sphere one layer thick is produced. Divisions in three planes usually result in a somewhat massive type of colony.

In most of the filamentous forms, with the exception of *Oscillatoria* and its relatives, differentiated cells, called *heterocysts,* appear in the colony. They may be seen in such common genera as *Nostoc* and *Anabaena* (Fig. 1*C*). A heterocyst is an enlarged vegetative cell that becomes thick-walled and transparent. Heterocysts usually occur singly but at rather frequent intervals, thus dividing the filament into segments called *hormogonia.* These become detached and move away from one another to form new colonies. A hormogonium is merely an isolated portion of the original filament. In *Oscillatoria* and related genera hormogonia are formed by the death of unmodified cells here and there in the colony (Fig. 1*D*).

Although none of the Cyanophyceae produces zoospores or gametes, most of the filamentous members form nonmotile resting spores. One kind, called an *akinete*, arises from a vegetative cell that enlarges by the accumulation of food and develops a thick cell wall (Fig. 3*A*, *B*). These cells are very resistant to unfavorable conditions. Akinetes may be separated in the filament or several may occur together. In some forms they always appear next to a heterocyst, either at the end or in the middle of the filament. Another kind of resting cell, called an *endospore*, is developed in some genera, as in *Chamaesiphon* and in the marine genus, *Dermocarpa* (Fig. 3*C*). Endospores are small thick-walled spores that

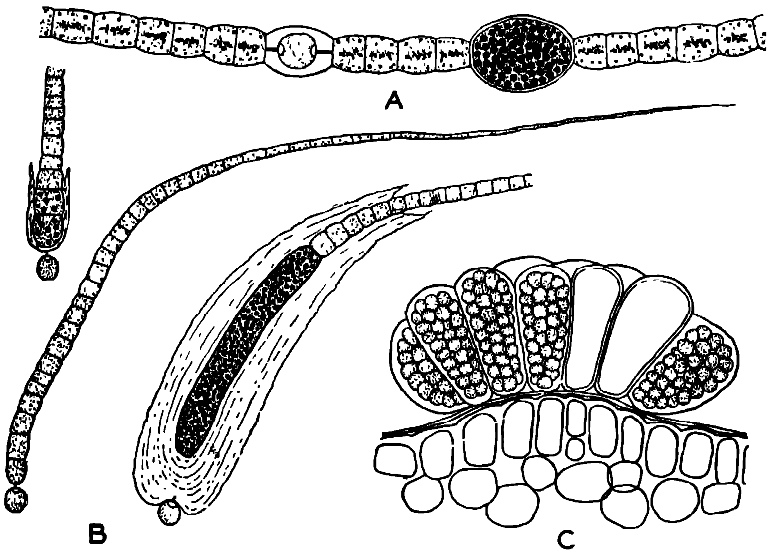

FIG. 3. Formation of resting spores in the blue-green algae. *A*, portion of filament of *Anabaena* with a heterocyst and an akinete containing many food granules, ×750; *B*, *Gloeotrichia*, showing a young filament and two stages in the development of an akinete, ×500; *C*, *Dermocarpa*, an epiphytic form, with two empty cells and others containing endospores. (*C*, *after Bornet and Thuret*.)

arise from a protoplast by divisions within the cell cavity and from which they later are liberated.

Rivularia is a filamentous form in which the basal cell of a filament is always a heterocyst, while the other cells become gradually smaller toward the very slender apex. A thick mucilaginous sheath, confined to the base of the filament, begins next to the heterocyst. *Gloeotrichia* is similar to *Rivularia* except that the first basal vegetative cell becomes transformed into an elongated akinete (Fig. 3*B*).

Branching. In some of the filamentous members branching occurs (Fig. 4). In *Tolypothrix* the filaments exhibit "false branching." Here the cells on one side of a heterocyst grow out beyond it to form a branch. In *Scytonema* the false branches arise laterally in pairs but usually not in connection with a heterocyst. In *Stigonema* a true branch arises as a lateral outgrowth from a single cell of the filament. This type of branching is rare in the Cyanophyceae, occurring in only a few genera.

Summary. The Cyanophyceae are an ancient group of plants showing an extremely primitive condition of structural organization. In addition to chlorophyll and carotinoids, a blue pigment (phycocyanin) is present and often a red pigment (phycoerythrin) as well. The plant body is unicellular, the cells nearly always forming colonies. The cell wall is

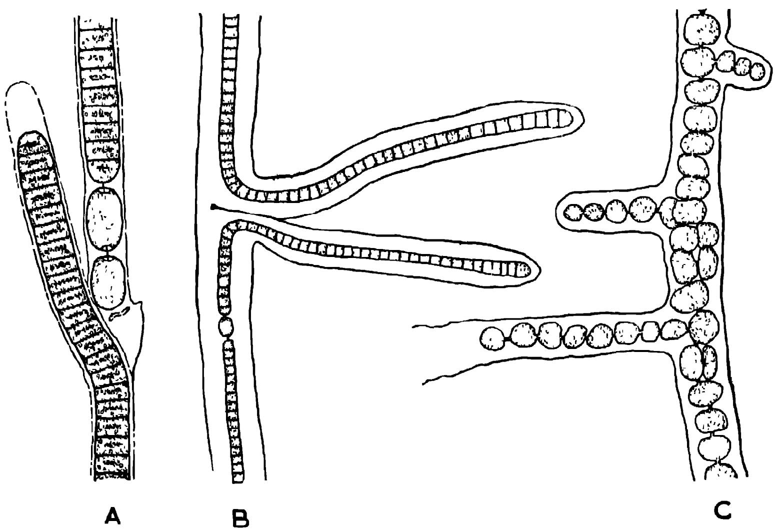

FIG. 4. False branching in *Tolypothrix* (*A*) and *Scytonema* (*B*), and true branching in *Stigonema* (*C*); *A*, ×750; *B*, ×200; *C*, ×300.

more or less unstable, usually producing abundant mucilage. The protoplast shows little organization. The pigments forming the characteristic blue-green color are diffused throughout the peripheral part of the protoplast, no plastids being present. Reserve carbohydrate food is stored as glycogen. A nucleus is represented only by scattered chromatin granules, there being no nuclear membrane or nucleolus. Reproduction occurs by fission and by nonmotile spores. It is entirely asexual. Ciliated cells are never produced. The resting cells (akinetes) are merely enlarged protoplasts with a thick wall. There is a tendency toward cellular differentiation, in some forms resulting in the establishment of a distinct apex and base. The relationships of the Cyanophyceae to the other algae are obscure. They appear to be closely related to the bacteria. In fact, the blue-green algae and bacteria are sometimes placed in the same group, the Schizophyta, and made an independent class of thallophytes.

2. EUGLENOPHYCEAE

Flagellates are unicellular organisms combining characters of both plants and animals. Zoologists regard them as one-celled animals, while botanists consider at least those with chlorophyll as plants, as well as certain colorless ones evidently derived from them. Nearly all flagellates are solitary and free-swimming, but some form loose gelatinous colonies and some are attached. Most of them live in fresh or salt water, some occur on damp earth, and some are parasitic. Formerly they were placed in a separate group, the Flagellatae, but they show so many differences among themselves that they are now distributed, so far as possible, into other groups. One of these, the Euglenophyceae, includes about 350 species of green or colorless, mainly fresh-water flagellates. The best-known genus, *Euglena*, is widely distributed and common in stagnant pools and ditches, often occurring in such abundance as to color the water a deep green.

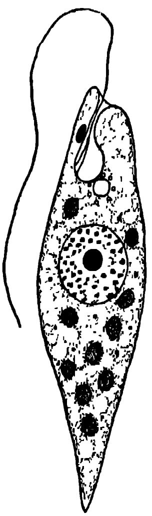

FIG. 5. *Euglena viridis*, ×750. The cell contains a large nucleus and a number of chloroplasts. At the anterior end is a long flagellum, a narrow gullet leading to the reservoir, a contractile vacuole, and an eyespot.

Cell Structure. *Euglena* is somewhat pear-shaped, being blunt at its anterior end and gradually tapering behind (Fig. 5). As in other flagellates, there is no cell wall, each cell consisting of a naked protoplast. In *Euglena* the outer part of the protoplast is differentiated into a thin *pellicle* that is somewhat firm but flexible enough to permit the cell to undergo frequent changes in shape. In some flagellates the pellicle is more rigid, giving the cell a constant form, while in others it is wanting. Some flagellates that lack a pellicle are amoeboid, putting out slender pseudopodia.

Flagellates are characterized by having, in the vegetative condition, one or two (rarely more) *cilia*—slender protoplasmic threads that lash back and forth in the water. Long whiplike cilia are called flagella,[1] the possession of which gives the flagellates their name. The flagella are generally borne at the anterior end of the cell and, where two are present, they are either equal or unequal in length.

Euglena has a single flagellum attached anteriorly. Near its base is a conspicuous red *eyespot*, which is thought to be sensitive to light. Although avoiding direct sunlight, the organism tends to swim toward the best-illuminated part of the water. At the anterior end of the cell

[1] If a distinction is to be made between cilia and flagella, the latter are not only longer than the cell that bears them but coarser and fewer in number. Cilium means "eyelash"; flagellum means "whip."

is a short narrow tube, called the *gullet*, that leads to a spherical cavity, the *reservoir*. The flagellum is inserted inside the reservoir and projects through the gullet. Near the reservoir is a *contractile vacuole* (more than one in some species), which alternately contracts and expands. The contractile vacuole discharges its contents into the reservoir. Contractile vacuoles, usually regarded as organs of excretion, are found in many one-celled animals, as well as in the motile cells of many algae.

Flagellates show an advance over the blue-green algae in having a definite nucleus. Moreover, their photosynthetic pigments, where present, are always confined to definite plastids. *Euglena* has many small green plastids (*chloroplasts*), but some flagellates, not belonging to the Euglenophyceae, have yellow or brown plastids. All these colored forms carry on photosynthesis. Other flagellates, some belonging to the Euglenophyceae, are colorless and live either as saprophytes, absorbing organic matter in solution through the plasma membrane, or as animals, ingesting solid particles of food either through the gullet or by means of pseudopodia. A few flagellates are parasitic on animals, one of these, *Trypanosoma*, causing a disease of man known as African sleeping sickness. Some forms with chlorophyll ingest solid food particles through the gullet. Some species of *Euglena* carry on photosynthesis in the light, but, if kept in darkness and supplied with organic matter in solution, become colorless and saprophytic. In all the Euglenophyceae food is stored as paramylon, a starch-like carbohydrate, and often as oil. The presence of paramylon granules is very characteristic, even in colorless cells. True starch is not formed. Flagellates belonging to other groups of algae differ with respect to the type of food stored.

Reproduction. As in all flagellates, reproduction in *Euglena* occurs by fission, the cell dividing longitudinally. In the presence of unfavorable conditions, encystment often occurs. The protoplasm retracts the flagellum, rounds up, secretes a thick gelatinous covering about itself, and goes into a resting stage. Although later the cyst usually produces a single motile protoplast, sometimes it divides internally into a number of smaller protoplasts that escape, develop flagella, and grow to mature size. Sexual reproduction in the Euglenophyceae is of doubtful occurrence.

Colacium, a member of the Euglenophyceae, is interesting in being an attached form lacking flagella in the vegetative condition. Its cells are surrounded by a gelatinous wall and are united into small irregular colonies. When reproduction occurs, the cell contents escape as a naked euglenoid protoplast with a flagellum.

Relationships. Flagellates are related on the one hand to various groups of algae and on the other hand to the Protozoa. The fact that they are intermediate between plants and animals strongly suggests that the earliest forms of life may have been similarly undifferentiated and that from such a common ancestry both plants and animals may have arisen. Although the relationship of the Cyanophyceae to the flagellates, if any, is very obscure, most of the higher algal groups are thought to have been derived from flagellate ancestors. Where intermediate forms occur, such a derivation seems almost certain.

Summary. The Euglenophyceae are a group of flagellates with bright green chloroplasts containing only chlorophyll and its associated carotinoids, the chlorophyll predominating, as in the green algae. Some members are colorless, these being either saprophytic or animal-like in their nutrition. All are unicellular and uninucleate, the cells being solitary or rarely in colonies. The cells have one or two cilia (flagella) that may be equal or unequal but are always attached anteriorly. Except in colonial forms, the cells are motile and lack a cell wall. Reserve food is stored as paramylon and often also as oil. Reproduction occurs by longitudinal fission. Resting cells (cysts) are commonly formed. Sexual reproduction is doubtful.

3. CHRYSOPHYCEAE

The Chrysophyceae, or golden-brown algae, are a small group numbering only about 200 species and occurring mainly in fresh water. Their plastids contain chlorophyll and an excess of yellow and brown carotinoid pigments, giving them a golden-brown color. Most members are flagellates, being unicellular motile forms without a cell wall. The cells are solitary or in colonies and may be either free-swimming or attached. Motile cells have one or two, rarely three, cilia (flagella) attached anteriorly. The two cilia may be equal or unequal in length. A few forms have a cell wall and are either filamentous or palmelloid, the latter with cells loosely held together in a gelatinous matrix. All members are uninucleate. Food is stored as oil or as leucosin, which is a protein-like substance of unknown composition. Some forms are colorless, while a few, with chlorophyll, may ingest solid food. Reproduction occurs by fission, mainly longitudinal. A characteristic feature is the occurrence of cysts with a silicified cell wall having a small plug at one end. Zoospores may be produced in members that are not flagellates. Sexual reproduction is of doubtful occurrence.

Chromulina is a motile unicellular form (Fig. 6). *Chrysamoeba* is amoeboid. *Synura* and *Uroglena* are globular free-swimming colonies. *Dinobryon* has species in which the cells form a dendroid colony. *Hydrurus* and *Phaeocystis* are palmelloid forms. *Phaeothamnion* is a branched filament and represents the highest type of organization attained by the group.

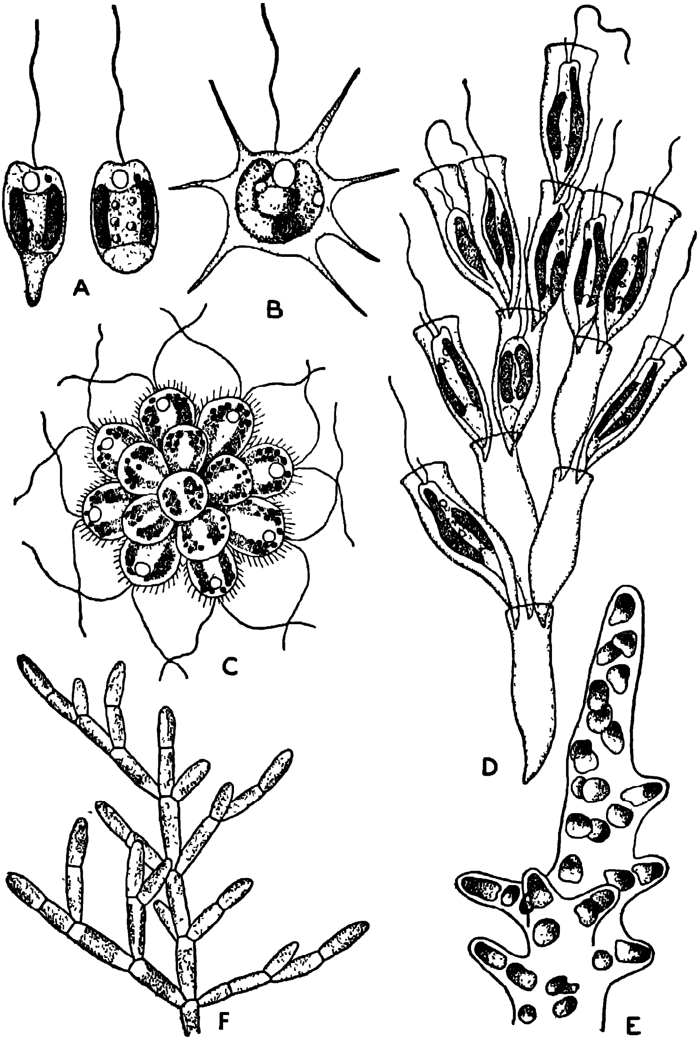

FIG. 6. Group of golden-brown algae. *A*, *Chromulina ovalis*, ×1,450; *B*, *Chrysamoeba radians*, ×960; *C*, *Synura uvella*, ×600; *D*, *Dinobryon sertularia*, ×900; *E*, *Hydrurus foetidus*, ×480; *F*, *Phacothamnion confervicolum*, ×440. (*A* and *B*, after Klebs; *C*, after Stein; *D*, after Senn; *E*, after Berthold; *F*, after G. M. Smith.)

Another group composed almost entirely of flagellates are the Cryptophyceae, yellow-green and brown forms that store food as starch or a related substance. Motile cells have two unequal cilia (flagella). Reproduction occurs by fission. Sexual reproduction has been reported in only one species. The Cryptophyceae comprise only 30 species, mostly occurring in fresh water, and are rarely seen. In some respects they resemble the next class.

4. DINOPHYCEAE

The Dinophyceae comprise a group of nearly 1,000 species of organisms, most of which are known as dinoflagellates. Although some occur in fresh water, most of them are free-swimming marine forms. A few have naked protoplasts, but nearly all have sculptured walls of cellulose usually composed of a definite number of jointed plates (Fig. 7). All the dinoflagellates are unicellular and most of them are solitary; some occur in chain-like colonies. The cells are small and generally have a pair of laterally attached cilia (flagella). A characteristic feature is the occurrence of two grooves, one encircling the cell transversely and the other extending longitudinally along one side. The cilia arise at the point of intersection of the grooves. One lies in the transverse groove and the other is directed backward.

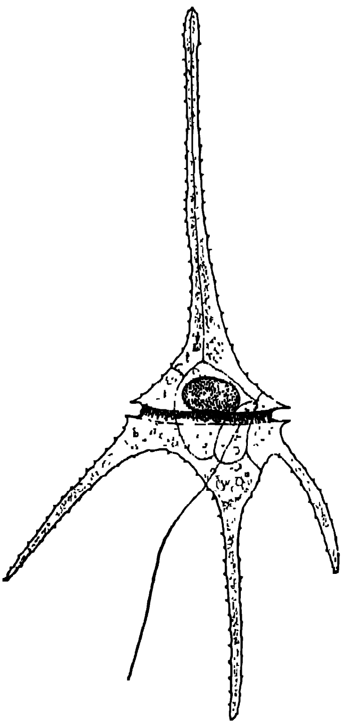

FIG. 7. *Ceratium hirudinella,* a fresh-water dinoflagellate, ×400.

The dinoflagellates have a definite nucleus and usually a number of brownish yellow plastids, in which there is a predominance of carotinoids over the chlorophyll. Some are colorless. The colorless forms live either as saprophytes or as animals, the latter ingesting solid food particles. Some are parasitic. Reserve food occurs either as starch or as oil. Many of the dinoflagellates are phosphorescent. The prevailing method of reproduction is by fission, but some members produce zoospores. As in the other flagellates, cysts are often formed. Sexual reproduction has been reported in only one member of the class.

In addition to the dinoflagellates, the Dinophyceae include a few forms with a higher type of cellular organization, such as *Gloeodinium,* a palmelloid form, and *Dinothrix* and *Dinocladium,* both of which are filamentous.

5. XANTHOPHYCEAE

The Xanthophyceae,[1] or yellow-green algae, are a small but distinct group of only about 200 species characterized by having an excess of

[1] Also called Heterocontae.

yellow pigments, especially carotin, in their plastids. *Xanthophyll* and *carotin* are the two carotinoid pigments associated with chlorophyll in other green plants, but here their proportions are different. Although a few are marine, most yellow-green algae are found in fresh water. They are either unicellular or multicellular. Many are flagellates. The group was formerly classified with the Chlorophyceae, but seems to have had an independent origin from a flagellate ancestry and to have followed a line of evolution parallel to that of the green algae. Three representative genera are *Chlorochromonas*, *Tribonema*, and *Botrydium*.

Chlorochromonas. This is a naked unicellular flagellate with two yellow-green plastids (Fig. 8). It has two cilia (flagella) of unequal length attached anteriorly, a contractile vacuole, and a central nucleus. It stores food as leucosin and probably also as oil. A leucosin granule, contained in a vacuole, lies at the posterior end of the cell. Reproduction takes place by fission. From such a form as *Chlorochromonas*, the other Xanthophyceae appear to have evolved.

FIG. 8. *Chlorochromonas minuta*, ×2,000. (*After Lewis.*)

Tribonema. This is a filamentous alga, widely distributed in fresh-water pools (Fig. 9). The filaments are unbranched and composed of elongated cylindrical cells. The walls are made up of two overlapping pieces that appear H-shaped in a longitudinal section. The cells contain a nucleus and a number of yellow-green plastids. Asexual reproduction occurs by the formation of aplanospores, akinetes, or zoospores. *Aplanospores* are nonmotile spores with a wall distinct from the wall of the parent cell. *Akinetes* are also nonmotile but are derived from an entire vegetative cell whose wall becomes the wall of the spore. *Zoospores* are ciliated and naked. In *Tribonema* one or more aplanospores may be produced within a cell, while the zoospores are usually formed singly. Sexual reproduction, which is rare, takes place by the fusion of isogametes formed in ordinary cells. Usually one gamete settles down before the other unites with it. The motile cells have two cilia of unequal length, attached anteriorly, and the reserve food is stored as oil or leucosin, never as starch.

Botrydium. *Botrydium* is a terrestrial alga often found on wet muddy flats. The vegetative body is unicellular and multinucleate, consisting of a balloon-shaped bladder about 1 to 2 mm. in diameter (Fig. 10). It is fastened to the soil by means of branched colorless rhizoids. The cytoplasm, containing many nuclei and, in the aerial portion, numerous yellow-green plastids, forms a thin layer lining the cell wall and enclosing a large central vacuole. Such a multinucleate body, without any cross walls, is called a *coenocyte*. Food is stored as oil or leucosin.

