repeatedly forked, with a basal stalk arising from a disk-like holdfast (Fig. 69). It is rather tough and leathery. In some species air bladders, giving buoyancy to the plant, are conspicuous. Growth occurs by means of an apical cell that occupies a notch at the end of each branch. The

FIG. 69. *Fucus furcatus.* Portion of thallus, showing conceptacles, two-thirds natural size.

apical cell is complex, having the form of a truncated quadrangular pyramid and cutting off cells in three planes. When the thallus branches, the apical cell divides vertically into two nearly equal parts, each of which becomes the apical cell of a new branch. Internally the thallus is differentiated into a firm outer cortex of photosynthetic tissue and a central colorless pith that is rather spongy. The only method of asexual reproduction is by fragmentation of the thallus. There are no spores of any kind.

Within the swollen tips of some of the branches are numerous flask-shaped pits or chambers, called *conceptacles*, each with a pore-like opening (Fig. 70). Sperms and eggs are produced inside the conceptacles, the sperms in antheridia and the eggs in oögonia. The antheridia are oval

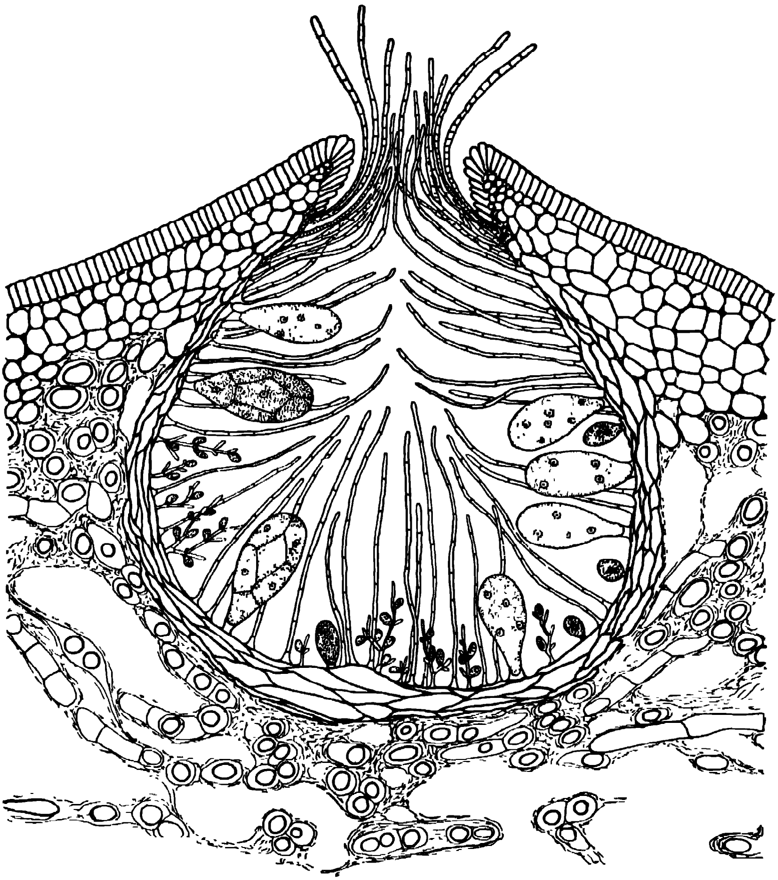


FIG. 70. Longitudinal section of a conceptacle of *Fucus furcatus*, showing oögonia in various stages of development, small branching filaments bearing antheridia, and numerous paraphyses, ×100.

and sac-like; they appear on special branching filaments that arise from the wall of the conceptacle (Fig. 71*A*). Each antheridium produces 64 small, laterally biciliate sperms. The antheridium is unicellular and, when young, is uninucleate. The number of chromosomes is reduced one-half when its nucleus divides. Free-nuclear divisions continue until there are 32 nuclei. Then the cytoplasm undergoes cleavage to form an equal number of uninucleate protoplasts, each of which divides again to produce two sperms. The sperms escape from the antheridium in a mass surrounded by a membrane that soon disappears.