Asexual reproduction may occur either by zoospores or aplanospores. When covered with water, the entire aerial portion may release numerous uninucleate zoospores through a terminal pore. The zoospores have two

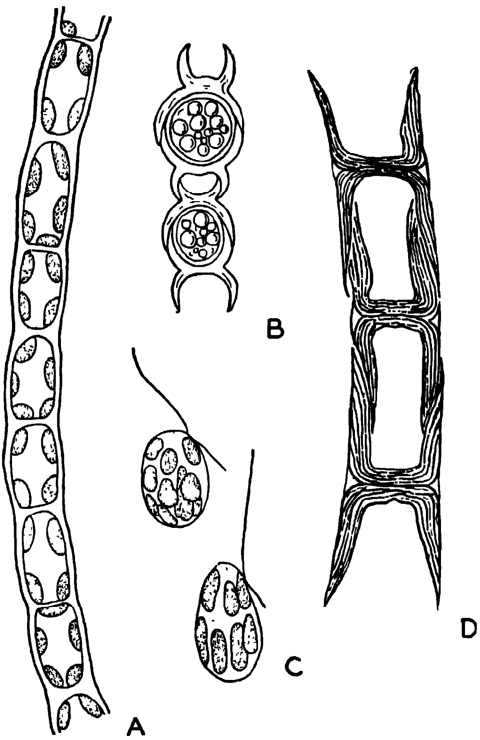

FIG. 9. *Tribonema bombycinum*, a yellow-green alga. *A*, portion of vegetative filament; *B*, aplanospores; *C*, zoospores; *D*, structure of cell wall, as revealed by special treatment. (*A*, *B*, *C*, *after Gay; D, after Bohlin.*)

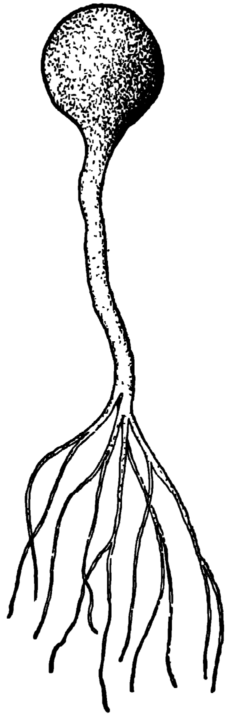

FIG. 10. *Botrydium granulatum*, showing balloon-shaped aerial portion and branched subterranean portion, ×20.

cilia of unequal length, attached anteriorly. They may either germinate immediately or form a wall and go into a resting stage. In the absence of sufficient moisture, the aerial portion may give rise to aplanospores or all the cytoplasm may move into the rhizoidal portion and there produce aplanospores. The aplanospores of *Botrydium* may be either uninucleate or multinucleate and, after a dormant period, may give rise either to zoospores or to new plants directly. Sexual reproduction is accomplished by small biciliate isogametes, each with a single nucleus, that fuse to form thick-walled zygotes. These germinate immediately, giving rise directly to a new vegetative body. Sometimes the gametes conjugate before being liberated.

6. BACILLARIOPHYCEAE

The Bacillariophyceae,[1] or diatoms, constitute an isolated group whose relationships to the other algae are very uncertain. They include over 5,000 species of unicellular plants occurring almost universally in fresh and salt water, as well as on damp soil. Some of the more common genera are *Melosira*, *Coscinodiscus*, *Biddulphia*, *Pinnularia*, *Surirella*, *Cocconeis*, *Navicula*, and *Pleurosigma*. Diatoms may be either free-floating or attached. Frequently they form slimy brown coatings on mud at the bottom of shallow bodies of water, as well as on sticks, stones, shells, other aquatic plants, etc. That they were more numerous in geologic times is shown by the great accumulations of diatomaceous earth found in various parts of the world. This consists of the shells (cell walls) of dead diatoms. Deposits of diatomaceous earth were formed mainly during the Tertiary, but the fossil record of diatoms extends as far back as the Jurassic.

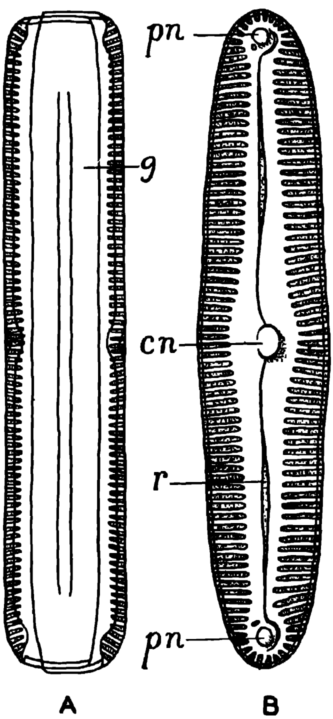

FIG. 11. Two views of the shell of *Pinnularia viridis*. *A*, girdle view; *B*, valve view; *g*, girdle; *pn*, polar nodule, *cn*, central nodule; *r*, raphe. (*After Pfitzer.*)

Although most diatoms are solitary, some form colonies of diverse types, the individuals being held together by a sheath of mucilage. Their color, usually a golden brown, is due to the presence of chlorophyll in association with an excess of carotinoids, particularly carotin and several brown xanthophyll pigments. Diatoms are distinguished from other algae by their silicified cell wall. This consists of two valves, one overlapping the other like the lid and bottom of a pillbox (Fig. 11). The place where the valves overlap is called the *girdle*. The cell wall is composed mainly of pectin impregnated with a large amount of silica. It is variously marked with numerous fine transverse lines that form regular and elaborate patterns. These make diatoms among the most striking and beautiful objects to be seen under the

[1] Also called Diatomeae.

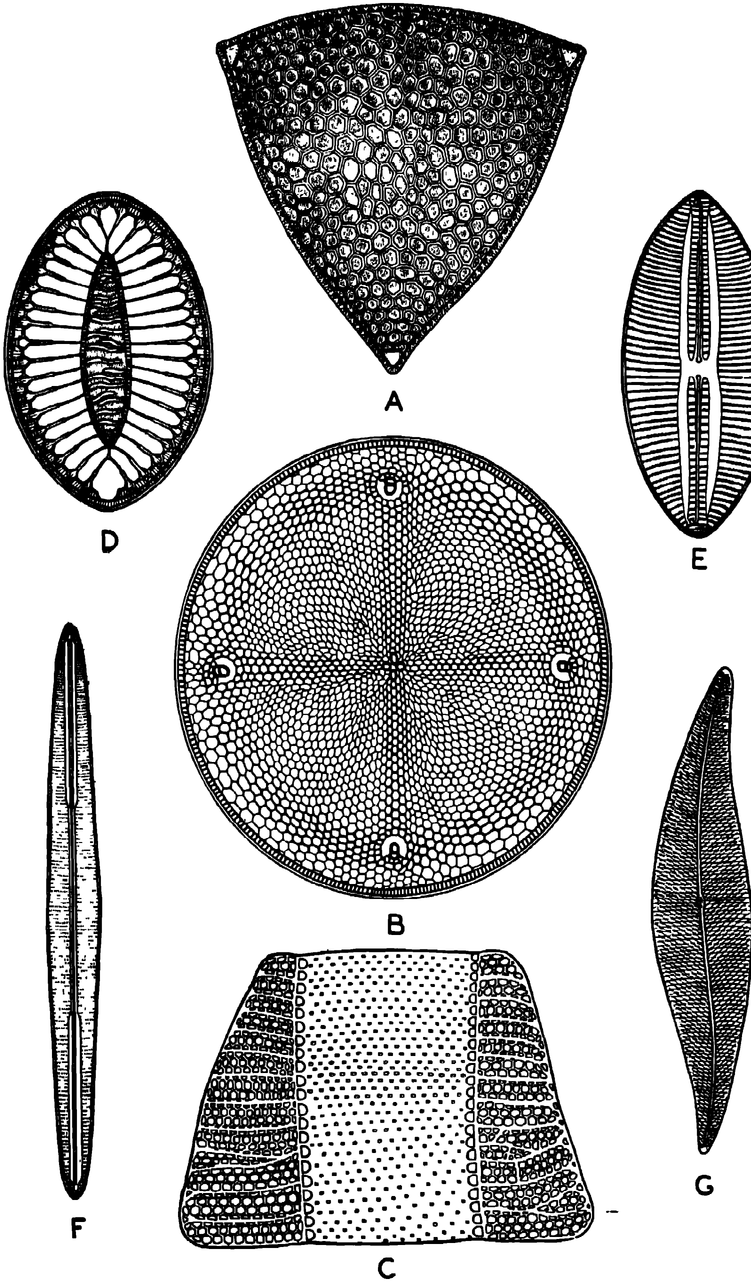

FIG. 12. Group of common diatoms. *A*, *Triceratium*; *B*, *Aulacodiscus*; *C*, *Isthmia*; *D*, *Surirella*, *E*, *Navicula*; *F*, *Amphipleura*; *G*, *Pleurosigma*. (*Adapted from a Turtox classroom chart.*)

microscope. A good microscope will show that the striations on the silicified cell wall generally consist of rows of very minute pores. They appear as lines because the pores are very close together.[1]

Two views of a diatom are possible—girdle (side) view and valve (top) view (Fig. 11). Many diatoms possess a *raphe*, which is a longitudinal slit extending down the center of the valve. Such forms have the power of locomotion, movement apparently being accomplished by a streaming of protoplasm along the raphe.

The Bacillariophyceae comprise two orders: (1) the Centrales, which are radially symmetrical in valve view, often circular, and have no raphe

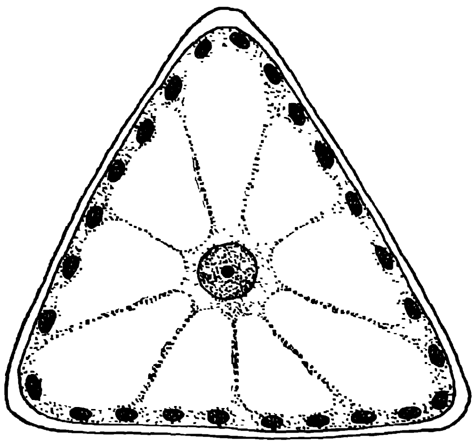

FIG. 13. *Triceratium*, a large marine diatom, as seen in optical section, ×400. The nucleus lies in the center of the cell, while numerous small plastids lie just inside the cell wall.

(Fig. 12*A–C*) and (2) the Pennales, which are usually bilaterally symmetrical, not circular, and generally have a raphe (Fig. 12*D–G*). The difference in symmetry is clearly shown by the pattern of markings on the valves, being radial in the Centrales and bilateral in the Pennales.

In most diatoms the nucleus is suspended in the center of the cell by slender strands or by a broad transverse band of cytoplasm connected with a thin layer lying next to the cell wall (Figs. 13 and 14*A*). Embedded in the peripheral layer are one or more plastids that are usually brown, frequently yellow, or rarely green. In the Centrales the plastids are small and numerous. In the Pennales they are large and few in number; commonly there are two. The plastids of diatoms vary greatly in shape, being often irregular and sometimes elaborately lobed. The cell contains no starch, food being stored mainly as oil.

[1] Some diatoms have striae so fine that they are used as test objects in determining the efficiency of microscope lenses. A good oil immersion objective will resolve markings that are as fine as five striae to the micron.

Reproduction occurs chiefly by fission, the cell always dividing in the plane of the valves (Fig. 14). The two valves separate and each daughter protoplast forms a new wall on its naked side, the new wall fitting inside the old one. One of the cells is always as large as the parent cell,

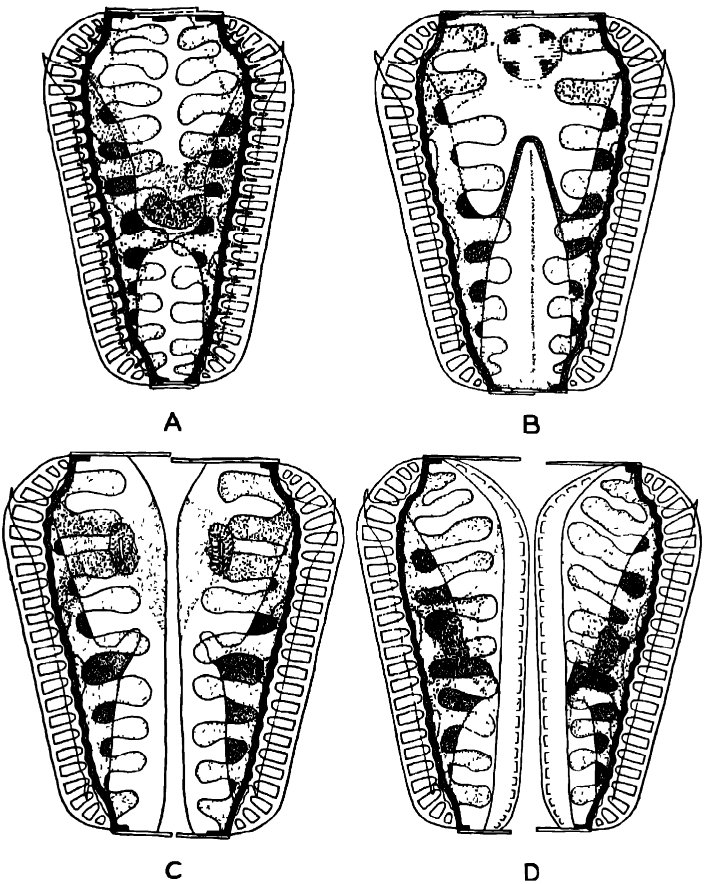

FIG. 14. Cell division in *Surirella calcarata*, ×275. *A* to *D*, successive stages. (*After Lauterborn.*)

but the other is smaller. Thus, as cell divisions continue, some of the individuals become constantly smaller. After a minimum size for the species has been reached, the original size is regained through the formation of *auxospores*.

In the Centrales an auxospore is formed by the escape from its cell wall of a protoplast that soon grows to the original size and develops a new cell wall. An auxospore may directly become a new individual or may form two new individuals by dividing in half. In most of the

Pennales auxospore formation is due to a fusion of cells. In some forms two vegetative protoplasts escape and conjugate to produce a single auxospore (Fig. 15). In other forms two diatoms unite to produce two auxospores. Here the two fusing cells lie within a gelatinous matrix and each produces two gametes. Then each of the gametes derived from one cell conjugates with one of those derived from the other cell. It is apparent that an "auxospore" formed by sexual fusion is really a zygote.

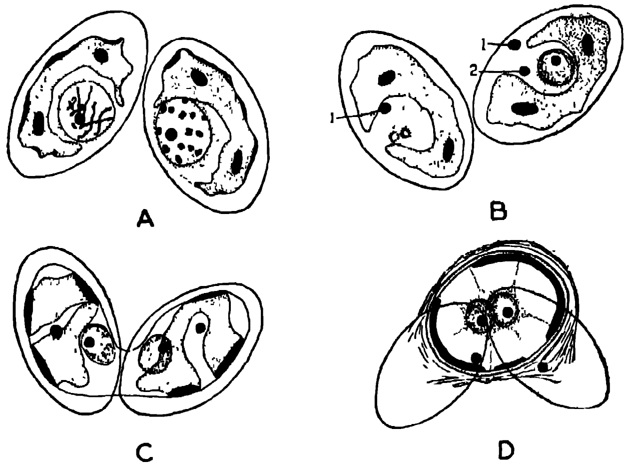

FIG. 15. Conjugation in *Cocconeis placentula*, ×1,500. *A* and *B*, meiosis in conjugating cells; *C*, fusion of protoplasts; *D*, zygote with sexual nuclei not yet fused. (*After Geitler.*)

Just previous to conjugation the nucleus of each of the pairing protoplasts undergoes a reduction of chromosomes, giving rise to four haploid nuclei. Some of these degenerate.

In some of the Centrales many small biciliate protoplasts arise within a vegetative cell and later escape into the water. These have been called "microspores." Some observers think that they function as zoospores, while others regard them as gametes, claiming that they fuse in pairs. The occurrence of these ciliated cells in the Bacillariophyceae suggests that the group may have been derived from flagellates with brown plastids. The connection, however, is a remote one.

7. CHLOROPHYCEAE

The Chlorophyceae, or green algae, are predominantly fresh-water forms whose plastids contain a preponderance of chlorophyll over its associated carotinoids, the green and yellow pigments occurring in approximately the same proportions as in the groups above the thallophyte level.[1] Only a comparatively few members are marine, but

[1] In a few members accessory pigments in the cell sap may mask the green color of the chloroplasts.

some of these are widely distributed and often abundant. Some green algae grow as scums on the surface of quiet water, while others are attached to various objects beneath the surface. A few forms grow on moist soil, rocks, or tree trunks. Most of the green algae are multicellular but some are unicellular, these occurring either as isolated cells or as colonies. The Chlorophyceae are generally regarded as the group of algae from which the bryophytes and other higher groups of green plants have been derived. Lime-secreting forms are known as fossils as far back as the Ordovician. The Chlorophyceae number over 5,000 species, nearly all of which are included in seven principal orders: Volvocales, Chlorococcales, Ulotrichales, Oedogoniales, Conjugales, Siphonocladiales, and Siphonales.

1. Volvocales

The Volvocales are a distinct group of primitive green algae that are widely distributed in fresh water. Only a few members are marine. They appear to have been derived from green flagellates, which they resemble in many ways, and to have given rise, in turn, to the other groups of Chlorophyceae. The Volvocales include about 50 genera and 300 species. The main genera are *Chlamydomonas*, *Sphaerella*, *Gonium*, *Pandorina*, *Eudorina*, and *Volvox*.

Chlamydomonas. This is a unicellular alga that does not form permanent colonies. It is widely distributed in pools and ditches and on damp ground. The vegetative cell, which is free-swimming, is generally spherical or egg-shaped (Fig. 16*A*). A cell wall is always present. At the anterior end are a pair of cilia, equal in length, a red eyespot, and two (rarely more) small contractile vacuoles. Surrounding the nucleus is a small mass of colorless cytoplasm lying in the depression of a large cup-shaped chloroplast. Embedded in the chloroplast is a conspicuous spherical *pyrenoid*. Pyrenoids are protein bodies that function as centers of starch formation. Although occurring in some members of certain other algal groups, they are especially characteristic of the Chlorophyceae.

Chlamydomonas reproduces asexually by means of *zoospores*. The vegetative cell becomes quiescent by retraction of the cilia and then its protoplast divides internally to form two, four, or eight daughter protoplasts, each of which, after enlarging slightly, forms a new cell wall and a pair of cilia while within the parent cell (Fig. 16*B*, *C*). By the breaking down of the original cell wall, the small cells are set free as zoospores, each soon undergoing further enlargement to become an adult vegetative cell (Fig. 16*D*). Under conditions unfavorable for vegetative activity, *Chlamydomonas* may pass into a "palmella" stage. The daughter cells, produced by the internal division of a vegetative cell, increase in number but, instead of escaping, become surrounded by abundant mucilage derived from the cell walls (Fig. 16*E*). Later, when favorable conditions return, the cells develop cilia and swim out of the mucilaginous matrix.

Sexual reproduction in *Chlamydomonas* occurs by the union of similar *gametes*. These arise from a quiescent vegetative cell by division of its protoplast into 16 or 32 daughter protoplasts (Fig. 16*F*). The gametes are smaller than the zoospores and are usually without a cell wall, but

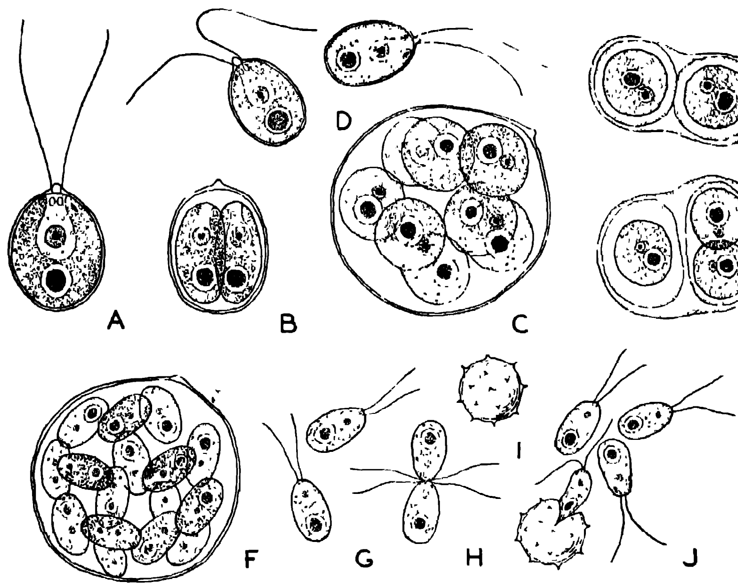

FIG. 16. *Chlamydomonas*, a free-swimming, unicellular green alga, ×1,000 *A*, vegetative cell, showing large cup-like chloroplast with embedded pyrenoid, nucleus, eyespot, two contractile vacuoles, and two cilia; *B* and *C*, formation of zoospores within parent cell wall; *D*, two escaped zoospores, *E*, "palmella" stage; *F*, formation of gametes; *G*, two escaped gametes; *H*, gametes fusing; *I*, zygote; *J*, four zoospores escaping from zygote.

otherwise have the same structural features. They escape and swim about in the water. Finally, they come together in pairs and fuse, each pair forming a zygote (Fig. 16*G*, *H*). The zygote soon loses its cilia, secretes a heavy wall about itself, and goes into a resting stage (Fig. 16*I*). While the wall is forming, the two nuclei inside the zygote unite. Upon germination, the protoplast of the zygote divides internally to form four zoospores that escape and enlarge to become new vegetative cells (Fig. 16*J*). The reduction in chromosome number from the diploid to the haploid state occurs in connection with the formation of the four zoospores from the zygote. Because, in most species, the pairing gametes are alike in size, *Chlamydomonas* is said to be *isogamous*. The fusing of similar gametes (*isogametes*) is known as *conjugation*.

In *Chlamydomonas eugametos* there are two sexually differentiated strains, designated as plus and minus. A zygote may be formed only by the union of a plus gamete with a minus gamete. Of the four zoospores arising from the zygote, two belong to the plus strain and two to the minus. These strains may soon undergo another sexual fusion or may be perpetuated asexually for an indefinite period. In *Chlamydomonas braunii* and a few other species the gametes of the plus strain are slightly larger than those of the minus strain, and so here a visible as well as a physiological sexual differentiation exists. Such species show that *Chlamydomonas* displays a slight tendency toward heterogamy.

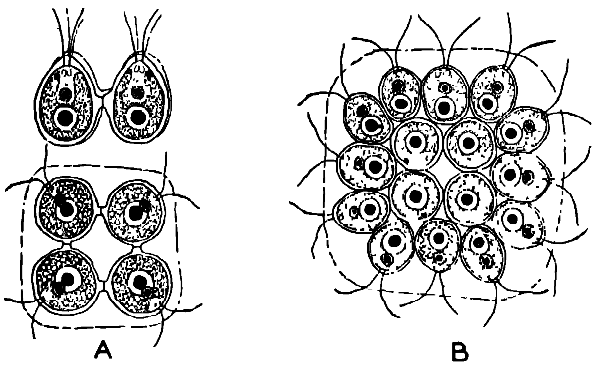

Fig. 17. Two species of *Gonium*, ×900. *A*, side and top views of four-celled colony of *Gonium sociale; B*, top view of sixteen-celled colony of *Gonium pectorale*.

In *Sphaerella*, a close relative of *Chlamydomonas* and common in rain-water pools, the inner portion of the cell wall is gelatinous and thick and is traversed by many delicate cytoplasmic strands. Generally it contains a bright red pigment, *haematochrome*, that masks the chlorophyll. This is present in the cell sap.