The eggs of *Fucus* are borne in groups of eight inside the oögonia, which are large oval or globular cells, each of which has a one-celled stalk (Fig. 71*B–D*). The young oögonium has a single nucleus, the division of which is reductional. Three simultaneous divisions result in the formation of eight free nuclei. Cytoplasmic cleavage follows and an egg is organized around each nucleus. The eggs are extruded from the oögonium in a

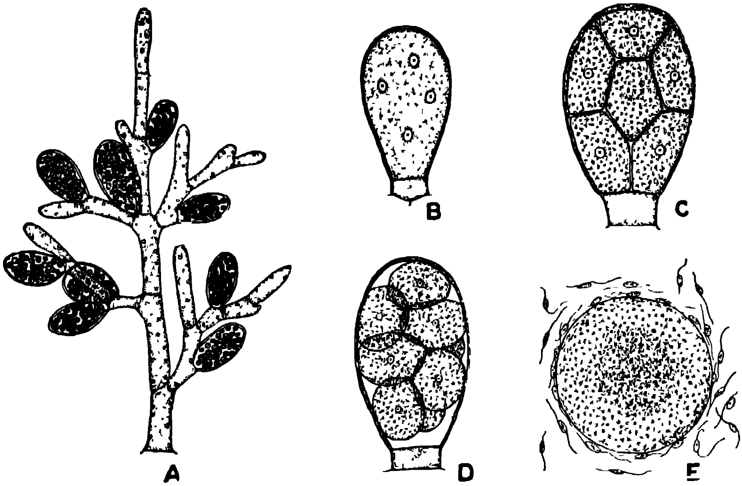



FIG. 71. Sex organs of *Fucus furcatus*. *A*, antheridial filament, ×320; *B*, young oögonium with four nuclei, ×160; *C*, longitudinal section of an older oögonium with eight nearly mature eggs, ×160; *D*, mature oögonium, ×160; *E*, escaped egg of *Fucus vesiculosus* surrounded by numerous sperms, ×240. (*E*, *after Thuret*.)

group surrounded by a membrane that soon ruptures. In *Ascophyllum* four eggs are organized in an oogonium, in *Pelvetia* two, and in *Sargassum* only one. In all the genera of Fucales, however, eight nuclei always arise in the oögonium, the nonfunctional nuclei either being extruded or degenerating. Thus *Fucus* represents the primitive condition from which the other genera, by progressive reduction, have been derived.

Depending on the species, the antheridia and oögonia of *Fucus* may occur in the same conceptacle, in different conceptacles on the same plant, or on different plants. In addition to the sex organs, the conceptacles contain numerous unbranched sterile filaments (paraphyses), some of which often project through the pore. Both the sperms and eggs escape from the conceptacles into the water but only the sperms are motile. The sperms surround the eggs in such vast numbers that they cause them to rotate (Fig. 71*E*). After fertilization has taken place, the zygote surrounds itself with a cell wall and divides at once to produce a new vegetative thallus. The reduction of chromosomes occurs when the nucleus of the young antheridium and that of the young oögonium divide. Thus from the four-nucleate stage to maturity the sex organs are haploid, the diploid condition arising at fertilization.

Although *Fucus* has no alternation of gametophyte and sporophyte plant bodies, there is a brief haploid phase and a prolonged diploid phase. Some botanists interpret the vegetative body of the Fucales as a sporophyte, the antheridia as microsporangia, and the sperms as microspores (small zoospores). They interpret the oögonia as megasporangia and the eggs as megaspores (large aplanospores). Then, to explain the sexual fusion, the microspores and megaspores are said to function directly as gametes. This interpretation implies that a gametophyte generation was once well developed and has become so reduced that it comprises only the haploid nuclei in the gametangia and the gametes themselves.

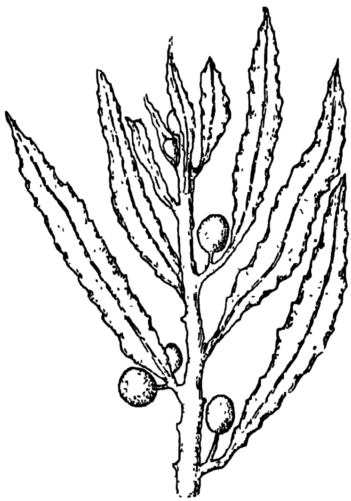


FIG. 72. Small portion of a plant of *Sargassum*, showing differentiation into stem, leaf-like blades, and berry-like air bladders, natural size.

**Sargassum.** This is a very large genus whose 250 species are widely distributed throughout tropical and subtropical seas, especially in the Southern Hemisphere. The vegetative body is more highly developed than that of *Fucus*, having distinct branches, leaf-like blades, and often small stalked air bladders as well (Fig. 72). *Sargassum* may live either in an attached or a floating condition. Like other rockweeds, it grows chiefly along seacoasts, but frequently plants are torn loose from the rocks and carried for hundreds of miles out to sea. The Sargasso Sea is a vast eddy lying west of the Canary Islands. Here great floating masses of "gulfweed," transported by the Gulf Stream from the West Indies and tropical America, accumulate and propagate themselves by fragmentation of the thallus.

**Summary.** The Fucales have a coarse, ribbon-like thallus that grows by means of an apical cell. Spores are not formed. The order displays well-developed heterogamy. The sex organs are unicellular, the antheridia producing numerous biciliate sperms, the oögonia producing one, two, four, or eight nonmotile eggs that escape before fertilization. The sex organs are borne in internal cavities (conceptacles). The Fucales are without a distinct alternation of generations.

## Summary of Phaeophyceae

The Phaeophyceae are algae having in their plastids an excess of carotin and a brown xanthophyll pigment (fucoxanthin) over the chlorophyll. All of them are multicellular, the thallus being filamentous, plate-like, or massive, often with differentiated tissues. The cells contain a definite nucleus, generally several or many plastids, and a distinct cell wall. Reserve food is stored chiefly as laminarin (a dextrin-like carbohydrate) or oil. Except in the Fucales, zoospores are produced or, in the Dictyotales, aplanospores. Gametic reproduction may occur either by isogametes or heterogametes. In the heterogamous forms the eggs may be ciliated but are generally nonciliated. All motile reproductive cells are laterally biciliate, the cilia being unequal in length. No resting cells are formed. Most members exhibit an alternation of generations, the Fucales, with only a diploid plant body, being a notable exception. The gametophyte and sporophyte are either similar or dissimilar vegetatively.

## 10. RHODOPHYCEAE

Like the Phaeophyceae, the Rhodophyceae, or red algae, are almost all marine in distribution but, as a rule, live in deeper and warmer waters than the brown algae. They include the majority of the seaweeds. Most of the Rhodophyceae are rose red or violet, but some are dark purple, reddish brown, or olive green. In addition to chlorophyll and its associated carotinoids, a red pigment, *phycoerythrin*, is present in the cells. This more or less obscures the chlorophyll. Many of the Rhodophyceae also contain a small amount of phycocyanin, the blue pigment of the Cyanophyceae. Except for several unicellular forms, whose inclusion in the group is doubtful, all the red algae are multicellular. Their bodies are not large, most of them being less than 30 cm. in length, while only a few are as long as 1 m. They are rather varied in form, however, being filamentous, ribbon-like, or plate-like, but never massive. They are always attached. Some are heavily impregnated with lime. Lime-secreting forms are known as fossils as far back as the Ordovician. The Rhodophyceae are the most highly specialized of all the algae. They are probably not related to any of the higher plants except, perhaps, to some of the fungi. They include about 3,000 species.