Gonium. This is a colonial form, each colony consisting of a flat plate of cells numbering either four or sixteen, according to the species (Fig. 17). The cells are regularly arranged and held together by a mucilaginous matrix derived from their cell walls. Each cell is biciliate and otherwise similar to an adult *Chlamydomonas*. By division of its protoplast, any cell may form a new colony that escapes from the parent cell. Sexual reproduction occurs by the fusion of similar gametes (isogametes), the two coming from separate colonies. The number of gametes formed in a cell corresponds to the number of cells in the colony. They escape separately. The zygote becomes thick-walled and dormant. Later it produces four biciliate zoospores. In the four-celled species these usually remain together as a colony; in the sixteen-celled species they separate and each forms a new colony.

Pandorina. This form is similar to *Gonium* except that the colony is spherical or nearly so and consists usually of 16 biciliate cells crowded together within a mucilaginous matrix and surrounding a small central cavity (Fig. 18*A*). Sometimes the colony consists of only 8 cells or, less frequently, of 32 cells. Each cell resembles that of *Chlamydomonas*. In asexual reproduction each cell divides simultaneously to produce a group of as many daughter cells as were in the parent colony (Fig. 18*B*). Each group then escapes as a new colony. In sexual reproduction each vegetative cell similarly produces a group of daughter cells as numerous as the cells in the colony, the groups separate, and the daughter cells escape individually as biciliate gametes. Although *Pandorina* is isogamous, one

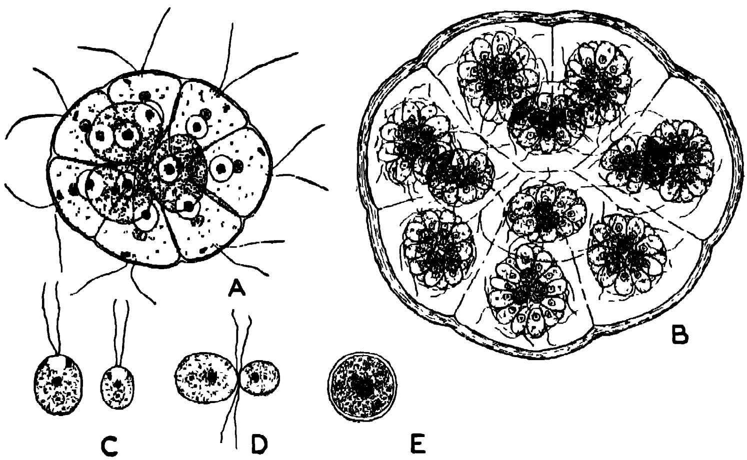

FIG. 18. *Pandorina morum*, ×750. *A*, free-swimming vegetative colony of 16 cells, those lying below not shown; *B*, colony undergoing asexual reproduction; *C*, a large and a small gamete; *D*, gametic union; *E*, a zygote.

of the fusing gametes is slightly larger and less active than the other, thus showing a tendency toward heterogamy (Fig. 18*C*, *D*). The zygote remains motile for a while, finally settling down and secreting a cell wall (Fig. 18*E*). Upon germination the zygote divides internally into four protoplasts, but generally only one becomes a zoospore. The zoospore produces a new colony.

Eudorina. *Eudorina* is a spherical colony usually consisting of 16, 32, or 64 biciliate cells, each like a cell of *Chlamydomonas*. The cells are loosely arranged in a single layer near the surface of a mucilaginous matrix. As in the preceding genera, any cell may give rise to a new colony by internal division of its protoplast, but an advance is seen in sexual reproduction (Fig. 19). Some of the cells divide to form groups of *sperms*, as many as 64 usually arising from a single vegetative cell. The other cells enlarge slightly by the accumulation of food and become *eggs*. Although both male and female gametes are biciliate, only the sperms escape from the colony and become free-swimming. At first the sperms hang together as a plate, but finally separate and fuse with the eggs. The union of a sperm and egg, called *fertilization*, results in the formation of a thick-walled resting zygote. Upon germination, the zygote produces four biciliate zoospores but only one functions, the other three degenerating inside the zygote. Because the pairing gametes are differentiated into sperms and eggs and are therefore unlike, *Eudorina*

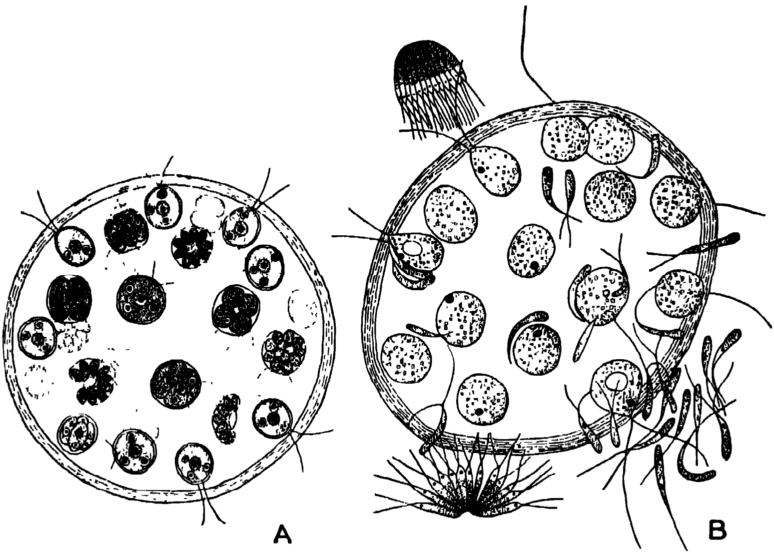

FIG. 19. *Eudorina elegans*. *A*, colony of 32 cells, many of which are dividing to form daughter colonies, ×500; *B*, a female colony surrounded by numerous sperms, two groups of which are still intact, while others, having separated, are uniting with the eggs. (*After Goebel*.)

is *heterogamous*. Some species show a further degree of sexual differentiation in being *dioecious*. Here all the cells in the male colony give rise to sperms, while all those in the female colony become eggs.

Volvox. This is the most highly developed member of the Volvocales. It lives in quiet bodies of fresh water, especially pools, ponds, and lakes. It consists of a hollow globular colony composed of hundreds or sometimes thousands of biciliate cells embedded in mucilage and arranged in a single layer (Fig. 20*A*). Often the colony reaches a diameter of nearly 2 mm. It is free-swimming, as in other members of the order. Each cell is like an adult *Chlamydomonas*, with two cilia, an eyespot, contractile vacuoles, a nucleus, and a single chloroplast with a pyrenoid. In most species the cells are connected by very fine protoplasmic strands, and thus the colony approaches the multicellular condition of organization. This is also shown by the fact that most of the cells function only vegetatively during the entire life of the colony, while others become reproductive cells. Such a "division of labor" is not seen in lower members of the order.

Volvox reproduces asexually by the formation of new colonies inside the old one. A few of the vegetative cells, seldom over 10 or 12, retract

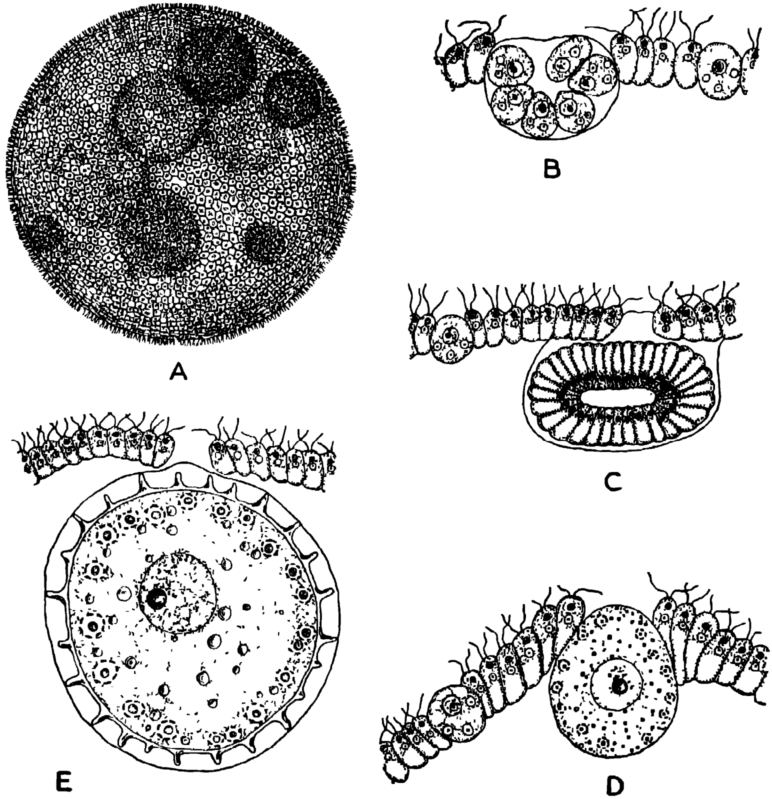

FIG. 20. *Volvox*. *A*, mature colony with young colonies inside; *B*, young colony in rim of mature colony; at the right, a vegetative cell has lost its cilia and is starting to form a new colony; *C*, a group of sperms derived from a single vegetative cell, one of which, to the left, has lost its cilia and is enlarging; *D*, an egg shortly before fertilization and, to the left, an egg beginning to develop from a vegetative cell; *E*, a mature zygote; *A*, ×170; *B* to *E*. ×780. (*After Chamberlain.*)

their cilia and increase slightly in size. Each divides to form a small group of cells that enter the colony and give rise to a new colony, remaining inside until the old colony dies (Fig. 20*B*).

In sexual reproduction, *Volvox* is heterogamous. Any cell may retract its cilia, enlarge by the accumulation of food, and become an egg (Fig. 20*D*). Another cell may enlarge and, at the same time, divide to form many small biciliate sperms (Fig. 20*C*). These arise as a hollow sphere or plate of cells that later separate. The sperms and eggs escape into the colony and there fertilization occurs. The zygote becomes heavy-walled and remains dormant for several months (Fig. 20*E*). In some species it then gives rise to a single biciliate zoospore, while in others it forms a new colony directly. In connection with the germination of the zygote, the number of chromosomes is reduced one-half. As is *Eudorina*, some species of *Volvox* are monoecious, others dioecious.

Summary. The Volvocales are distinguished from the other Chlorophyceae by the fact that their vegetative cells are ciliated and motile. They exhibit a range of development from single isolated cells to complex globular colonies. Each cell has one nucleus and generally one chloroplast. Asexual reproduction occurs by zoospores and by the formation of a new colony from a single parent cell. The number of cells in the colony is definite and is determined during early development. It is not subsequently increased by vegetative cell divisions. Sexual reproduction shows an advance from isogamy to heterogamy, while dioecism is attained by some species of *Eudorina* and *Volvox*.

2. Chlorococcales

The Chlorococcales constitute a large order of diverse forms that are probably not closely related. They are chiefly fresh-water algae, only a few occurring in the ocean. Some live in moist places on land. Some are endophytic in the intercellular spaces of certain seed plants, while others live symbiotically in the lower animals. Others are lichen formers. The order contains 90 genera and approximately 700 species. Some characteristic genera are *Chlorococcum, Chlorella, Scenedesmus, Pediastrum, Hydrodictyon,* and *Protosiphon.*

Chlorococcum. This simple alga grows on damp soil or rocks. It is unicellular, spherical, and nonmotile. At first it has a single nucleus and a large cup-like chloroplast with one or more pyrenoids (Fig. 21). Later the cell becomes multinucleate and the protoplast divides to form a variable number of biciliate zoospores that escape. After coming to rest, a zoospore loses its cilia, secretes a wall, and becomes a vegetative cell. Asexual reproduction may also occur by aplanospores. These arise in the same way as zoospores but have no cilia and develop a cell wall before being freed. As in *Chlamydomonas*, a "palmella" stage may develop by gelatinization of the cell walls in a group of cells. Sexual reproduction is accomplished by the production of a large number of biciliate isogametes by a vegetative cell. These escape and fuse in pairs. In general, *Chlorococcum* is like *Chlamydomonas* except that the vegetative cells have lost their motility.

Chlorella. *Chlorella* lives on the bark of trees, damp walls, and soil; also in various infusoria, the fresh-water sponge, and the green hydra. It can be grown easily in water cultures and is much used in experiments on photosynthesis. The cells are spherical and solitary. They have a single nucleus and a cup-shaped peripheral chloroplast usually without a pyrenoid. *Chlorella* resembles *Chlorococcum* except that it produces only aplanospores, no motile cells of any kind. A protoplast divides to form as many as 16 daughter protoplasts, each of which, before escaping, secretes a cell wall. Gametes are unknown.

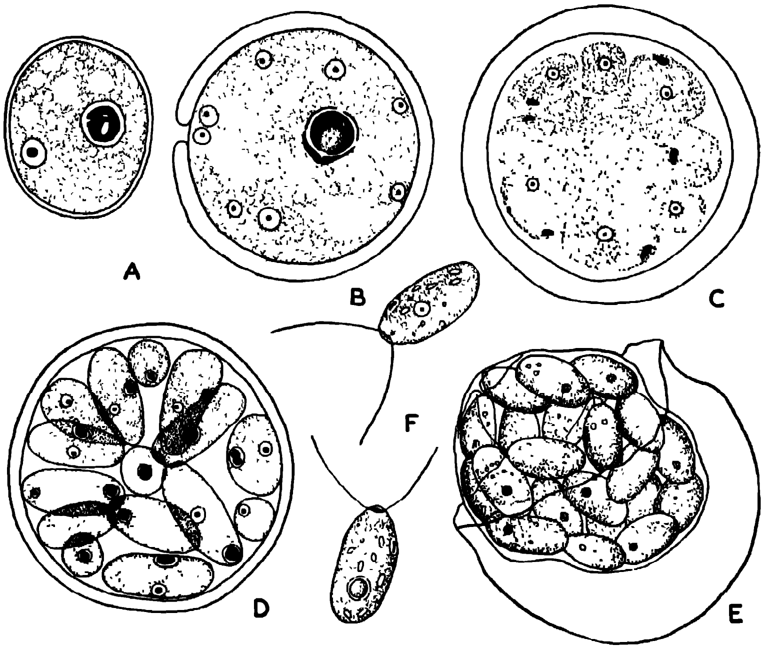

FIG. 21. *Chlorococcum infusionum.* *A*, section of vegetative cell with single nucleus and pyrenoid; *B*, multinucleate stage; *C*, appearance of cleavage furrows, isolating uninucleate protoplasts with a pyrenoid fragment; *D*, section of nearly mature sporangium; *E*, escape of zoospores in a gelatinous vesicle; *F*, two zoospores; *A*, ×2,000; others, ×2,700. (*After Bold.*)

Scenedesmus. This alga is common and widely distributed in fresh water. It is a colonial form with generally four or eight cells arranged in a short row (Fig. 22). The end cells often bear conspicuous spine-like projections. Each cell contains a single nucleus, a large peripheral chloroplast, and a pyrenoid. In reproduction, a protoplast divides within its own cell wall to form a new colony that escapes as a whole. Neither zoospores nor gametes are produced.

Pediastrum. *Pediastrum* is a free-floating form widely distributed in fresh water. It consists of a colony of cells symmetrically arranged in a flat plate (Fig. 23). The number of cells may be 2, 4, 8, etc., up to 128, but is most commonly 16 or 32. The cells are nearly all alike, except that the peripheral ones often bear short spine-like projections.

In young colonies the cells are uninucleate but later become multinucleate (coenocytic), as many as eight nuclei being present. Young cells have a single peripheral chloroplast with one pyrenoid, while older cells have several pyrenoids, the chloroplast becoming diffuse.

In asexual reproduction a protoplast divides generally into as many daughter protoplasts as there are cells in the colony, but often into twice as many. These become biciliate zoospores that escape as a group enclosed in a common membrane (Fig. 24*A*). The zoospores then come together and form a new colony within the membrane (Fig. 24*B*, *C*).

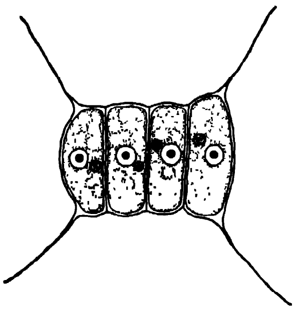

FIG 22. Four-celled colony of *Scenedesmus*, ×750. Each cell contains a small nucleus and a large peripheral chloroplast with a pyrenoid.

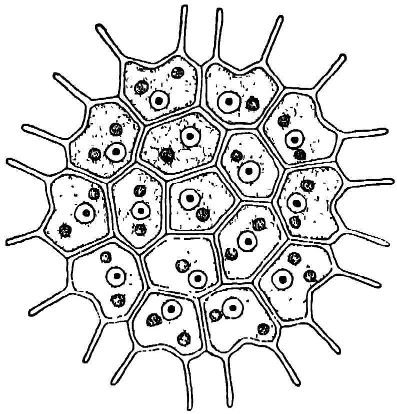

FIG. 23. Young colony of *Pediastrum boryanum*, its cells forming a plate, ×750. Some of the cells have become binucleate Each has a peripheral chloroplast and a pyrenoid.

Sexual reproduction also takes place, *Pediastrum* being isogamous. Division of a vegetative protoplast results in the formation of many biciliate gametes. These escape separately and fuse in pairs to form zygotes. After increasing in size, the zygote gives rise to a group of zoospores. These escape into the water, swim freely and, after coming to rest, develop into thick-walled polyhedral cells (Fig. 24*D*). The polyhedrons enlarge and divide internally to form a group of zoospores that escape in a common membrane, within which they construct a new colony by coming together without further division (Fig. 24*E*–*G*).

Hydrodictyon. This remarkable alga, common in fresh water, is a free-floating colony having the form of a large hollow net, the polygonal meshes of which are made up of elongated cylindrical cells arranged end to end (Fig. 25*A*). Each mesh consists usually, but by no means always, of six cells. A single colony may reach a length of 20 to 30 cm. At first each cell contains a single nucleus and a chloroplast with one pyrenoid, but later there are many nuclei and a large number of pyrenoids, the chloroplast becoming reticulate and diffuse (Fig. 25*B*). Mature cells have a peripheral layer of cytoplasm surrounding a large central vacuole. In asexual reproduction as many as 7,000 to 20,000 biciliate zoospores may arise from a single vegetative cell by progressive cleavage of its protoplast. These do not escape but swim around within the parent cell, finally coming together to form a new net (Fig. 25*C*). Later the cell walls of the old net dissolve and the young colonies are set free. These grow to the adult size without any cell division.

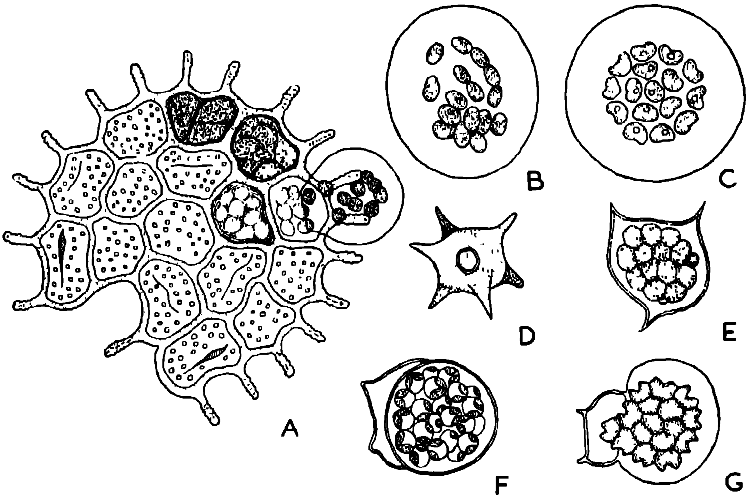

Fig. 24. *Pediastrum boryanum.* *A*, formation of zoospores and escape of one group in a common vesicle; *B* and *C*, zoospores forming a new colony; *D*, a thick-walled resting cell (polyhedron); *E*, *F*, *G*, zoospores within a polyhedron forming a new colony. (*A*, *B*, *C*, after *A. Braun*; *D* to *G*, *after Askenasy*.)

In sexual reproduction a single protoplast may give rise to as many as 30,000 to 100,000 biciliate isogametes. These escape from the parent cell through a small pore and fuse in pairs to form thin-walled zygotes (Fig. 25*D*–*F*). After undergoing a short resting period, the zygote turns green and increases in size. It then produces four large zoospores and, in connection with their formation, the number of chromosomes is reduced one-half (Fig. 25*G*, *H*). As in *Pediastrum*, the zoospores escape into the water, settle down, and become large heavy-walled polyhedrons (Fig. 25*I*). These remain dormant until the following spring and represent the real resting stage. Upon germination, a polyhedron produces 200 to 300 small zoospores that escape enclosed in a membrane, where they arrange themselves to form a new net (Fig. 25*J*). These nets are much smaller than the ones developed later by the zoospores arising within the vegetative cells of the colony.