There are seven orders of Rhodophyceae. These, together with one or more representative genera, are as follows: (1) Bangiales—*Bangia, Porphyra, Porphyridium;* (2) Nemalionales—*Nemalion, Batrachospermum,* (3) Gelidiales—*Gelidium;* (4) Cryptonemiales—*Corallina, Lithothamnion;* (5) Gigartinales—*Plocamium, Gracilaria, Chondrus, Gigartina;* (6) Rhodymeniales—*Rhodymenia;* (7) Ceramiales—*Callithamnion, Ceramium, Polysiphonia, Delessaria.*

**Porphyra.** *Porphyra* is a typical member of the Bangiales, the most primitive order of Rhodophyceae. It is widely distributed along rocky seashores, occurring on both coasts of North America. It grows in the intertidal zone on rocks and other algae. The thallus is plate-like and attached by means of a small basal holdfast (Fig. 73*A*). It is only one or

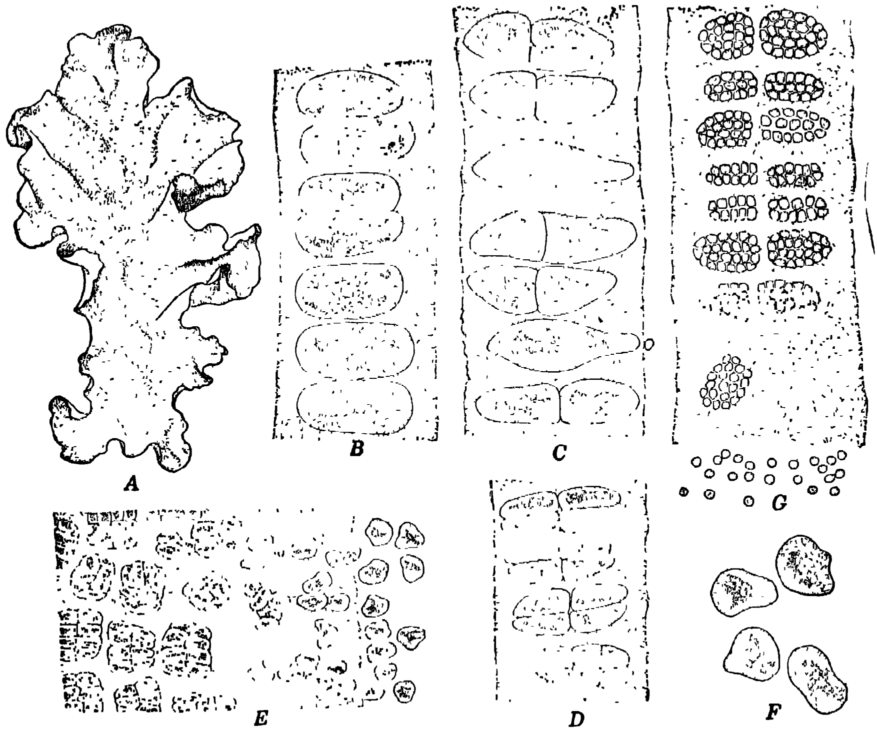



FIG. 73. *Porphyra perforata.* *A*, thallus, one-half natural size; *B*, vertical section of vegetative portion of thallus; *C* and *D*, vertical sections of thalli with carpogonia and developing carpospores; *E*, surface view, showing liberation of carpospores; *F*, amoeboid carpospores; *G*, vertical section through portion of a thallus liberating spermatia. (*From Gilbert M. Smith.*)

two layers of cells in thickness and, in most species, is less than 50 cm. long. The cells lie in a tough gelatinous matrix derived from their walls. They are without apparent cytoplasmic connections (Fig. 73*B*). Each cell has a nucleus that divides by a primitive type of mitosis. It also has a single large plastid with a central pyrenoid.

Some species of *Porphyra* are monoecious but most of them are dioecious. The antheridia develop directly from the vegetative cells. A cell undergoes repeated divisions in three planes until 64 or sometimes 128 small cells are formed. The walls gelatinize and free the protoplasts, which function as male gametes (Fig. 73*G*). Such naked, nonmotile male cells, a feature of all the red algae, are called *spermatia*. The female sex organs, or *carpogonia*, also arise from ordinary vegetative cells but without undergoing division, the protoplast functioning directly as an egg (Fig. 73*C*).