Protosiphon. *Protosiphon* is a unicellular coenocytic alga occurring on damp earth. It shows a striking resemblance to *Botrydium*, one of the Xanthophyceae, and often grows with it in the same habitat. The plant has a green aerial portion that is tubular or bladder-like and a

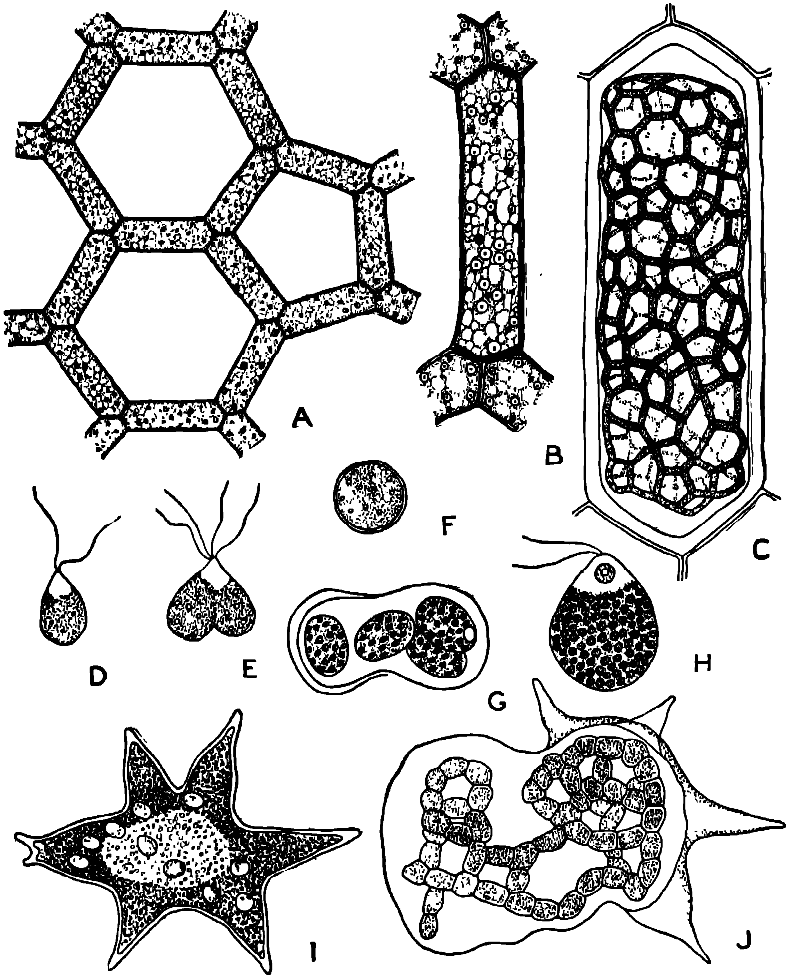

FIG. 25. *Hydrodictyon reticulatum.* *A*, portion of colony, ×150; *B*, single cell with many nuclei and pyrenoids, ×350; *C*, young net formed within a parent cell, *D*, a gamete; *E*, gametes fusing; *F*, zygote; *G*, four zoospores escaping from zygote; *H*, a zoospore escaped from zygote; *I*, polyhedron formed by a zoospore; *J*, young net escaping from polyhedron. (*C* to *F*, *after Klebs; G to J*, *after Pringsheim.*)

colorless underground portion that resembles a rhizoid (Fig. 26*A*). It is entirely without cross walls. The cytoplasm, in a thin layer surrounding a large central vacuole, contains numerous scattered nuclei (Fig. 26*B*). When young, the cell has a large reticulate chloroplast with many pyrenoids; later there may be several chloroplasts. Reserve food occurs chiefly as starch. The aerial portion may bud off new plants that later become detached. When covered with water, the protoplast may give rise to a number of biciliate zoospores or isogametes that escape

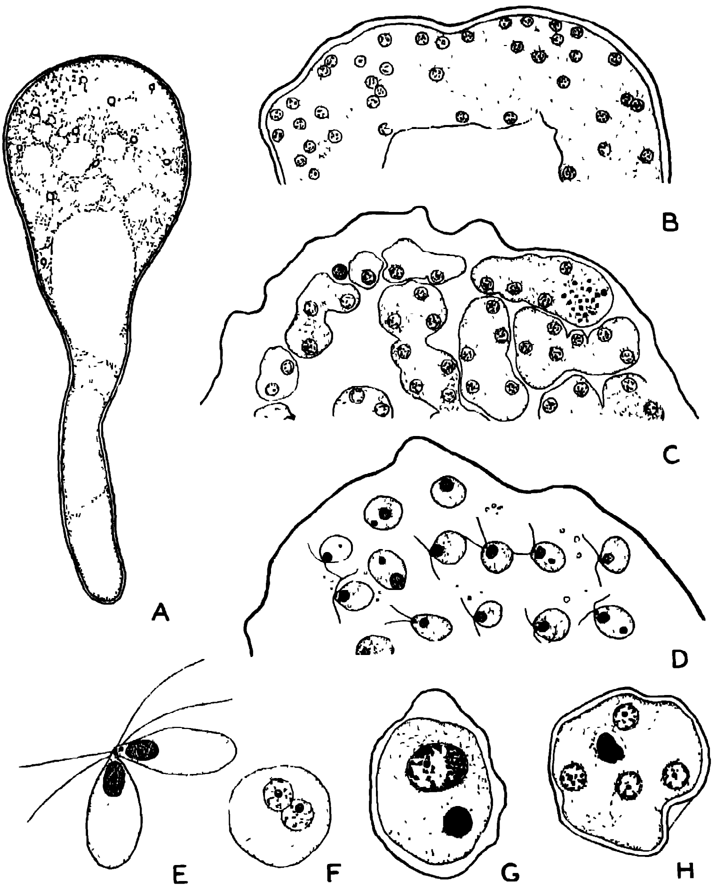

FIG. 26. *Protosiphon botryoides.* *A*, longitudinal section of vegetative plant; *B*, upper portion, showing scattered nuclei; *C*, an older stage, the cytoplasm undergoing progressive cleavage; *D*, formation of zoospores; *E* and *F*, gametic union; *G*, a zygote; *H*, germinating zygote with four nuclei. (*After Bold.*)

through an apical pore (Fig. 26*C–H*). Gametes from the same plant may pair and fuse. The zygote, which becomes thick-walled and dormant, produces a new plant directly. If the soil becomes dry, the vegetative protoplast may form aplanospores by progressive cleavage of the cytoplasm. These may be either small and uninucleate or larger and multinucleate. The latter, upon germination, usually give rise to zoospores or isogametes, but may develop into a new vegetative plant directly.

Summary. The Chlorococcales range from simple isolated cells to complex colonies. In this and succeeding orders nonmotility is the permanent condition of the vegetative cells. Although usually uninucleate, frequently these are multinucleate and often contain more than one chloroplast. Colonies are formed by the coming together of free cells (usually zoospores) derived from a single parent cell and there is no subsequent division of vegetative cells. Cell division occurs only in connection with the formation of reproductive cells. Reproduction is accomplished by zoospores, aplanospores, or akinetes, and usually also by isogametes.

3. Ulotrichales

The Ulotrichales have been called the representative group of the Chlorophyceae. Most of them live in fresh water but some are marine.

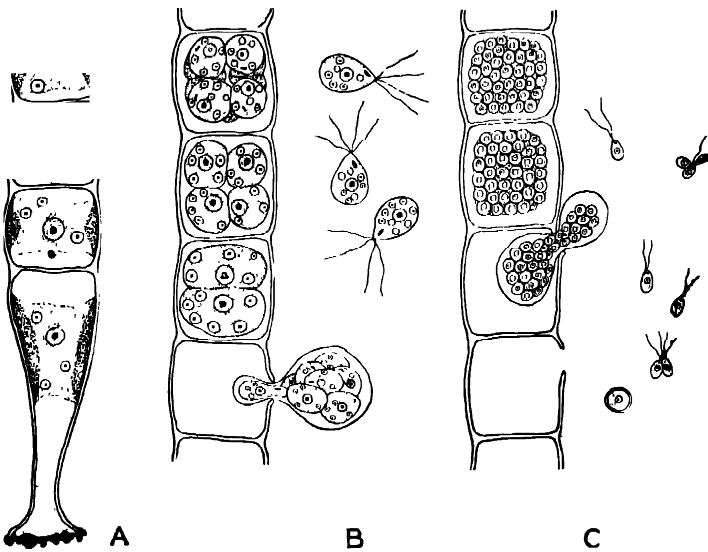

FIG. 27. *Ulothrix zonata*, vegetative and reproductive stages, ×700. *A*, basal portion of filament, showing holdfast cell and three vegetative cells, each with a single nucleus and a peripheral band-like chloroplast with many pyrenoids; *B*, formation and escape of zoospores; *C*, formation and escape of gametes, some of which are pairing.

A few live in damp places on land. *Trichophilus* grows inside the hair of the South American sloth. To this order belong 85 genera and approximately 500 species, the principal genera being *Ulothrix*, *Chaetophora*, *Draparnaldia*, *Stigeoclonium*, *Protococcus*, *Ulva*, and *Coleochaete*.

Ulothrix. This alga is of widespread occurrence in streams, lakes, and ponds, where it grows attached to objects in the water. A few of its species are marine. The plant body is multicellular, consisting of a simple unbranched filament (Fig. 27*A*). The basal cell is elongated and modified to serve as a holdfast, but all the other cells are alike, being shortly cylindrical. Each contains a central nucleus and a peripheral band-like chloroplast usually with many pyrenoids. The chloroplast may form either a complete or a partial band. Any cell in the filament, except the basal one, may divide by the formation of a cross wall between two daughter protoplasts, thus resulting in growth of the filament.

In asexual reproduction, the contents of any vegetative cell, except the holdfast, may divide to form mostly 2, 4, 8, or 16 zoospores (Fig. 27*B*). These escape through a pore in the cell wall and swim by means of four equal cilia attached apically. When discharged, the zoospores are enclosed in a common membrane that soon disappears. As in the vegetative cells of the Volvocales, each zoospore has a red eyespot and a contractile vacuole. After a period of free swimming, a zoospore comes to rest, withdraws its cilia, and secretes a cell wall. It then gives rise to a new filament by repeated cell divisions. Sometimes aplanospores are formed instead of zoospores. They frequently germinate within the parent cell.

Sexual reproduction takes place in *Ulothrix* by the conjugation of isogametes (Fig. 27*C*). These originate from the vegetative cells in the same way as the zoospores do, but are smaller, more numerous (usually 32 or 64 in a cell), and have only two cilia. They escape through a pore in the cell wall, enclosed in a common membrane that soon breaks down. Following pairing and fusing of the gametes, the resulting zygotes secrete a heavy wall and generally do not germinate until the following spring. Then each produces 4 to 16 zoospores (or sometimes aplanospores) that, in turn, give rise to new vegetative filaments. The zygote is the only diploid cell in the life history. When its nucleus divides, the chromosome number is reduced one-half. Although isogamous, *Ulothrix* shows some degree of sexual differentiation in that the gametes of one filament fuse only with those of another.

Chaetophora. Some of the Ulotrichales are branching filaments, often with cells showing a differentiation in size. One such member is *Chaetophora*, frequently found in standing water attached to submerged objects. The cells of the branches become progressively smaller and end in hair-like appendages that taper to a point. In a closely related form, *Draparnaldia*, common in clear, cool streams, the cells of the main filament are much larger than those of the branches (Fig. 28). Cell structure and reproduction in both genera are much the same as in *Ulothrix*. *Stigeoclonium*, another relative of *Chaetophora*, is differentiated into a cushion-like basal portion from which arise a number of sparingly branched upright filaments. When exposed to dry conditions, the cells round off and separate, giving rise to a "palmella" stage. These cells are thick-walled and divide in any plane. They may remain in groups or become separate. With the return of favorable conditions, they produce a new filamentous body.

Protococcus. One of the commonest and most widely distributed of the green algae is *Protococcus*,[1] a terrestrial form growing on the shaded side of damp tree trunks, moist rocks, walls, etc. It is a unicellular alga,

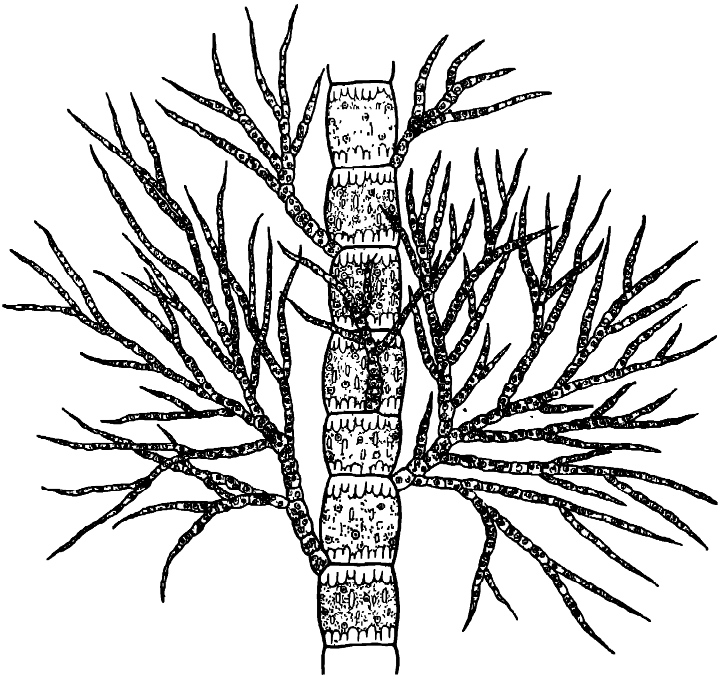

FIG. 28. *Draparnaldia*, portion of plant, a branching filament with a marked differentiation in size of vegetative cells, ×200. Each cell has a central nucleus obscured by the peripheral band-like chloroplast with many pyrenoids.

consisting of a spherical protoplast enclosed by a cell wall (Fig. 29). It has a small nucleus and a large, peripheral, irregularly lobed chloroplast usually without pyrenoids. Reproduction occurs entirely by cell division, spores and gametes being unknown. Permanent colonies are not formed but, instead of separating immediately, the cells usually hang together temporarily in small groups. In the presence of excessive moisture, the number of cells in a group is greatly increased and sometimes some of them grow into short filaments.

In most unicellular algae the division of a cell involves the formation of a new cell wall completely around each daughter protoplast and the disintegration of the wall of the parent cell. In *Protococcus*, however, a

[1] Often called *Pleurococcus.*

cross wall is developed across the parent cell, a method characteristic of *Ulothrix* and multicellular algae in general. If a second wall appears in one or both of the daughter cells before they separate, it comes in at right angles to the first one. Later divisions may be in the third plane. Thus there is a slight tendency in *Protococcus* toward the development of a multicellular body.

Protococcus is now generally regarded, not as a primitive form, but as one that has become reduced from more highly developed ancestors, probably as a result of its terrestrial mode of life. This is indicated by

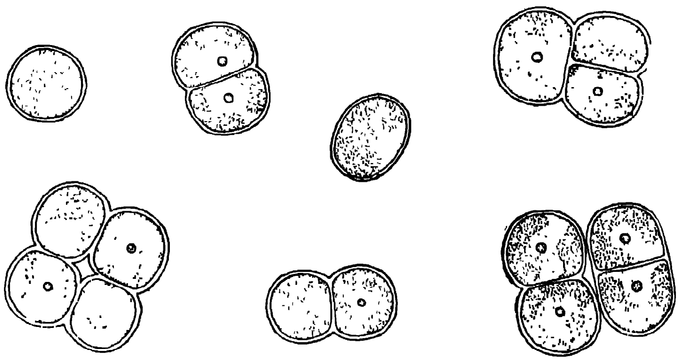

FIG. 29. *Protococcus viridis*, a unicellular green alga, ×1,000. Some of the cells have divided to form small temporary groups. Each cell has a central nucleus and a peripheral lobed chloroplast.

its advanced method of cell division combined with a failure to develop an extensive multicellular plant body like that of other Ulotrichales and by the absence of zoospores and gametes, which even such truly primitive forms as *Chlamydomonas* possess.

Ulva. This is a widely distributed marine alga commonly known as "sea lettuce." It grows along seacoasts between the high- and low-tide lines. The vegetative body consists of a plate-like thallus two layers of cells in thickness (Fig. 30). It is attached to rocks and other objects in the water by means of a basal holdfast consisting of long colorless rhizoids. The thallus may reach a length of 30 cm. or more. Each cell is uninucleate and has a single chloroplast with a pyrenoid.

Reproduction in *Ulva* closely resembles that of *Ulothrix*. Zoospores arise from ordinary vegetative cells situated along the thallus margin, four or eight zoospores being produced in each cell. They are liberated into the water through an opening in the cell wall and swim by means of four cilia. Upon germination, a zoospore gives rise to a plant that produces only gametes. These are smaller than the zoospores, more numerous (16 or 32 in a cell), and biciliate. Two similar gametes[1] coming from

[1] Although some species of *Ulva* are strictly isogamous, others produce two kinds of gametes that differ slightly in size.

separate plants unite to form a zygote. Instead of becoming a thick-walled resting cell, the zygote germinates immediately and produces a plant that bears only zoospores.

Thus *Ulva* illustrates the phenomenon of *alternation of generations*. Two separate plants, one producing gametes and the other spores, are involved in each life cycle and, although they look alike, the gamete-producing plants are haploid and the spore-producing plants are diploid.

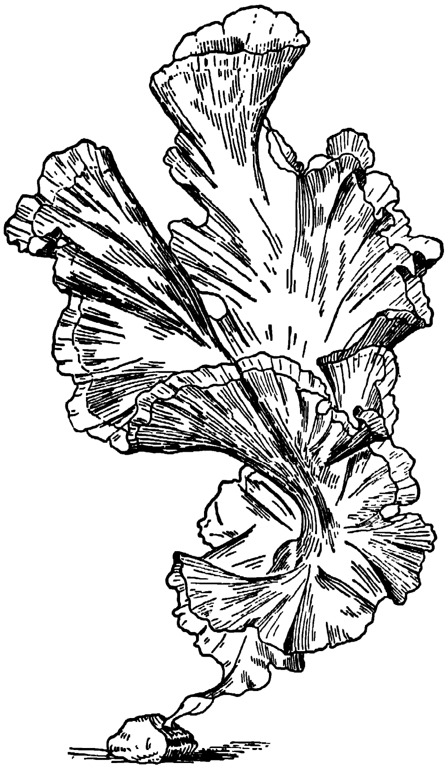

FIG. 30. *Ulva lactuca*, the sea lettuce, about one-half natural size. The bright green thallus is only two layers of cells thick. (*After Thuret.*)

The doubling of chromosomes, resulting from the conjugation of two gametes, is carried over by the zygote to the cells of the spore-producing plant. The reduction of chromosomes takes place when the zoospores are produced. These haploid spores give rise to the gamete-producing plants. The haploid plants are called *gametophytes* and the diploid plants *sporophytes*. Because the two kinds of plants are alike vegetatively, *Ulva* displays an *isomorphic* alternation of generations.

Coleochaete. *Coleochaete* is a small fresh-water alga that usually grows attached to leaves and stems of aquatic seed plants, such as water lilies and cattails. Depending on the species, the vegetative body is either a branching filament, a cushion with free branches, or a circular disk with radiating rows of cells (Fig. 31*A*). When disk-like, it rarely exceeds 5 mm. in diameter. Some of the cells bear hair-like outgrowths,

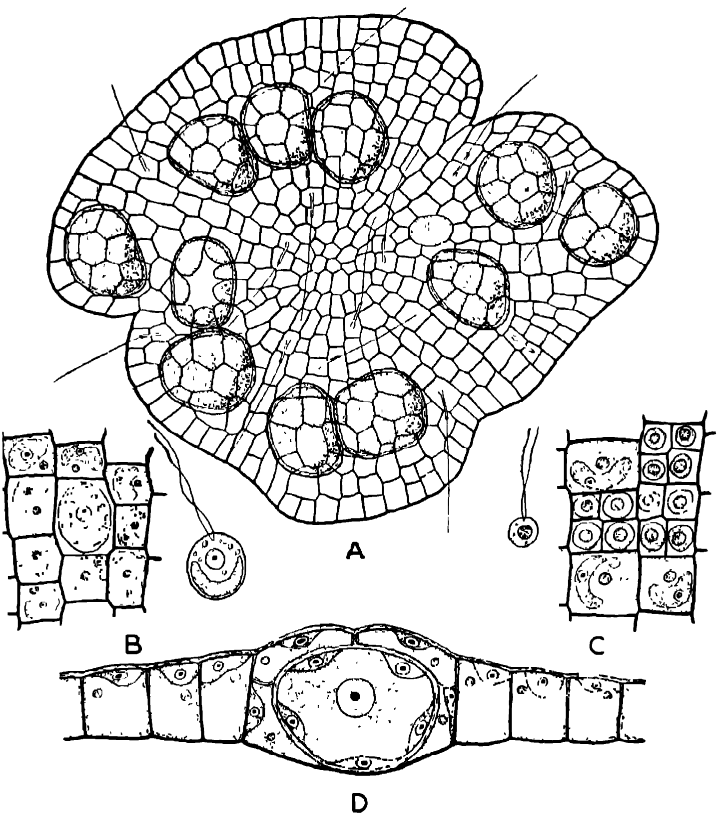

FIG. 31. *Coleochaete scutata*, a discoid species. *A*, a small vegetative plant with numerous zygotes overgrown by the surrounding cells, ×150; *B*, a small group of vegetative cells, one of which is giving rise to a zoospore, and an escaped zoospore, ×500; *C*, vegetative cells giving rise to antheridia, and an escaped sperm, ×500; *D*, cross section of portion of thallus, showing a zygote, ×350.

each with a sheath at its base. Each cell has a single nucleus and a chloroplast with one or sometimes two pyrenoids. Growth is always apical, in the discoid species occurring by means of a marginal meristem. Biciliate zoospores, formed singly, may arise in any vegetative cell (Fig. 31*B*). They escape through a pore in the cell wall.

In being heterogamous, *Coleochaete* makes an advance over the other Ulotrichales that have been considered. In the discoid species *antheridia* are formed by the division of a vegetative cell into smaller cells, the protoplasts of which escape into the water as biciliate *sperms* (Fig. 31*C*). An *oögonium* is formed near the margin of the thallus by the enlargement of a vegetative cell, its protoplast becoming a nonmotile *egg*. In the branched species the antheridia and oögonia are borne at the ends of separate branches. Here the oögonium has a long, slender extension (trichogyne) with a terminal opening. A few species are dioecious.

A sperm enters the oögonium and fertilizes the egg, the zygote enlarging and becoming thick-walled. At the same time adjacent vegetative cells grow up around the oögonium and form a case (Figs. 31*D* and 32*A*).

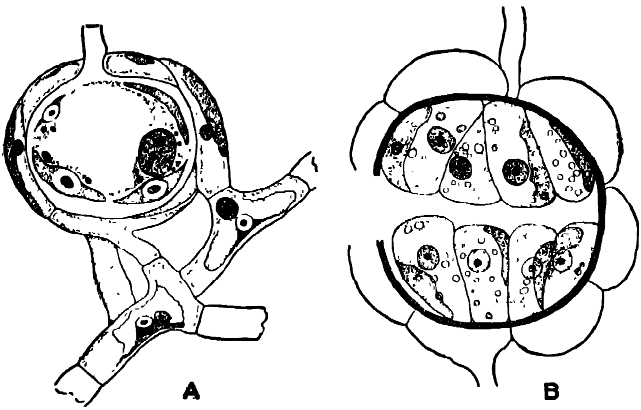

FIG. 32. *Coleochaete pulvinata*. *A*, section of oögonium containing a zygote and surrounded by jacket produced by adjacent vegetative cells; *B*, section of oögonium containing a group of cells derived from the zygote, each of which gives rise to a zoospore. (*After Oltmanns*.)

After undergoing a period of rest, the zygote germinates inside the oögonium and produces a spherical body consisting of 16 or 32 cells, each cell in turn producing a biciliate zoospore (Fig. 32*B*). This escapes and gives rise to a new vegetative plant. In the discoid species the zygote produces an eight-celled body. The reduction of chromosomes takes place when the zygote germinates. Consequently, the body of spore-producing cells that develops from it is haploid and so cannot be regarded as a sporophyte. Thus *Coleochaete* is without a true alternation of generations.

Summary. The plant body of the Ulotrichales is multicellular (except in *Protococcus*), being either a simple filament, a branched filament, or a flat plate-like thallus. The cells contain one nucleus and a single chloroplast. Growth occurs by division of the vegetative cells. Nearly all members produce zoospores, these being either biciliate or quadriciliate. Asexual reproduction may also occur by aplanospores or by akinetes. Sexual reproduction ranges from isogamy to heterogamy.

4. Oedogoniales

The Oedogoniales are related to the Ulotrichales and are often classified with them. They are a fresh-water group including only 3 genera and approximately 400 species. The two chief genera are *Oedogonium* and *Bulbochaete*, both occurring throughout the world.