A spermatium, carried by water currents to the carpogonium, enters and fuses with the egg. The zygote divides at once to form a group of spores, usually 8 or 16, that are freed by the breaking down of the surrounding cell walls (Fig. 73*C E*). These naked cells are *carpospores* and, like the gametes, are nonciliated. The freed carpospores exhibit an amoeboid movement (Fig. 73*F*). After coming to rest, each carpospore forms a cell wall and develops into a new thallus. The reduction of chromosomes occurs when the zygote germinates, and so the vegetative plant is haploid.

As compared with the higher orders of Rhodophyceae, the Bangiales have a simple type of nucleus and cells without evident protoplasmic continuity. They display intercalary rather than apical growth. The carpogonium either lacks a trichogyne or has a very short one. The zygote is transformed directly into carpospores. An alternation of generations is not present.

*Porphyridium* is a unicellular alga whose relationships are uncertain. It forms a reddish gelatinous layer on damp soil and moist walls. It was formerly placed in the Cyanophyceae but, because it has a true nucleus and a distinct plastid, is now included in the Rhodophyceae. The cells are spherical and surrounded by a mucilaginous matrix. Fission is the only known method of reproduction.

**Nemalion.** Although showing a considerable advance over *Porphyra*, this form is much simpler than members of the higher orders. *Nemalion* is widely distributed, growing on rocks between the high- and low-tide lines. The thallus, up to 60 cm. in length, consists of a slimy mass of branching filaments that are interwoven to form a worm-like cylinder. This is composed of a central core of slender colorless filaments from which tufts of larger chlorophyllose filaments radiate outward. The cells of the latter have a small nucleus and a large plastid with a conspicuous pyrenoid. As in all the algae except the Bangiales, growth is apical. Furthermore, the vegetative protoplasts are connected by a conspicuous strand of cytoplasm that passes through a pore in the cell wall.

*Nemalion* is monoecious, the sex organs occurring at the ends of short branches. The antheridium consists of a single small cell that is budded off laterally from an antheridial branch (Fig. 74*A*). Its protoplast, the *spermatium*, is discharged into the water. The female organ, called a *procarp*, consists of two parts, the *carpogonium* and the *trichogyne* (Fig. 74*B*). The protoplast of the carpogonium functions as an egg. The trichogyne is a long thread-like cell at the upper end of the carpogonium.

Its nucleus degenerates. The nonmotile male cell, or spermatium, is carried by water currents. After coming in contact with the trichogyne, it becomes binucleate. Both of the male nuclei may enter the trichogyne but only one passes into the carpogonium, where it fuses with the egg nucleus. The other male nucleus does not function.