Oedogonium. This widely distributed alga, comprising nearly 300 species, generally lives in ponds, lakes, and quiet streams, often attached to sticks, stones, and other aquatic plants. It consists of a simple unbranched filament that, when young, has a basal holdfast cell but later is usually free-floating. The cells are elongated and uninucleate. Each contains a peripheral chloroplast with many pyrenoids. The chloroplast is band-like and reticulate. Any vegetative cell except the basal one may divide.

Oedogonium has a peculiar method of cell division seen only in the other members of its order (Fig. 33). It results in the formation of distinctive "apical caps." The nucleus divides near the upper end of the cell, where simultaneously a ring-like thickening of cellulose is developed on the inside of the lateral wall above the dividing nucleus. A groove appears in this ring and the cell wall splits transversely opposite the groove. A thin cross wall now appears between the daughter nuclei and the protoplast is divided in half. The ring stretches into a cylinder as each daughter protoplast elongates, the new cross wall moving upward to the top of the parent cell, where it unites with the lateral wall very close to where the transverse split occurred. The upper cell, which has a new cell wall, continues to elongate until it reaches the size of the lower cell, which possesses the old cell wall.

Asexual reproduction occurs by the formation of large zoospores, each of which arises from the entire contents of an ordinary vegetative cell (Fig. 34*A*, *B*). This escapes as a naked protoplast that bears a crown of cilia. The liberation of the zoospore is accompanied by a transverse splitting of the cell wall at the apical end. After a period of free swimming, the zoospore comes to rest with its ciliated end downward, retracts its cilia, forms a cell wall, and gives rise by repeated divisions to a new filament. *Oedogonium* may also produce akinetes, although these are relatively uncommon. The akinetes may occur either singly or in a linear series. They germinate directly into new filaments.

Oedogonium is heterogamous. An antheridium arises as a short cell that is cut off at the apex of an ordinary vegetative cell. It may remain the only one, but generally more (from 2 to 40) are produced by continued division of the lower cell or by division of antheridia already formed (Fig. 34*C*). Each antheridium gives rise to one or, more commonly, to two sperms, either by a vertical or a transverse division of the protoplast, depending on the species. The sperms escape into the water and, like the zoospores, swim by means of a crown of cilia. An oögonium also commonly arises from the smaller upper cell produced by the division of an ordinary vegetative cell, but this cell subsequently enlarges by the accumulation of food (Fig. 34*D*). The oögonia may occur separately or

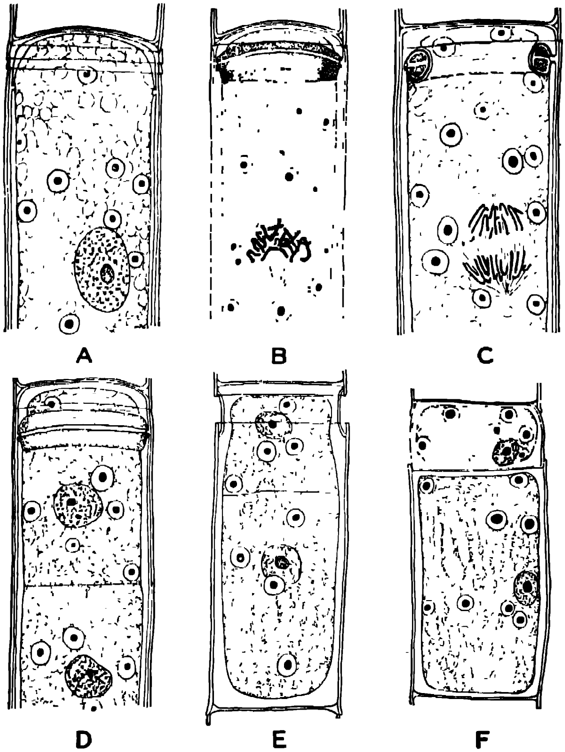

FIG. 33. Nuclear and cell division in *Oedogonium grande*, ×320. *A*, elongation of nucleus and appearance of young ring; *B*, metaphase, *C*, anaphase; *D*, formation of cross wall and separation of nuclei; *E*, broken outer layer of cell wall and stretching of ring; *F*, straightening of ring and migration of cross wall upward to unite with inner layer of cell wall. (*After Ohashi.*)

several may be cut off in a series. The entire protoplast of the oögonium becomes a large nonmotile egg.

A sperm enters an oögonium through a pore in its wall and unites with the egg. The zygote becomes a heavy-walled resting cell that later produces four zoospores (Fig. 34*E*, *F*). When liberated, these are enclosed by a common membrane that soon disappears. From each of the zoospores a new filament is developed. The reduction of chromosomes occurs in connection with the germination of the zygote, and so the four zoospores are haploid.

Some species of *Oedogonium* are monoecious, the antheridia and oögonia occurring in the same filament. Other species are dioecious, the two kinds of sex organs being borne on separate filaments. In some dioecious species the male and female filaments are approximately equal in size.

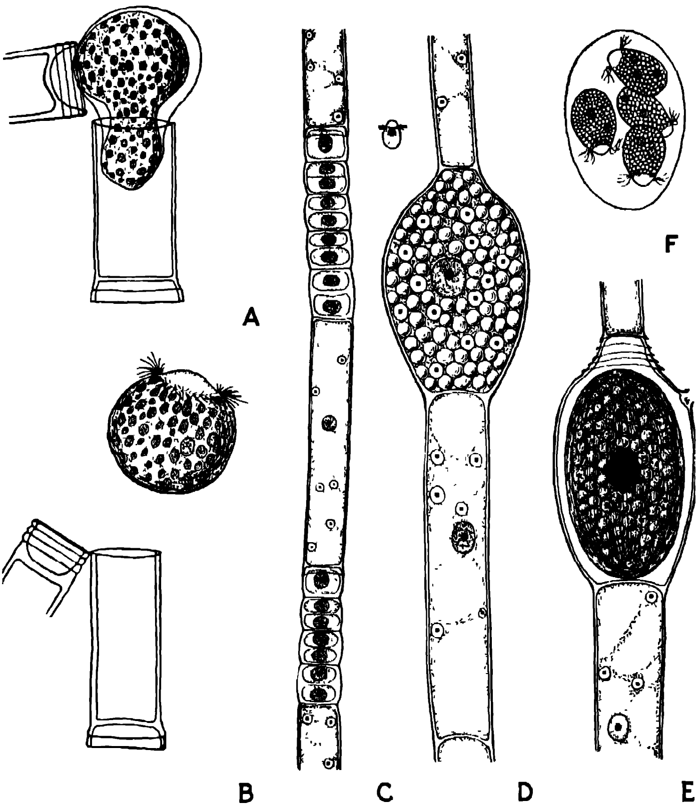

FIG. 34. Reproduction in *Oedogonium*, × 500 *A* and *B*, the entire contents of a vegetative cell escaping as a zoospore; *C*, portion of filament with two groups of antheridia, also a single escaped sperm; *D*, portion of filament with an oogonium containing a mature egg in which are many pyrenoids and starch grains; *E*, heavy-walled zygote still within the oögonium; *F*, group of four zoospores produced by the zygote. (*A and B, after Hirn; F, after Juranyi.*)

In others the male filaments are very small, consisting of only a few cells. These dwarf filaments are produced by special small zoospores, called *androspores*, that originate singly in rows of small cells resembling antheridia. The androspores germinate on the female filaments near or on an oögonium (Fig. 35). The dwarf filament usually consists of a single vegetative cell that cuts off one or several terminal antheridia, each producing two sperms. Figure 35 shows three dwarf filaments of different ages. In the one on the right the single vegetative cell has cut off a small, undivided, antheridial cell. In the middle filament a second antheridium has been formed by the vegetative cell, while the first antheridium has produced two sperms. In the male filament on the left two sperms have escaped from the upper antheridium, but two more have been formed in the lower one.

Bulbochaete is a genus closely resembling *Oedogonium*, differing chiefly in having branches, most of the cells of which bear long one-celled hairs that are swollen at the base.

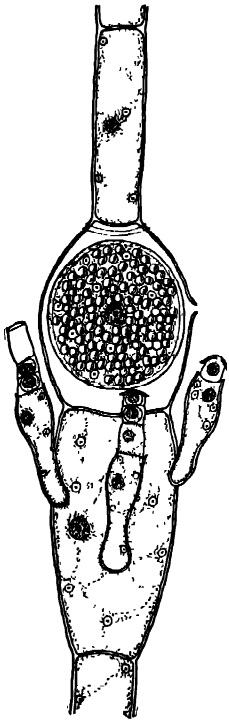

FIG. 35. A species of *Oedogonium* having dwarf male filaments, three of which have developed on the cell below the oögonium, ×300.

Summary. The Oedogoniales are a small order differing from the Ulotrichales mainly in having a peculiar method of cell division and motile reproductive cells with a crown of cilia. The vegetative body is multicellular and filamentous, the cells having one nucleus and a single chloroplast. Asexual reproduction occurs by zoospores, sometimes by akinetes. All the members are heterogamous.

5. Conjugales

The Conjugales constitute a distinct and highly specialized order of green algae that occupy an isolated position. In fact, they are sometimes removed from the Chlorophyceae and made an independent class. All of them occur in fresh water. They include 38 genera and over 2,400 species. Some representative genera are *Closterium*, *Cosmarium*, *Mougeotia*, *Spirogyra*, and *Zygnema*.

Desmids. These algae are widely distributed in bogs, ponds, and small lakes, usually becoming abundant late in the season. They number about 2,250 species. *Closterium* is a genus of nearly 200 species, while *Cosmarium* has over 800. The desmids are unicellular and the cells display a great variety of form. Like the diatoms, they have won the favor of microscopists by their great beauty. Desmids are typically solitary, but some develop into filamentous colonies. Many desmids have the power of movement, which appears to be caused by exudation of mucilage through pores in the cell wall.

In most desmids the cell is organized into two symmetrical halves that are generally separated by a median constriction called the *isthmus* (Figs. 36 and 37). In each half there is usually one large chloroplast (sometimes two) with one or more pyrenoids. The chloroplast is often elaborately lobed. The nucleus lies in the isthmus. In *Closterium*, at each end of the cell, is a small group of calcium sulphate crystals that show Brownian movement. In some desmids, the outer surface of the cell wall displays warts, spines, ridges, or other markings, most of which show a regular arrangement.

Asexual reproduction occurs mainly by fission, rarely by aplanospores. Zoospores have never been observed. In cell division the nucleus divides

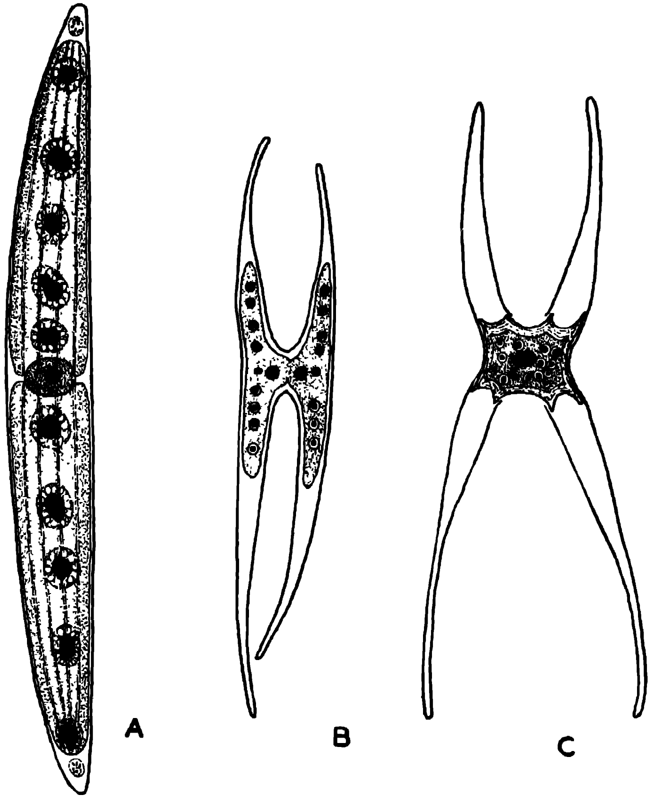

FIG. 36. *Closterium*, a common desmid. *A*, vegetative cell, showing nucleus at isthmus, a large lobed chloroplast with a row of pyrenoids in each half of the cell, and at each end a vacuole containing a few crystals, ×300; *B* and *C*, another species, showing two stages in conjugation, ×200.

first and then a cell wall is formed across the isthmus. Each of the two chloroplasts splits transversely. The daughter cells then separate and each forms a new half similar to itself. In sexual reproduction two cells come together and secrete a common mucilaginous sheath (Fig. 36*B*, *C*). Their walls generally break at the isthmus. Then the protoplasts escape and fuse to form a zygote. In a few desmids each cell sends out a short tube. These meet, become continuous, and the two protoplasts fuse in the tube. The desmids are isogamous but their gametes, each represent-

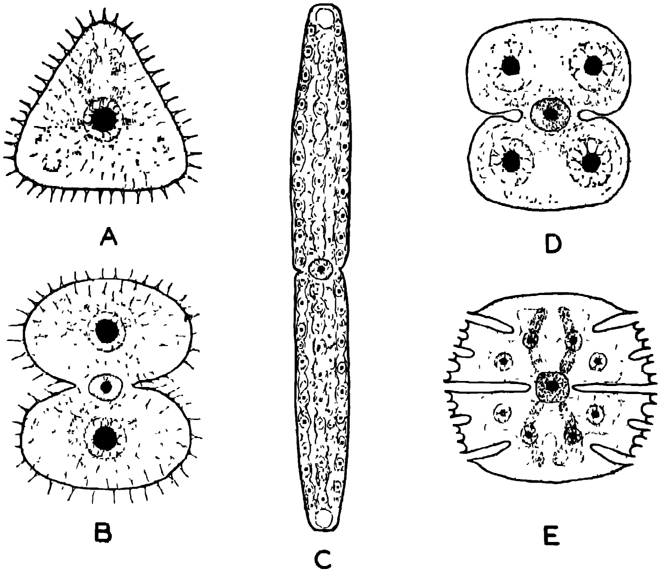

FIG. 37. Several desmids, showing variety of form. *A*, end view and *B*, front view of *Staurastrum*; *C*, *Docidium*; *D*, *Cosmarium*, *E*, *Micrasterias*; *C*, X250; others, X400.

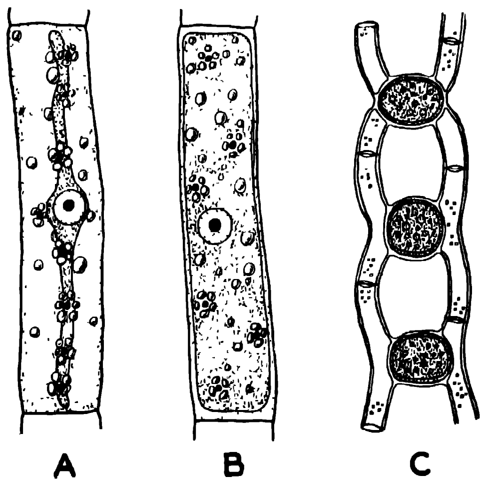

FIG. 38. Single cells of *Mougeotia*, showing the plate-like chloroplast as seen in side (*A*) and face (*B*) views, X500; *C*, conjugating filaments, with three zygotes formed in the conjugating tubes. (*C*, *after Wittrock*.)

ing an entire vegetative protoplast, are nonciliated. The zygote becomes thick-walled and, after a period of rest, its protoplast escapes and divides generally into two daughter protoplasts, each of which becomes a new individual. As a result of two successive divisions of the zygote nucleus, during which the reduction of chromosomes occurs, each daughter protoplast has two haploid nuclei. Then one nucleus in each protoplast degenerates.

Mougeotia. This alga consists of a delicate unbranched filament. Each cell displays a nucleus and a peculiar, axial, plate-like chloroplast containing two or more pyrenoids (Fig. 38*A*, *B*). The chloroplast can change its position in the cell, presenting its flat surface to dull light and

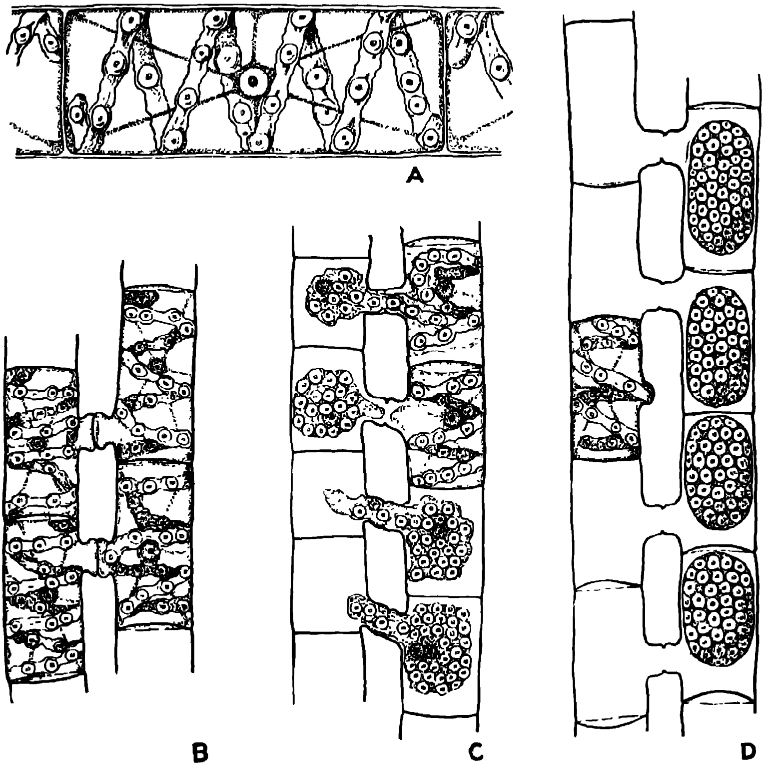

FIG 39. *Spirogyra.* *A*, a vegetative cell, showing the central nucleus and the peripheral, band-like, spiral chloroplast with many pyrenoids, ×500; *B*, *C*, *D*, stages in conjugation, ×250.

its edge to bright light. Reproduction occurs by fragmentation, aplanospores, and by the conjugation of isogametes. The cells of two filaments lying parallel to each other put out short bud-like outgrowths that come into contact and form tubes. The protoplasts of two conjugating cells pass into one of these tubes and there fuse, producing a heavy-walled zygote (Fig. 38*C*). Upon germination, four cells are formed. Three of these die, the fourth producing a new filament. It is probable that the chromosome reduction takes place when the zygote germinates.

Spirogyra. *Spirogyra* is a well-known green alga very common in ponds, lakes, and streams, where it forms slimy bright green masses on or beneath the surface of the water. It is a large genus of over 100 species. The vegetative body is an unbranched filament with cylindrical cells that are usually elongated. Each cell has a single nucleus suspended in the center by strands of cytoplasm (Fig. 39*A*). It also has one or more peripheral, ribbon-like chloroplasts with many pyrenoids. The chloroplasts have the form of spiral bands, the number in each cell depending

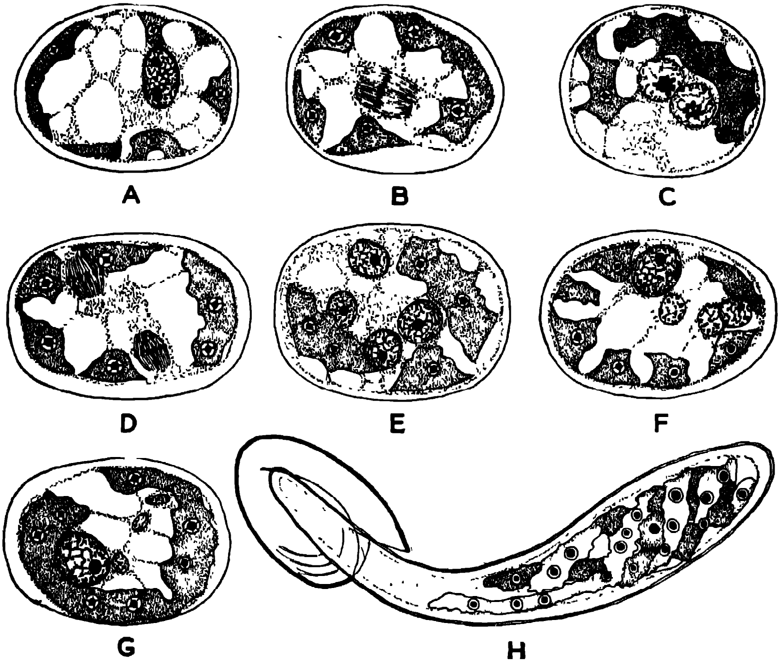

FIG. 40. Nuclear changes in the zygote of *Spirogyra longata* (*A* to *G*) and germination of the zygote of *Spirogyra neglecta* (*H*). *A*, *B*, *C*, first meiotic division of fusion nucleus in the zygote; *D* and *E*, second division; *F* and *G*, degeneration of three of the haploid nuclei. (*After Tröndle.*)

on the species. Any cell may divide by the formation of a cross wall, thus resulting in growth of the filament. In some species the cross walls possess characteristic infoldings.

In sexual reproduction the cells of the two filaments lying side by side put out lateral projections that come in contact (Fig. 39*B–D*). The contiguous portions of the cell walls at the ends of these projections then break down and form tubes leading from one filament to the other. Through these conjugating tubes the protoplasts of one filament pass to fuse with those of the other filament, forming zygotes. An entire vegetative protoplast thus becomes a large gamete. The zygote develops a heavy wall and goes into a resting stage. Upon germination, which usually occurs in the following spring, it directly produces a new filament

(Fig. 40*H*). The zygote becomes diploid by the fusion of the two nuclei derived from the conjugating protoplasts. When germination takes place, the fusion nucleus undergoes two successive divisions that result in a reduction of chromosomes (Fig. 40*A*–*G*). Of the four haploid nuclei thus formed, three degenerate, leaving one to function. In this way the zygote gives rise to a haploid filament.

Zoospores are never produced in *Spirogyra*. If conjugation fails to occur, a protoplast may round up and become a heavy-walled cell that, after a period of rest, gives rise to a new filament. Such a cell is often

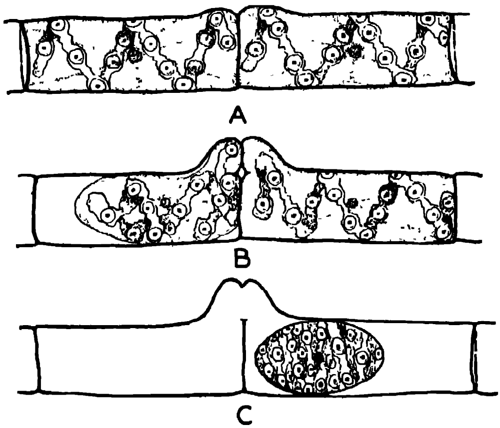

FIG. 41. A species of *Spirogyra* with lateral conjugation, gametic union occurring between adjacent cells of the same filament. *A*, *B*, *C*, development of conjugating tubes and formation of zygote, ×300.

called an aplanospore but would be more appropriately designated as a gamete that develops without undergoing conjugation.

Spirogyra, like the other Conjugales, is peculiar because an entire vegetative protoplast becomes a single large gamete that is not ciliated and does not escape into the water. Although the gametes show no differentiation in size, the active ones are regarded as male and the passive ones as female. The ordinary type of conjugation is known as *scalariform* (ladder-like) conjugation. In a few species *lateral* conjugation occurs (Fig. 41). In this type conjugating tubes are developed between adjacent cells of the same filament. At its completion a zygote is formed in one of the conjugating cells.

Zygnema. This is a genus closely related to *Spirogyra* and resembling it in many ways. Both forms grow in the same sort of places and look much alike to the naked eye. The filaments of *Zygnema* are unbranched and consist of cylindrical, more or less elongated cells (Fig. 42). Each has two spherical chloroplasts between which, at the center of the cell, lies the nucleus. Each chloroplast has a single pyrenoid surrounded by radiating starch grains. As in *Spirogyra,* sexual reproduction takes place by the passage of isogametes, each representing an entire vegetative protoplast, through conjugating tubes and their fusion in the cells of one of the filaments. There is also the same degeneration of three of the haploid nuclei derived from the nucleus of the zygote.

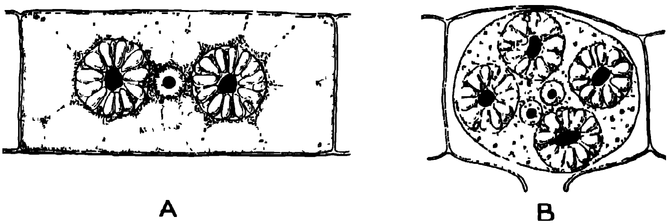

FIG. 42. Single cells of *Zygnema,* ×750. *A,* vegetative cell, showing central nucleus and two spherical chloroplasts, each with a pyrenoid surrounded by radiating starch grains; *B,* young zygote with four chloroplasts and the two gametic nuclei not yet fused.

Summary. The Conjugales are an aberrant order of green algae showing no close relationship to any of the other orders. The plant body may be either unicellular or multicellular, in the latter case consisting of a simple unbranched filament. The cells are uninucleate and have one or more peculiar chloroplasts. The distinguishing feature of the order is the absence of all ciliated cells in the life history. No zoospores are produced, but aplanospores may occur. Sexual reproduction is accomplished by the conjugation of two nonciliated isogametes, each derived from the entire protoplast of a vegetative cell. These either escape and fuse, unite in a conjugating tube, or pass through a conjugating tube and fuse in one of the cells.

6. Siphonocladiales

This is a group whose members are often distributed among other orders, although its characters are rather well defined. They are represented in both fresh and salt water, but most of them are marine, being found principally in tropical and subtropical seas. Many of the marine forms are incrusted with lime. Representatives of the group have been found as fossils as far back as the Ordovician. The Siphonocladiales include about 37 genera and 450 species, the best-known genera being *Cladophora, Sphaeroplea,* and *Acetabularia.*

Cladophora. *Cladophora* is a genus of about 150 species, world-wide in distribution. It is found in great abundance in streams, ponds, and lakes, usually attached to stones and piers. Some of its species are marine. The vegetative body is filamentous and much branched, its cells being elongated and cylindrical (Fig. 43*A*). A branch originates as an outgrowth from the upper end of a cell lying near the end of a filament. Each cell is a coenocyte, containing many nuclei. The cytoplasm usually surrounds a large central vacuole. When young, a cell has a large, peripheral, reticulate chloroplast with many pyrenoids. Later the chloroplast often appears to break up into numerous small chloroplasts, some of which have pyrenoids.

Many quadriciliate zoospores are formed, usually in cells at or near the ends of branches (Fig. 43*B*). The zoospores, which are uninucleate,

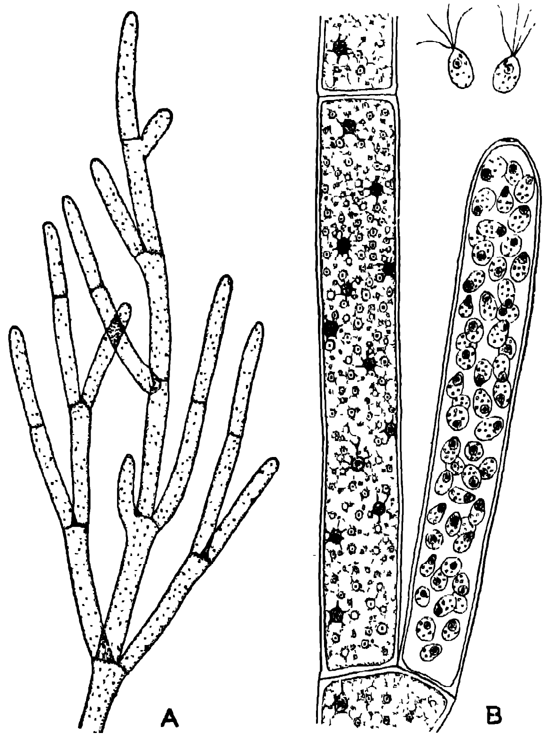

FIG. 43. *Cladophora*. *A*, portion of plant, a branching filament, ×65; *B*, a vegetative cell, a sporangium, and two escaped zoospores, ×300 Each vegetative cell has many nuclei and a large, peripheral, reticulate chloroplast with a large number of pyrenoids.

escape singly through a small pore in the cell wall. They develop into new filaments, but these, in turn, produce only isogametes. The gametes may arise in any vegetative cell. They escape into the water and swim by means of two cilia. The gametes pair and fuse, but fusion occurs, as a rule, only between gametes coming from different plants. The zygote, without undergoing a period of rest, gives rise to a new filament directly. This plant produces only zoospores. Although alike vegetatively, the gamete-producing plants are haploid and the spore-producing plants are diploid. The reduction of chromosomes occurs in connection with the formation of zoospores. Thus, as in *Ulva*, the life cycle of *Cladophora* involves a distinct alternation of generations of the isomorphic type.

Sphaeroplea. This is a fresh-water alga that grows in wet meadows and occasionally in pools. Although widely distributed, it is not common. The vegetative body consists of an unbranched filament with very long cylindrical cells, each containing numerous nuclei and chloroplasts (Fig. 44). The chloroplasts, some of which have pyrenoids, are parietally placed and grouped into wide annular bands of cytoplasm separated by

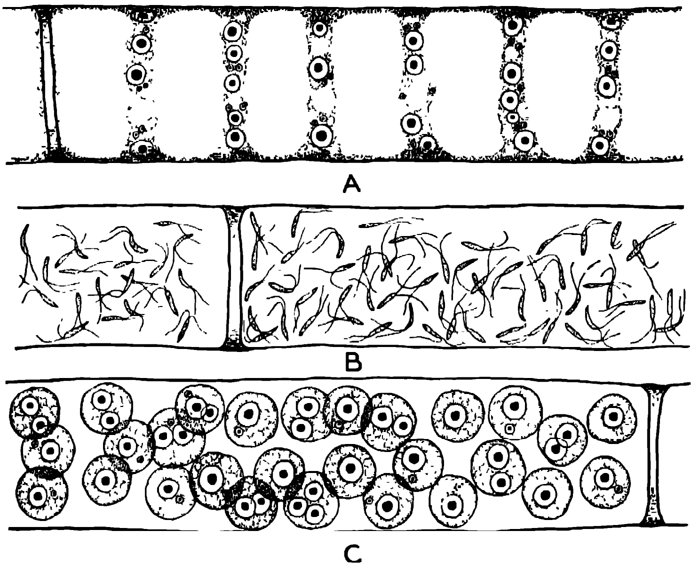

FIG. 44. *Sphaeroplea annulina*, ×400. *A*, portion of a vegetative cell with ring-like bands of cytoplasm containing many small nuclei, chloroplasts, and pyrenoids; *B*, antheridia producing sperms; *C*, portion of an oogonium with many eggs ready for fertilization.

wide vacuoles. The vegetative cells of *Sphaeroplea* do not produce any zoospores. Sexual reproduction is heterogamous, the two kinds of sex organs usually being borne in different filaments. Any vegetative cell, without undergoing a change in shape, may become an antheridium or an oögonium. The antheridium produces a large number of small biciliate sperms, while the oögonium gives rise to many large nonmotile eggs. The eggs are at first multinucleate, but later all the nuclei degenerate except one. The sperms escape through small pores in the cell wall, enter the oögonium through similar pores, and there fertilization takes place. Each zygote becomes thick-walled and, after undergoing a long resting period, gives rise usually to four biciliate zoospores. Each of these forms a new filament. The reduction of chromosomes occurs when the zygote germinates, and so the spores and vegetative filaments are haploid.

Acetabularia. This is a marine genus occurring in tropical and subtropical regions. It is called the mermaid's-wineglass. *Acetabularia crenulata* is a common species off the coast of Florida and throughout the West Indies. Its vegetative body, reaching a height of 6 to 9 cm., consists of a stalk bearing rhizoid-like holdfasts below and expanded above into a cup-like disk about 1 cm. in diameter (Fig. 45). The disk is composed of a whorl of elongated branches that are laterally coherent, each branch being a coenocyte. The plants are more or less incrusted with lime. At first the plant has a single nucleus that soon gives rise to many small nuclei. These pass up the stalk and enter the disk, which has now become divided into cells.

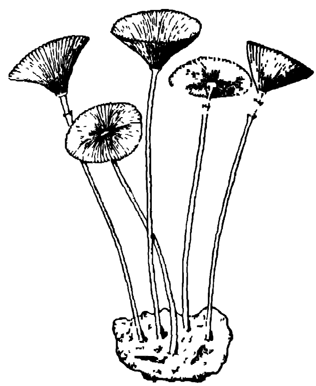

Fig. 45 *Acetabularia crenulata*, natural size.

Reproduction begins by the formation of a large number of aplanospores (cysts) within the fertile branches composing the disk. The aplanospores are at first uninucleate but later become multinucleate. They are liberated into the water and, after a resting period, each gives rise to a large number of biciliate isogametes that escape and fuse in pairs. The zygote germinates immediately to form a new plant. The vegetative plant is diploid, the reduction of chromosomes occurring when the nucleus of the aplanospore divides.

Acetabularia has been widely used by students of genetics and development, especially in experiments on regeneration and polarity.

Summary. The Siphonocladiales are multicellular algae with large multinucleate cells, these usually containing many small chloroplasts. The plant body is thus partially coenocytic. Vegetative growth takes place by cell division. Asexual reproduction usually occurs by zoospores, aplanospores, or akinetes. Sexual reproduction may be either isogamous or heterogamous. This order is related both to the Chlorococcales and to the Siphonales.

7. Siphonales

The Siphonales are a distinct group of mostly marine algae, only a few being found in fresh water. They are especially abundant in tropical seas. As in the Siphonocladiales, many marine forms secrete lime. Fossil members are known as far back as the Ordovician. The order includes 50 genera and about 350 species. Representative genera are *Vaucheria, Codium, Bryopsis,* and *Caulerpa.*

Vaucheria. This well-known alga grows in felt-like masses in fresh water and on damp soil. Some of its species live in brackish water and some live in the ocean. The plant body consists of a sparsely branched coenocytic filament without any cross walls in the vegetative portion. It is attached by means of colorless rhizoid-like holdfasts. Numerous small nuclei and chloroplasts are scattered throughout the cytoplasm, which surrounds a large central vacuole. There are no pyrenoids or starch grains, but oil droplets are usually present in abundance. In this respect *Vaucheria* differs from the other Siphonales.

Vaucheria displays three methods of vegetative reproduction, as follows: (1) A branch may be constricted at the base, thus producing a

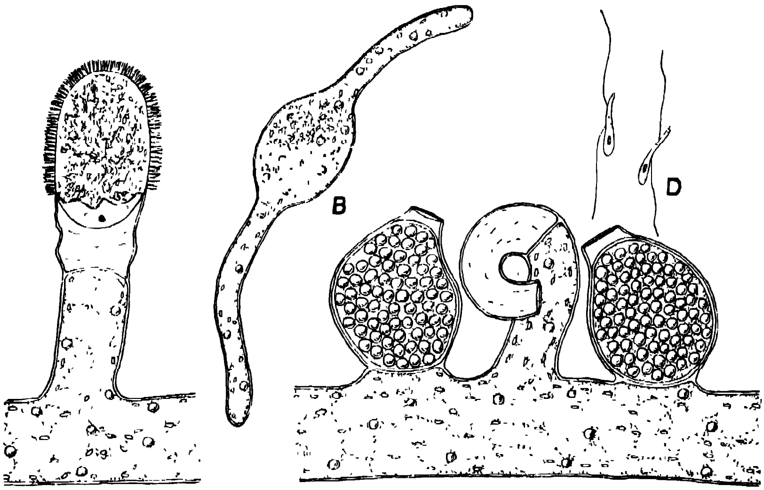

FIG. 46. *Vaucheria*, a coenocytic green alga, ×250. *A*, an escaping zoospore covered with many cilia; *B*, a zoospore giving rise to a new vegetative filament; *C*, two oogonia of *Vaucheria sessilis*, each with a zygote; also an antheridium that has discharged its sperms; *D*, two sperms, more highly magnified.

new plant body directly. (2) The tip of a branch may swell slightly and become cut off by a cross wall to form a club-shaped sporangium (Fig. 46*A*). The multinucleate protoplast in the branch rounds up and becomes a large zoospore entirely covered by cilia. The cilia are in pairs and beneath each pair is a nucleus. For this reason the zoospore is regarded as compound. It escapes into the water through a terminal pore and, upon germination, gives rise to a new filament (Fig. 46*B*). (3) The contents of an entire filament may break up into aplanospores, each developing a thick wall.

Vaucheria is heterogamous. The antheridia and oögonia are not transformed vegetative cells but are developed on special branches of the filament (Fig. 46*C*). In most species a short branch, sooner or later cut off by a wall, becomes a globular oögonium. Its protoplast is organized as an egg, which becomes uninucleate. It is uncertain whether this is accomplished by the degeneration of all its nuclei except one, as some observers have claimed, or, as others contend, by the passage back into the filament of all but one nucleus before the wall is formed at the base of the oögonium. Arising close to the oögonium is a longer and more slender branch, its curved tip being cut off by a wall to form an antheridium. In some species both kinds of sex organs are borne on the same branch, the antheridium being terminal and surrounded by two or more oögonia (Fig. 47). The antheridium produces many small biciliate sperms that are liberated into the water through a terminal pore. A sperm

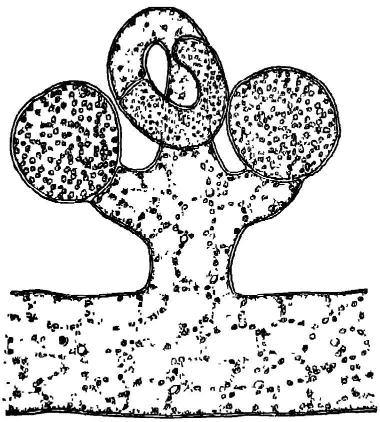

FIG. 47. Sex organs of *Vaucheria geminata*, two oögonia and an antheridium borne on the same branch, ×250.

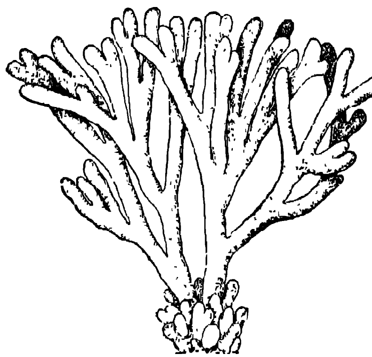

FIG. 48. Thallus of *Codium fragile*, one-half natural size.

enters an oögonium through a terminal pore in its wall and fuses with the egg to produce a heavy-walled zygote. After remaining dormant, it gives rise to a new filament directly. The reduction of chromosomes probably occurs during germination of the zygote.

Codium. *Codium* is a widely distributed marine alga that grows on rocks between tide lines. The thallus is dark green and spongy, consisting of thick cylindrical branches composed of a dense mass of interwoven filaments (Fig. 48). It is anchored by means of a basal disk-like holdfast. Like other members of the order, the vegetative body is without cross walls. The cytoplasm is peripheral and has numerous small nuclei and chloroplasts. There is no asexual reproduction by means of spores. Two kinds of gametangia are produced, generally on different plants. They arise on the sides of large club-shaped branches that form a sort of cortex, and are cut off by a basal wall. The male gametangium, which is smaller than the female one, liberates many thousands of biciliate male gametes. In the female gametangium some of the nuclei degenerate, while others enlarge. Several hundred biciliate female gametes are organized. These escape through a terminal pore and are fertilized in the water. The zygote gives rise at once to a vegetative plant. The vegetative plants of *Codium* are diploid and the reduction of chromosomes takes place in connection with the formation of the gametes.

Bryopsis. Some of the marine Siphonales are highly branched, one of these being *Bryopsis*. The thallus is composed of a prostrate rhizome-like portion, anchored by rhizoids, and an upright feathery portion, the

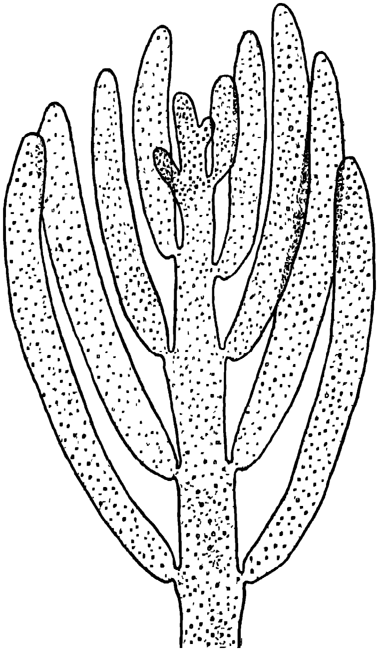

FIG. 49. A small portion of the vegetative body of *Bryopsis*, showing branches of limited growth, ×75.

latter consisting of an axis with branches of limited growth (Fig. 49). In the formation of a gametangium, a branch is cut off by a cross wall and gives rise to numerous bicilate gametes. A gametangium produces either male or female gametes and these are usually borne on different plants. The female gametes are about three times as large as the male ones. Both escape into the water, where they pair and fuse. The zygote secretes a cell wall and germinates immediately to form a new vegetative plant. There are no spores of any kind in the life cycle. The reduction of chromosomes occurs when the gametes are formed, and thus the vegetative plant is diploid.

Caulerpa. This is a marine form of interest because of the high degree of differentiation of its coenocytic plant body (Fig. 50). It consists of a creeping axis with root-like holdfasts and erect leaf-like shoots of various form. In some species the shoots reach a height of 30 cm. Cross walls are absent in the vegetative part of the plant, but the central cavity is traversed by numerous slender strands. Asexual reproduction occurs only by fragmentation, sexual reproduction by biciliate isogametes.

Summary. The Siphonales are characterized by a completely coenocytic plant body that is usually much branched and often differentiated in form. Cross walls appear only in connection with the formation of

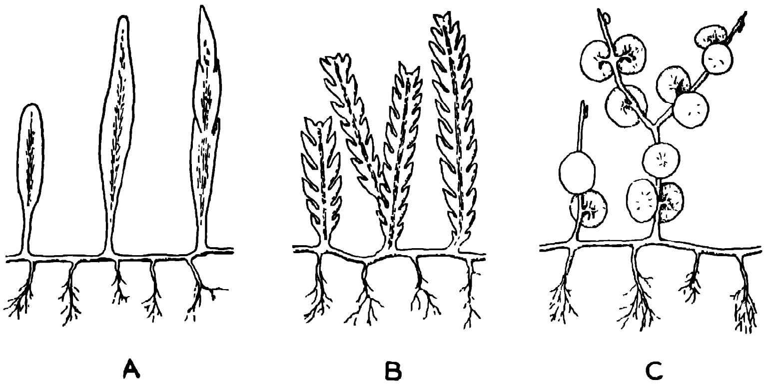

FIG. 50. Three species of *Caulerpa*, a coenocyte with a high degree of structural differentiation, one-half natural size. *A*, *Caulerpa prolifera*, *B*, *Caulerpa crassifolia*; *C*, *Caulerpa macrodisca*.

reproductive organs. The vegetative body contains innumerable nuclei and small chloroplasts. It is really a single multinucleate cell. Asexual reproduction may be accomplished by fragmentation of the thallus, by zoospores, aplanospores, or akinetes. Sexual reproduction ranges from isogamy to heterogamy. This is a highly specialized order related both to the Chlorococcales and the Siphonocladiales.

Summary of Chlorophyceae

The Chlorophyceae are algae with only chlorophyll and its associated carotinoids in their plastids, these being present in the same proportions as in the higher plants. In vegetative organization they are highly diversified. Some are unicellular but most of them are multicellular, the thallus being most commonly filamentous, sometimes plate-like, and rarely massive. Some are partially or completely coenocytic. There is relatively little cellular differentiation. A definite cell wall composed of cellulose is nearly always present, this seldom becoming mucilaginous. The cells contain a well-organized nucleus (often more than one) and one or more distinct plastids. Pyrenoids are usually present. Reserve food is stored generally as starch, sometimes as oil. Asexual reproduction occurs by fission (in some unicellular forms), fragmentation, or by zoospores, aplanospores, and akinetes. Sexual reproduction is either isogamous or heterogamous. In the heterogamous forms the sperms are ciliated, the eggs nearly always nonciliated. Motile reproductive cells generally have two or four cilia, equal in length and apically attached. The zygote nearly always becomes a resting cell.

Within the Chlorophyceae, three main evolutionary trends can be recognized. The occurrence of ciliated reproductive cells in practically all members, except the Conjugales, indicates that the common ancestor of the group must have been a form like *Chlamydomonas*. The Volvocales, retaining motility in vegetative cells, represent one line of evolution. It emphasizes the ciliated colonial type of organization that culminates in *Volvox*.

A second line of development, represented by the Chlorococcales, also emphasizes the colony but shows a loss of motility by the vegetative cells. A tendency toward the formation of multinucleate cells appears in this order. This leads to the development of coenocytic bodies, which reaches a climax in the Siphonales. *Protosiphon* is a connecting link between the Chlorococcales and Siphonales. Some regard the Siphonocladiales as a transitional stage leading to the evolution of the Siphonales; others consider them an offshoot of that order, the incomplete formation of walls being a recent development. Still others think that at least some of the Siphonocladiales have arisen from the Ulotrichales.

A third line of development within the Chlorophyceae is represented by the Ulotrichales, an order in which several different types of multicellular bodies have appeared. All of these grow by division of uninucleate vegetative cells. The Oedogoniales may represent an offshoot from this order, but a connection between the Conjugales and the Ulotrichales seems rather remote, the lack of ciliated cells and peculiar type of sexual reproduction in the Conjugales being the chief obstacles. The Ulotrichales are of great interest in being the order of green algae most closely resembling the probable ancestors of the higher green plants. The occurrence of plate-like forms is particularly significant, inasmuch as the vegetative body of the simpler bryophytes is a plate-like thallus.

CHAPTER III

THALLOPHYTA: ALGAE (CONTINUED)

8. CHAROPHYCEAE

The Charophyceae, or stoneworts, constitute a very isolated group of highly organized green thallophytes with uncertain affinities. Although often included in the Chlorophyceae, they are so distinct that they belong in a separate and coordinate class. The Charophyceae are multicellular plants in which the only pigments present are chlorophyll and its associated carotinoids, these occurring in essentially the same proportions as in the green algae. They include 6 genera and about 200 species, nearly all of which belong to *Chara* and *Nitella*. The stoneworts grow in streams, ponds, and lakes attached to the bottom. They also live in brackish water but not in the ocean. Most species of *Chara* extract calcium carbonate from the water and deposit it in their walls, thereby becoming rough and brittle. Fossils belonging to the Charophyceae have been identified in deposits of the Cretaceous and later geologic periods. There is some evidence of their existence even as far back as the Devonian.

Vegetative Body. The vegetative body of the stoneworts consists of a slender cylindrical stem bearing many short branches in whorls (Fig. 51*A*). It grows erect and often reaches a height of 20 to 30 cm. The stem is attached to the substratum by means of colorless branched rhizoids. It is made up of short nodes and long unicellular internodes, the branches arising from the nodes. There are two kinds of branches: branches of unlimited growth, comprising the main axes, and branches of limited growth, the so-called leaves, in whose axils the main axes arise. All the cells contain numerous small spherical chloroplasts without pyrenoids. Reserve food is stored as starch.

Both kinds of branches grow by means of an apical cell, hemispherical in shape, that cuts off a longitudinal series of segments by successive transverse walls (Fig. 51*B*). Each segment again divides transversely into two cells, the lower one becoming the long internodal cell and the upper one the nodal cell. The latter, by vertical divisions, gives rise to a plate of cells that produce the branches. The internodal cell, often attaining a length of 10 cm., may become coenocytic by fragmentation of its nucleus. Its cytoplasm gives a striking demonstration of protoplasmic streaming. In *Chara* the internodal cells become ensheathed by cells that arise from the nodes and form a one-layered cortex. Half of the cortical cells are derived from the node below and half from the node above, the two halves meeting in a zigzag line midway between the nodes. In *Nitella* the internodes remain uncovered.

Reproduction. No spores are produced in the Charophyceae. The nodes of the branches of limited growth bear unicellular branches and the sex organs, which are the most complex of all the algae. Most species are

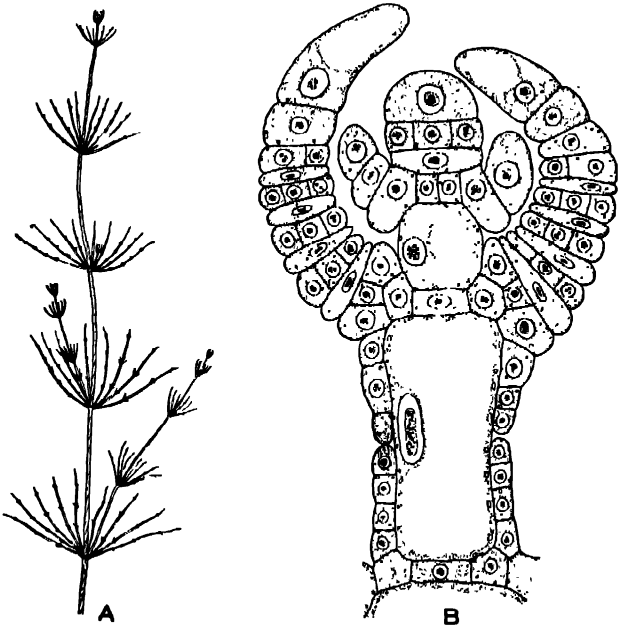

FIG. 51. *Chara.* *A*, upper portion of plant, showing branches of limited and unlimited growth, natural size; *B*, median longitudinal section through the stem tip, showing prominent apical cell and alternating nodes and internodes derived from it, $\times 200$. The large internodal cell below is being ensheathed by a layer of cortical cells arising from adjacent nodes.

monoecious, an antheridium lying below an oögonium at the same node (Fig. 52). The antheridium is a stalked globular body that is brilliant red or yellow. It develops from a single initial cell that at first divides in three planes to produce octants. Each octant then undergoes two periclinal divisions to form an outer, a middle, and an inner cell. A jacket of eight triangular plate-like cells, called *shields*, is derived from the outer cells. The rapid enlargement of the shields results in the formation of a cavity within the antheridium. Projecting inward from the center of each shield is an elongated cell, the *manubrium*, that bears a rounded terminal cell, called a *primary capitulum*, which often divides in two. The manubria and primary capitula are derived from the middle and inner cells, respectively, of the young antheridium (Fig. 53*A*). The primary capitulum forms about six *secondary capitula*. Each of these gives rise to a pair of long filaments consisting of 100 to 200 small cells, from every one of which a sperm is liberated (Fig. 53*B*). At maturity, the entire antheridium falls apart. A single antheridium of *Chara* produces 20,000 to 50,000 sperms. These are coiled and biciliate, resembling the sperms of bryophytes.

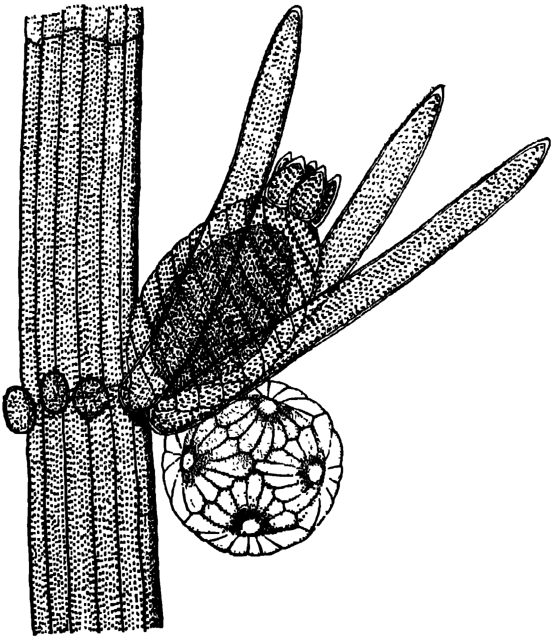

FIG. 52. Branch of *Chara* bearing an oögonium, with sterile jacket and crown, and an antheridium, with interlocking, shield-like wall cells, $\times 50$.

An oögonium is an enlarged apical cell. It produces a single large egg. A unique feature of the oögonium is the presence of five elongated, spirally wound cells that arise below and completely surround it (Figs. 52 and 53*A*). At the top of the oögonium each jacket cell cuts off a small cell, these five cells forming a crown. In *Nitella* each spiral cell cuts off two crown cells, making ten in all. When the egg is ready for fertilization, the spirally twisted cells separate slightly just below the crown, forming five slits through which the sperms enter the oögonium. After a sperm nucleus has united with the egg nucleus, the walls of the surrounding cells harden, the whole structure becoming nut-like. In this condition the zygote rests. Before germination, the fusion nucleus gives rise to four nuclei. Each probably has the haploid number of chromosomes, although this has not been definitely established. Three of these nuclei degenerate. Upon germination, the zygote sends out a simple green filament and a colorless rhizoid. The adult shoot arises from this filament as a lateral branch.

Summary. The Charophyceae are an aberrant group, standing apart from the other algae. They resemble the Chlorophyceae in containing an excess of chlorophyll over the carotinoids and in storing starch as reserve food. The vegetative body is distinctive, being an erect thallus differentiated into nodes and internodes and with two kinds of branches

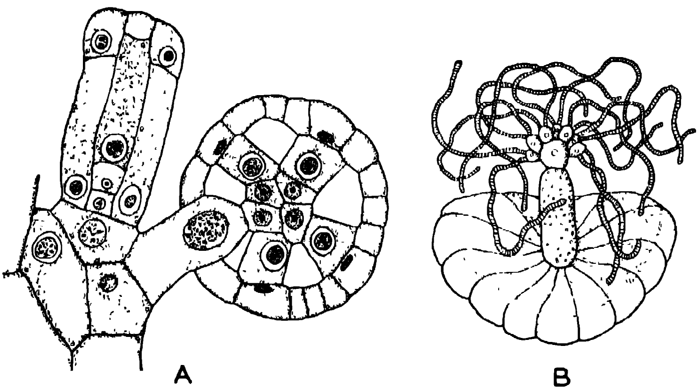

FIG. 53. *Chara.* *A*, longitudinal section of a young oogonium, invested by a sterile jacket, and a young antheridium, the latter consisting of a stalk cell, an outer layer of shield cells, four middle cells (manubria), and four inner cells (primary capitula), ×200; *B*, a shield cell from a mature antheridium with manubrium projecting from it. At the tip of the manubrium is a primary capitulum to which are attached smaller secondary capitula, each bearing a pair of spermatogenous filaments.

arising at the nodes. There is no reproduction by spores. The sex organs are multicellular and complex, both being enclosed by a jacket of sterile cells. In this respect the Charophyceae resemble the bryophytes, although the development of the sex organs in the two groups is very different. The sperms are also like those of bryophytes.

9. PHAEOPHYCEAE

The Phaeophyceae, or brown algae, are nearly all marine in distribution, occurring along most seacoasts but reaching their greatest display in cool waters. They range in color from olive green to dark brown as a result of the presence in their cells of chlorophyll and an excess of carotin and a unique xanthophyll, *fucoxanthin*, which is brown. There are no unicellular brown algae. Their multicellular bodies may be filamentous, plate-like, or may reach massive proportions and be highly differentiated in form. They are always attached. The Phaeophyceae are a specialized group, probably derived independently from flagellate ancestors and apparently not related to any of the higher plants. There is no satisfactory fossil evidence of their existence before the Jurassic. The Phaeophyceae number almost 1,000 species, nearly all of which are contained in six main orders: Ectocarpales, Sphacelariales, Cutleriales, Dictyotales, Laminariales, and Fucales.

1. Ectocarpales

The Ectocarpales include the simplest of the brown algae. They occur along all rocky seacoasts, growing attached to rocks, piers, and other plants. They include over 60 genera and 300 species, forming a diverse assemblage that is often broken up into several smaller orders. Of the many genera, perhaps the two that are best known are *Ectocarpus* and *Pylaiella*.

Ectocarpus. *Ectocarpus* is a simple brown alga, widely distributed along seacoasts, where it grows attached to rocks or to other algae. It is filamentous and usually much branched, the older portions sometimes being surrounded by rhizoid-like branches. Otherwise the body is strictly *monosiphonous*, each branch consisting of a single filament. An alga composed of parallel bundles of filaments is said to be *polysiphonous*. Growth of the filaments occurs mainly by intercalary cell divisions. Each cell contains a single nucleus and a number of small brown plastids.

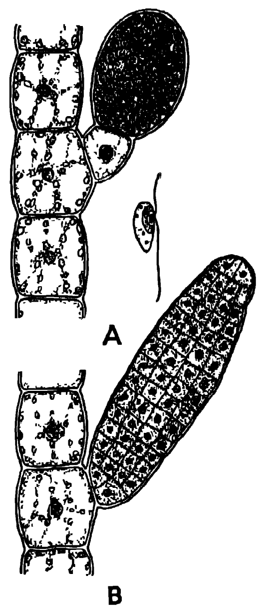

FIG. 54. A sporangium (*A*) and a gametangium (*B*) of *Ectocarpus*, ×400; also a single escaped zoospore, more highly magnified.

Zoospores and isogametes are borne in sporangia and gametangia, respectively. These develop from the terminal cell of a short lateral branch, but may be either stalked or sessile. The sporangium is globular or somewhat elongated (Fig. 54*A*). It is unicellular and contains many (32 or 64) zoospores. It is at first uninucleate, becoming multinucleate and forming zoospores by cleavage of the cytoplasm. The gametangium is longer than the sporangium and often ovate or cylindrical (Fig. 54*B*). It is divided by cell walls into many small cubical cells, in each of which an isogamete is formed. Both the zoospores and gametes are laterally biciliate, the cilia being of unequal length. The pairing gametes are generally of the same size but, in some species, one is slightly larger than the other and swims less vigorously. Where this slight tendency toward heterogamy exists, all the gametes in a gametangium are either smaller (male) or larger (female). As in all the brown algae, the zygote germinates without going into a resting stage.

Ectocarpus displays a primitive type of alternation of generations and one that is not well established. Although all the plants of a species are alike vegetatively, some are gametophytes and some are sporophytes. The gametophytes, producing gametangia, are haploid. The zygotes give rise to sporophytes, which are diploid. These produce two kinds of sporangia. One is multicellular and looks like a gametangium but gives rise to diploid zoospores that develop into other sporophytes. The other is the unicellular sporangium already described. The division of the nucleus in the young unicellular sporangium is reductional, and so the zoospores that it produces are haploid. These haploid zoospores always give rise to gametophytes. Sometimes gametes, without pairing and fusing, develop directly into other haploid plants. It is apparent that much variation occurs in the behavior of the spores and gametes.

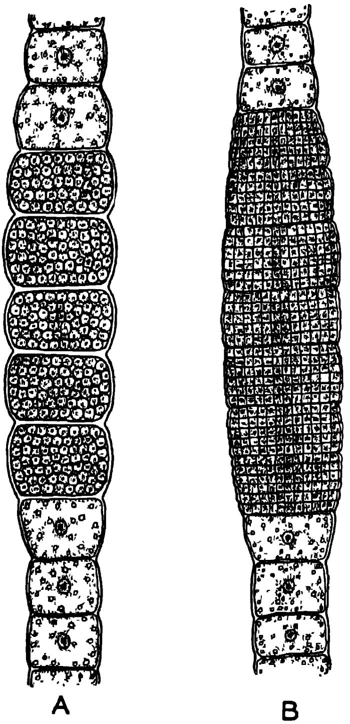

FIG. 55. A row of sporangia (*A*) and gametangia (*B*) of *Pylaiella*, ×500.

Pylaiella. This alga resembles *Ectocarpus* in its habitat and general structure. It differs chiefly in that the filaments are usually only slightly branched and any cell may become a sporangium or gametangium (Fig. 55). Consequently the reproductive organs are intercalary in position and usually appear in a linear series. They have the same structure as those of *Ectocarpus*, the sporangia being unicellular and the gametangia multicellular. Sometimes multicellular sporangia are produced on the plants bearing unicellular ones. Although *Pylaiella* is essentially isogamous, one of the pairing gametes is slightly larger than the other. An alternation of generations is seen also in this genus, the gamete-producing plants being haploid and the spore-producing plants diploid. The reduction of chromosomes occurs in the young unicellular sporangium.

Summary. The thallus of the Ectocarpales is usually composed either of freely branching filaments or wholly or in part of a plate-like or solid body composed of interlacing filaments. In some forms the thallus is parenchymatous. Vegetative growth is mainly intercalary, often being confined to basal portions of the branches. Reproduction occurs typically by zoospores borne in unicellular (and multicellular) sporangia and by motile isogametes borne in multicellular gametangia. There is an alternation of generations, the haploid plants being either similar to the diploid plants in size and vegetative structure, or much smaller and simpler.

A few heterogamous forms with unicellular sex organs borne on minute gametophytes, but otherwise resembling the Ectocarpales, are now segregated into two small orders: the Sporochnales and Desmarestiales. Some authors also segregate into the Chordariales, Punctariales, and Dictyosiphonales isogamous forms with multicellular gametangia but with dissimilar haploid and diploid plants.

2. Sphacelariales

The Sphacelariales are a small but distinct order related to the Ectocarpales. They are all littoral algae numbering 10 genera and 60 species, chiefly tropical but also occurring in temperate regions. The two chief genera are *Sphacelaria* and *Stypocaulon*.

Sphacelaria. This alga grows in small tufts attached to rocks and other algae. It occurs along both coasts of North America but is rather uncommon. The vegetative body is differentiated into a flat, plate-like, prostrate portion and a filamentous erect portion that is freely branched, the branches increasing in length by means of a large apical cell (Fig. 56). This cuts off a series of transverse segments that then divide both longitudinally and transversely to form a polysiphonous thallus. In most algae, growth is intercalary, which means that it occurs by division of all or many of its cells. Where there is an apical cell, all the cells of the body are descendants of it, even though some may later divide independently.

The sporangia and gametangia of *Sphacelaria* are similar to those of *Ectocarpus*, the sporangia being unicellular and the gametangia multicellular. Both are short-stalked and borne on the axes. The zoospores and gametes are laterally biciliate and, in some species, one of the pairing gametes is slightly larger than the other. As in *Ectocarpus*, there is an alternation of vegetatively similar generations and the number of chromosomes is reduced one-half in the young unicellular sporangium. A form of vegetative reproduction common in *Sphacelaria* involves the production of *propagules*. These are short, flattened, modified branches that become detached and give rise to new plants.

Summary. The thallus of the Sphacelariales is filamentous, being monosiphonous near the tips and polysiphonous below. Growth takes place by means of an apical cell. Reproduction occurs by zoospores borne in unicellular sporangia and motile isogametes borne in multicellular gametangia. The order displays an isomorphic alternation of generations.

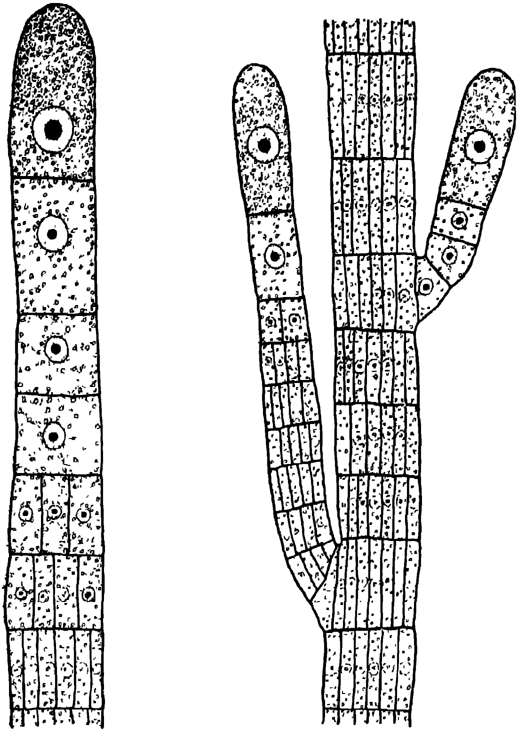

FIG. 56. *Sphacelaria*, ×200. *A*, tip of filament, showing large apical cell and segments derived from it; *B*, slightly older portion of thallus, showing development of branches.

3. Cutleriales

The Cutleriales are a very small order including only *Cutleria*, with 3 species, and *Zanardinia*, with 1. Both genera occur in the Mediterranean Sea, while *Cutleria* has been reported also from Florida and the West Indies. The Cutleriales are more advanced than the two preceding orders, although apparently related to them.

Cutleria. The best-known species of *Cutleria* is found in the warmer parts of Europe. The plants grow just below the low-tide mark. *Cutleria* displays a *heteromorphic* alternation of generations, the gametophyte and sporophyte being unlike vegetatively. In fact, they are so different in general appearance that, before they were known to belong to the same life history, they were placed in separate genera. The gametophyte was called *Cutleria* and the sporophyte *Aglaozonia*. The sporophyte is a small, flat, lobed disk several layers of cells in thickness and about 2 to 5 cm. in diameter (Fig. 57*E*). The lower side bears numerous rhizoids. On the upper side are enormous numbers of elongated unicellular sporangia in crowded clusters. Each sporangium has a one-celled stalk and produces 8, 16, or 32 laterally biciliate zoospores (Fig. 57*F*). At first the sporangium has a single nucleus, the first two divisions of which result in a reduction of chromosomes. After three, four, or five simultaneous free-nuclear divisions have occurred, uninucleate protoplasts are

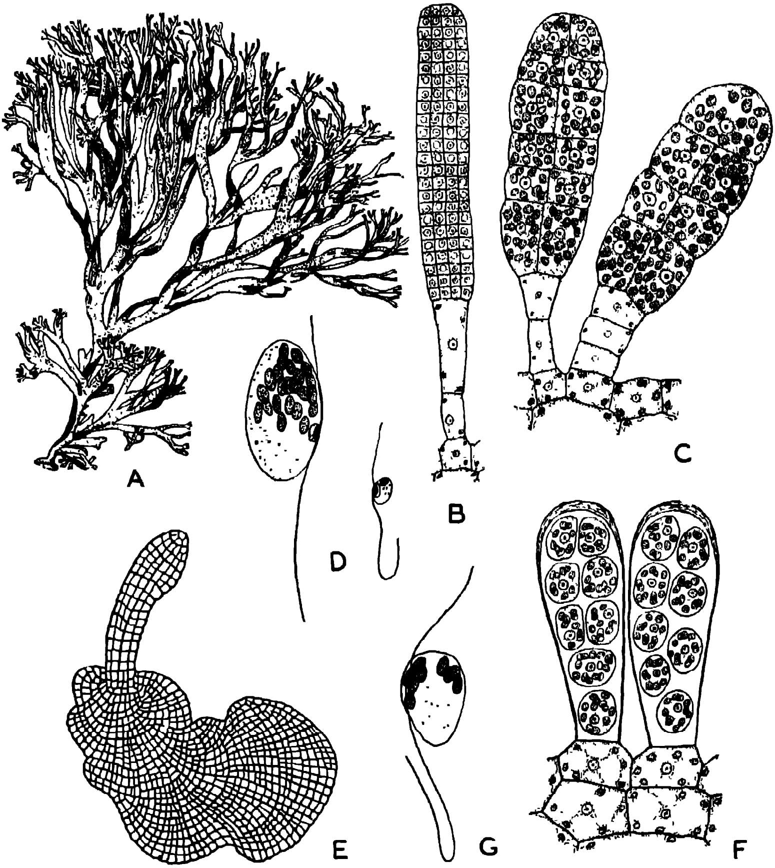

FIG. 57. *Cutleria multifida.* *A*, gametophyte, one-third natural size, *B*, male gametangium, ×600; *C*, two female gametangia, ×600; *D*, an egg and a sperm in the living condition; *E*, young sporophyte 30 days after fertilization; *F*, two nearly ripe sporangia, ×600; *G*, a zoospore in the living condition. (*A*, *after Thuret; D*, *E*, *G*, *after Yamanouchi.*)

formed by cleavage of the cytoplasm. Thus the zoospores are haploid (Fig. 57*G*).

The gametophytes, which are produced by the zoospores, are either male or female but are alike vegetatively (Fig. 57*A*). They are erect, ribbon-like, and dichotomously branched, reaching a length of about 20 cm. They are several layers of cells in thickness. The male and female gametangia, which are somewhat similar in appearance, are borne in clusters on both sides of the thallus, intermixed with sterile hairs called *paraphyses*. Each has a short stalk and a number of gamete-producing cells. The male gametangium (antheridium) is a club-shaped organ consisting of over 200 small cells arranged in many tiers (Fig. 57*B*). Each cell produces a single sperm. The female gametangium (oögonium) has fewer cells, about 20 to 60, each giving rise to an egg (Fig. 57*C*). The eggs are considerably larger than the sperms but both are laterally biciliate and free-swimming (Fig. 57*D*). The eggs are less active than the sperms, however, and usually come to rest first. The zygote germinates at once, giving rise to a sporophyte.

Zanardinia. This genus differs from *Cutleria* in several ways. The gametophyte and sporophyte are alike vegetatively, both being disk-like, several layers of cells thick, and about 5 cm. or more in diameter. Each sporangium produces four large biciliate zoospores, the reduction of chromosomes occurring when they are formed. The gametophytes are monoecious, the two kinds of gametangia being intermixed. The male gametangium produces about 250 sperms, the female gametangium about 12 to 36 eggs. The gametes resemble those of *Cutleria,* both being laterally biciliate.

Summary. The Cutleriales have a flat plate-like thallus that may be either erect or prostrate. Its growth is entirely or partially intercalary. The zoospores are borne in unicellular sporangia, the gametes in multicellular gametangia. The group has well-marked heterogamy, but both the sperms and eggs are ciliated. A distinct alternation of generations is present, the gametophyte and sporophyte being either vegetatively similar (*Zanardinia*) or dissimilar (*Cutleria*).

4. Dictyotales

The Dictyotales are a distinct group of brown algae occupying a somewhat intermediate position with respect to the other groups. They are found in both tropical and temperate seas but always grow in warm waters. There are 18 genera and about 100 species. *Dictyota, Padina,* and *Zonaria* are well-known members.

Dictyota. Although found along both the Atlantic and Pacific coasts of North America, this genus does not occur north of about 35° latitude. The plants grow attached to rocks in tidepools and are always submersed. The vegetative body consists of a thin, flat, dichotomously branched thallus with a basal holdfast (Fig. 58). It is composed of three layers of cells: an upper and a lower layer of small photosynthetic cells with a layer of large colorless cells between them. The thallus grows by means of a large apical cell, one of which lies at the tip of each branch (Fig. 59). The sporophyte and gametophyte are alike vegetatively, and so alternation of generations is isomorphic.

Numerous unicellular sporangia are scattered over both surfaces of the sporophyte (Fig. 60). Each sporangium, borne on a one-celled stalk, produces four nonmotile spores (aplanospores). In connection with the formation of four free nuclei from the single nucleus of the young sporangium, the number of chromosomes is reduced one-half. Two of the

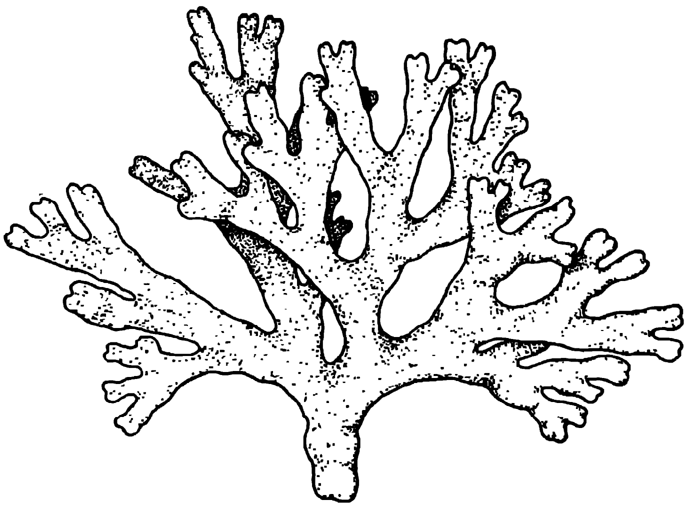

FIG. 58. *Dictyota binghamiae.* Portion of plant showing dichotomous branching, three fourths natural size.

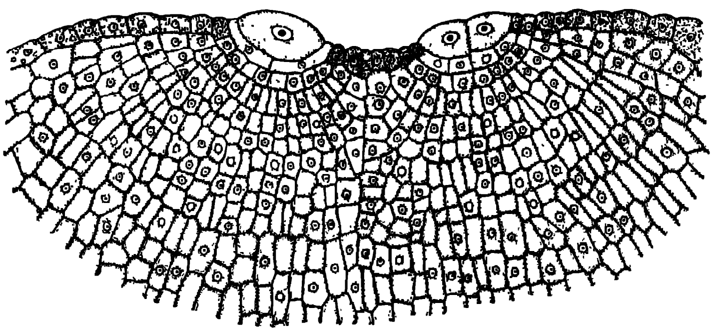

FIG. 59. Longitudinal section of a bifurcating thallus of *Dictyota dichotoma*, cut parallel to its flat surface. The branch tip on the left shows a large undivided apical cell, while the one on the right has just undergone a second dichotomy.

spores from each sporangium give rise to male plants and two to female plants.

Like other members of the order, *Dictyota* displays well-developed heterogamy. The antheridia are borne in clusters of about 100 to 300 on both surfaces of the male plants (Fig. 61*A*). The clusters are surrounded by several rings of sterile cells. Each antheridium is composed of a stalk

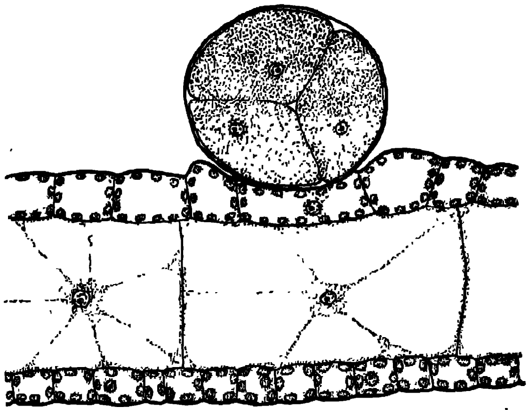

FIG. 60. *Dictyota dichotoma.* Cross section of thallus with a sporangium, showing three of the four spores. (*After Mottier, Textbook of Botany, The Blakiston Company.*)

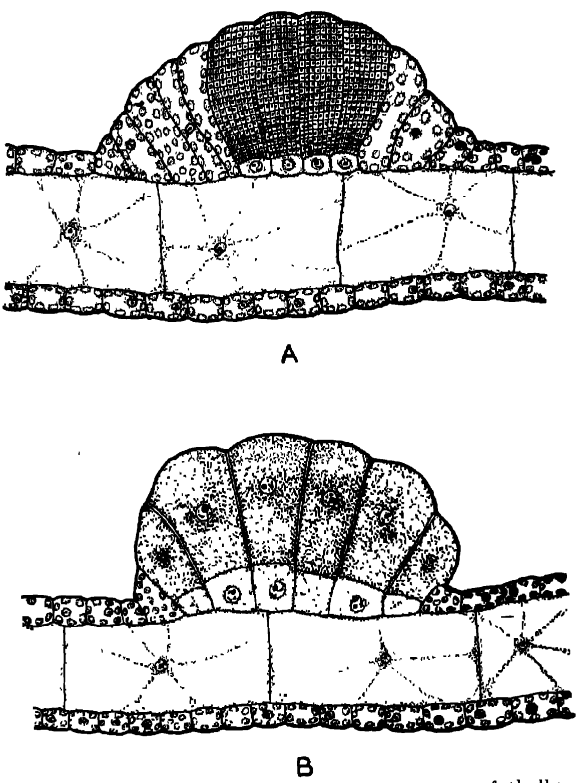

FIG. 61. Sex organs of *Dictyota dichotoma.* *A*, cross section of thallus with group of antheridia; *B*, cross section of thallus with group of oögonia. (*After Mottier, Textbook of Botany, The Blakiston Company.*)

cell and about 1,500 small cells, each of which produces a sperm. Although the sperms are laterally biciliate, one cilium is very short. The oögonia are borne in groups of about 25 to 50 on both sides of the female plants (Fig. 61*B*). The groups are not surrounded by sterile cells. Each

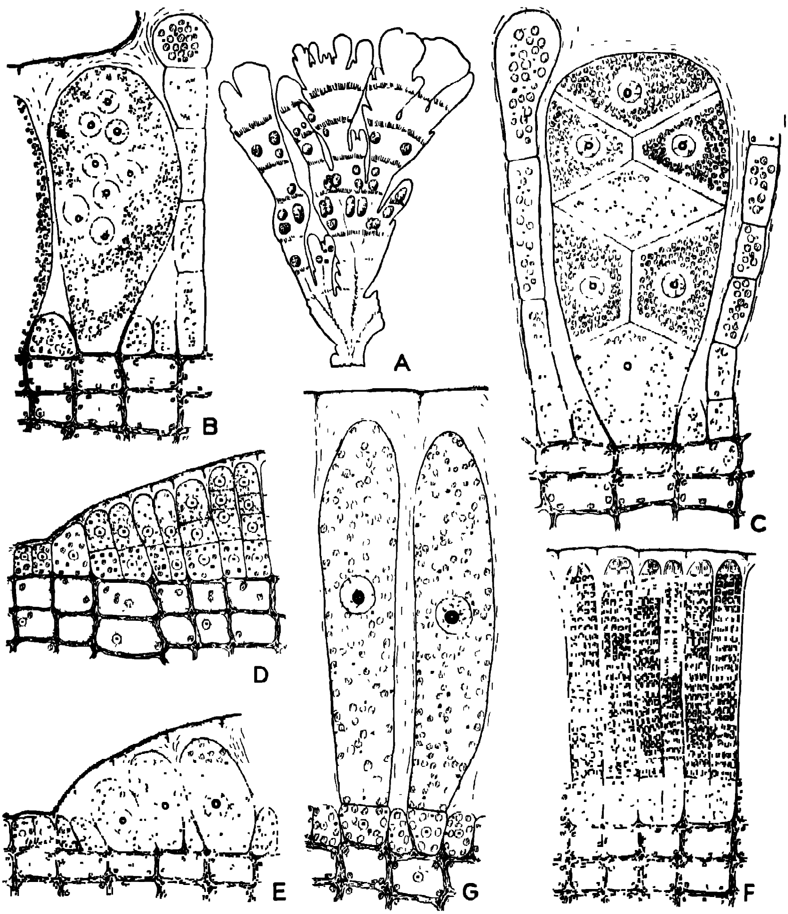

FIG. 62. *Zonaria farlowii*. *A*, portion of thallus with numerous groups of sporangia, ×1½; *B*, young sporangium with eight free nuclei; *C*, mature sporangium, the eight aplanospores cut off by walls; *D*, young antheridia; *E*, young oögonia; *F*, mature antheridia; *G*, two mature oögonia; *B* to *G*, ×300. (*After Haupt*.)

oögonium consists of a small stalk cell and a single large nonmotile egg. The eggs are discharged into the water and there fertilized. The zygote gives rise to the sporophyte without undergoing any resting period.

Zonaria. *Zonaria* has about the same distribution along both coasts of North America as *Dictyota*. The thallus consists of an erect fan-like cluster of thin flat branches arising from a stalk-like portion that is attached by a disk-shaped mass of rhizoids (Fig. 62*A*). It grows by means of a row of apical cells extending around the distal margin of each branch. The mature thallus is about eight layers of cells in thickness. The diploid sporophytes bear groups of sporangia intermixed with paraphyses. Each sporangium, lacking a stalk cell, gives rise to eight large haploid aplanospores (Fig. 62*B*, *C*). These produce the gametophytes, which are either male or female and resemble the sporophytes vegetatively. The antheridia and oögonia are, in general, similar to those of *Dictyota* (Fig. 62*D–G*). The zygote produces a sporophyte.

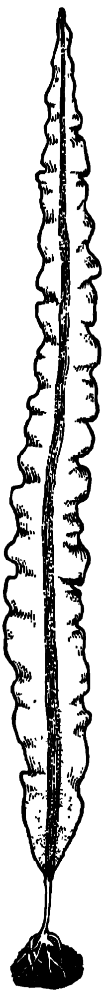

FIG. 63. *Laminaria*, a small kelp with a blade, stipe, and holdfast, about one-half natural size.

Summary. The thallus of the Dictyotales is flat, plate-like, and erect. It grows by means of a single apical cell or a marginal row of apical cells. Reproduction occurs by aplanospores, four or sometimes eight being developed in a unicellular sporangium, and by heterogametes. Small biciliate sperms are borne in multicellular antheridia and large nonmotile eggs are borne singly in unicellular oögonia. A distinct alternation of generations is present, the gametophyte and sporophyte being similar vegetatively.

5. Laminariales

The Laminariales comprise the kelps, the largest of the brown algae. They are widely distributed throughout temperate and arctic regions, occurring mainly in cool waters and making their greatest display along shores bordering the North Pacific Ocean. Most of the Laminariales grow below the low-tide line. They include about 30 genera and 100 species. Some of the best-known members are *Laminaria*, *Macrocystis*, *Nereocystis*, *Postelsia*, and *Egregia*. *Laminaria*, with 30 species, is the largest genus.

Laminaria. Common along both coasts of North America, in cooler waters, are various species of *Laminaria*. Some are not more than 30 cm. long, while others reach a length of 9 to 12 m. They live attached to rocks just below the low-tide line. Alternation of generations is heteromorphic. The large vegetative plant is a sporophyte (Fig. 63). It consists of a long blade and a thick leathery stipe anchored by means of a branching basal holdfast. According to the species, the blade may be entire or divided lengthwise into segments. The cells of the stipe show a differentiation into an outer cortical region of photosynthetic tissue and a central pith that usually contains storage cells. Many of the central cells are elongated and have pores in their end walls, thus resembling the sieve tubes of vascular plants. Vegetative growth is not apical but results

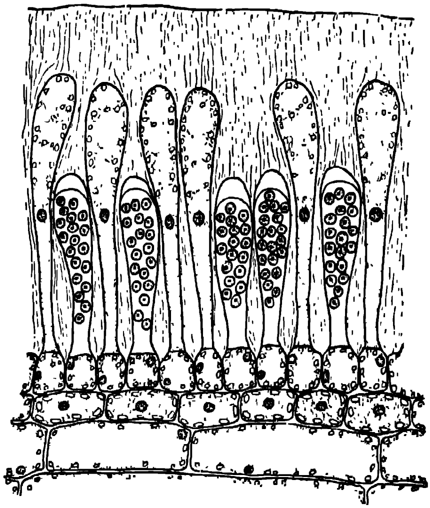

FIG. 64. Sporangia of *Laminaria*, intermixed with paraphyses, ×400.

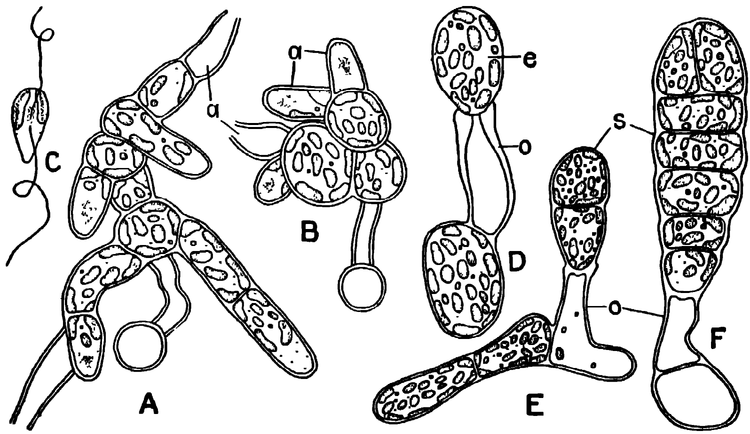

FIG. 65. Gametophytes of *Laminaria yendoana*. *A* and *B*, male gametophytes, ×1,200; *C*, a sperm, ×1,200; *D*, *E*, *F*, female gametophytes, ×800; *a*, antheridia, some empty; *e*, egg; *o*, oögonia; *s*, young sporophytes arising from the fertilized egg. (*After Kanda.*)

from the activity of a meristem situated at the junction of the blade and stipe. The meristem forms a new blade each year, replacing the old one, which dies off.

Numerous unicellular, club-shaped sporangia, intermingled with long sterile cells (paraphyses), arise in large patches on both sides of the thallus (Fig. 64). They produce 32 or 64 small, laterally biciliate zoospores. The reduction of chromosomes results from the division of the nucleus of the young sporangium. After four or five simultaneous free-nuclear divisions have taken place, the contents of the sporangium undergoes cleavage into uninucleate protoplasts, the zoospores. These are liberated

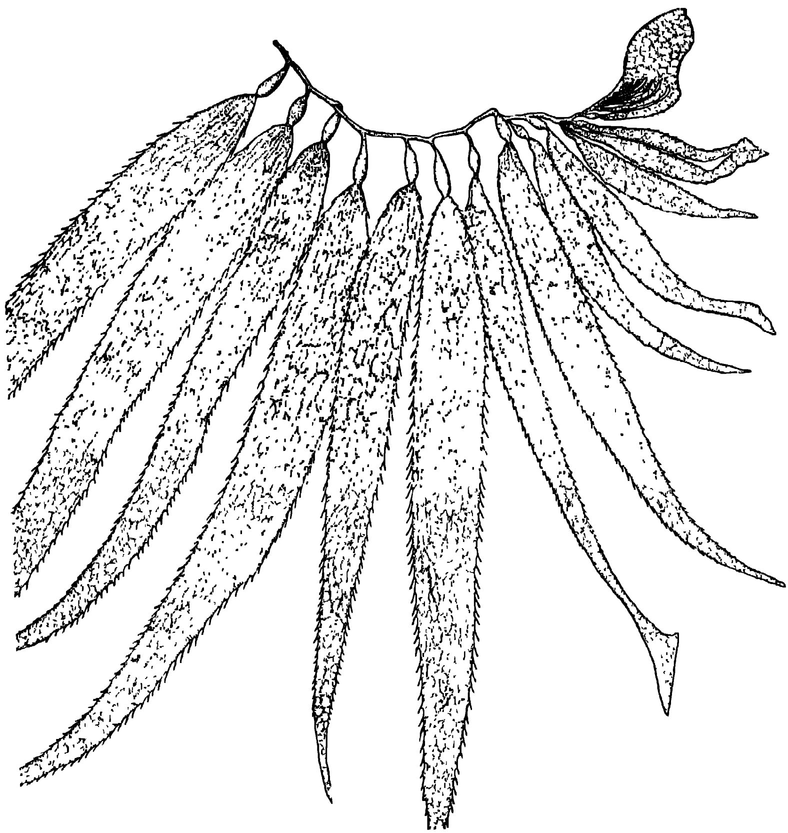

FIG. 66. Apical portion of a plant of *Macrocystis pyrifera*, one-fifth natural size.

and develop into minute male and female gametophytes (Fig. 65). The sperms are laterally biciliate and are borne singly in antheridia that arise at the ends of short, branched filaments. The female plant usually consists of only a few cells, one of which becomes an oögonium. This produces a single nonmotile egg that is extruded through a terminal pore, to which it remains attached. The zygote germinates at once, giving rise to the large sporophyte,

Other Kelps. As in *Laminaria*, the bodies of nearly all the other kelps are differentiated into holdfast organs, stout stalks, and flat blades often much divided into narrow segments. Air bladders are frequently present. Reproduction is similar in all members of the order. The greatest variety and largest of the kelps occur along the Pacific coast of North America, where they live in water 10 to 30 m. deep, their stalks attached to rocky reefs and their blades often floating on the surface. *Macrocystis* may reach a length of 30 to 50 m. A single plant consists of a stalk with many blades, each blade having a float (Fig. 66). Another large kelp is *Nereocystis*, with a large hollow bulb at the end of a thick stalk and a number of blades arising from the bulb (Fig. 67). It reaches a length of 25 to 30 m. *Postelsia*, known as the "sea palm," has a stout stalk up to 60 cm. long bearing at its tip numerous branches terminating in narrow blades (Fig. 68). *Egregia*, the "feather-boa kelp," has a long stalk that bears two rows of lateral blades and floats, the blades producing sporangia being much narrower than the sterile ones.

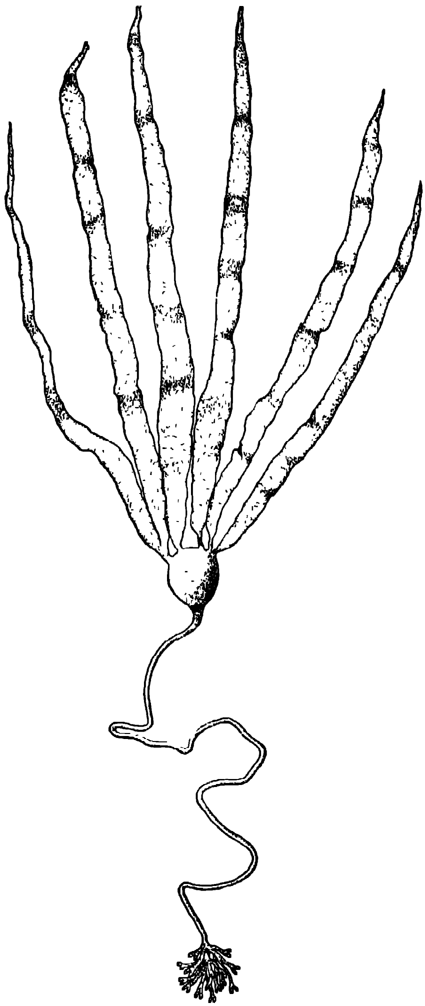

FIG. 67. Young plant of *Nereocystis luetkeana*, one-quarter natural size.

Summary. The vegetative body of the Laminariales is highly differentiated both externally and internally. It consists of a massive thallus usually with a holdfast, stipe, and one or more blades. Growth is due to an intercalary meristem. The large plant body is a sporophyte bearing unicellular sporangia that contain many zoospores. The gametophytes are microscopic, dioecious, and heterogamous. The sperms are biciliate and produced singly in unicellular antheridia. The eggs are nonmotile and borne in unicellular oögonia. The Laminariales have a heteromorphic alternation of generations.

FIG. 68. A sea palm (*Postelsia palmaeformis*) growing on a rock exposed at low tide, about one-quarter natural size.

6. Fucales

The Fucales, commonly known as rockweeds, are a highly specialized order of brown algae standing apart from the others. They are widely distributed throughout tropical and temperate regions, most of them growing along rocky seacoasts in the intertidal zone. They comprise 32 genera and 325 species, representative forms being *Fucus*, *Pelvetia*, *Ascophyllum*, and *Sargassum*.

Fucus. *Fucus* is widely distributed in cool waters, being represented along both the eastern and western coasts of North America. The thallus, rarely exceeding a meter in length, is coarsely ribbon-like and