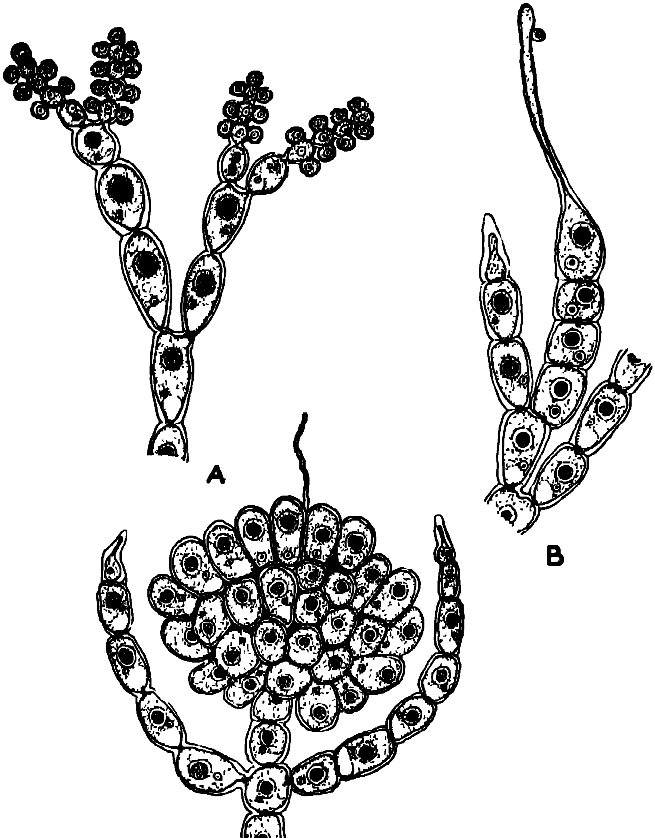



FIG. 74. *Nemalion lubricum*, ×700. *A*, portion of plant with four antheridial branches consisting of groups of small cells, each producing a single spermatium; *B*, a carpogonial branch, terminating in a carpogonium with its slender trichogyne to which a spermatium is attached; *C*, a cystocarp, composed of fertile filaments that cut off terminal carpospores.

Following fertilization, many short filaments, called *gonimoblasts*, arise from the carpogonium and at the tip of each a carpospore is organized. After a carpospore is shed, another may be cut off from the cell behind it. It is only in the Bangiales that carpospores are produced by direct division of the zygote. In *Nemalion* the carpogonium, fertile filaments, and carpospores collectively form the *cystocarp* (Fig. 74*C*). The carpospores, upon being set free as naked, nonmotile cells, develop into sexual plants.

The reduction of chromosomes occurs just after fertilization, when the fusion nucleus in the carpogonium divides. Thus the gonimoblasts, carpospores, and sexual plants are haploid. There is no true alternation of generations.

**Batrachospermum.** This is a widely distributed fresh-water alga, growing in streams attached to rocks along the bottom. The plants are blue-green, olive green, violet, or reddish. The variation in color is primarily a result of differences in light intensity, plants growing in shallow water being greener than those in deeper water. *Batrachospermum* is related to *Nemalion* but differs from it in several respects. The vegetative body consists of long branching filaments of unlimited growth bearing whorls of dwarf branching filaments of limited growth (Fig. 75). The long filaments consist of an axial row of cells which, in the older portions of the body, is covered by a layer of small-celled filaments that form a sheath around it. The cells of the sheath arise from the basal cells of the dwarf filaments. Growth occurs by means of an apical cell.

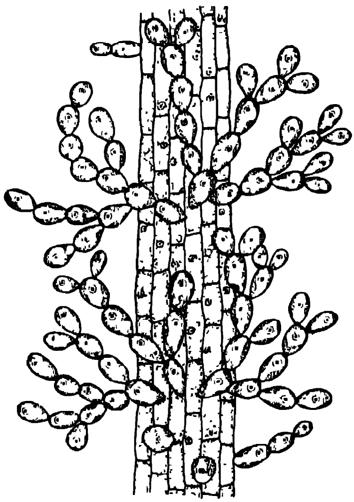


FIG. 75. Small portion of the vegetative body of *Batrachospermum*, showing dwarf filaments arising in whorls from the cylindrical main axis, ×400.

The sex organs are borne at the ends of some of the dwarf filaments and resemble those of *Nemalion* (Fig. 76). After coming in contact with the trichogyne, the spermatium remains uninucleate instead of becoming binucleate. Moreover, following fertilization, the cells at the base of the carpogonium send out loose filaments that grow up around and invest the cystocarp while the carpospores are being produced.

The germinating carpospore gives rise to a branching filamentous body that is much simpler than the gamete-producing plant. This plant, which represents a juvenile stage in the life cycle, may multiply by *monospores*, which are formed singly within sporangia at the ends of short lateral branches. Finally a special branch appears that becomes a gamete-producing plant. As in *Nemalion*, the chromosome number is reduced one-half when the fusion nucleus divides in the fertilized carpogonium. Consequently, the juvenile plant is not a sporophyte and there is no alternation of generations.

**Polysiphonia.** *Polysiphonia* is a widespread genus of about 150 species. It is abundant along the Atlantic coast of North America but is less common along the Pacific coast. It grows in tide pools on rocks and on other algae. It is a more highly developed but more typical red alga than any of the others that have been discussed. The plant body, reaching a length of 25 cm., is filamentous and polysiphonous, being made up of an

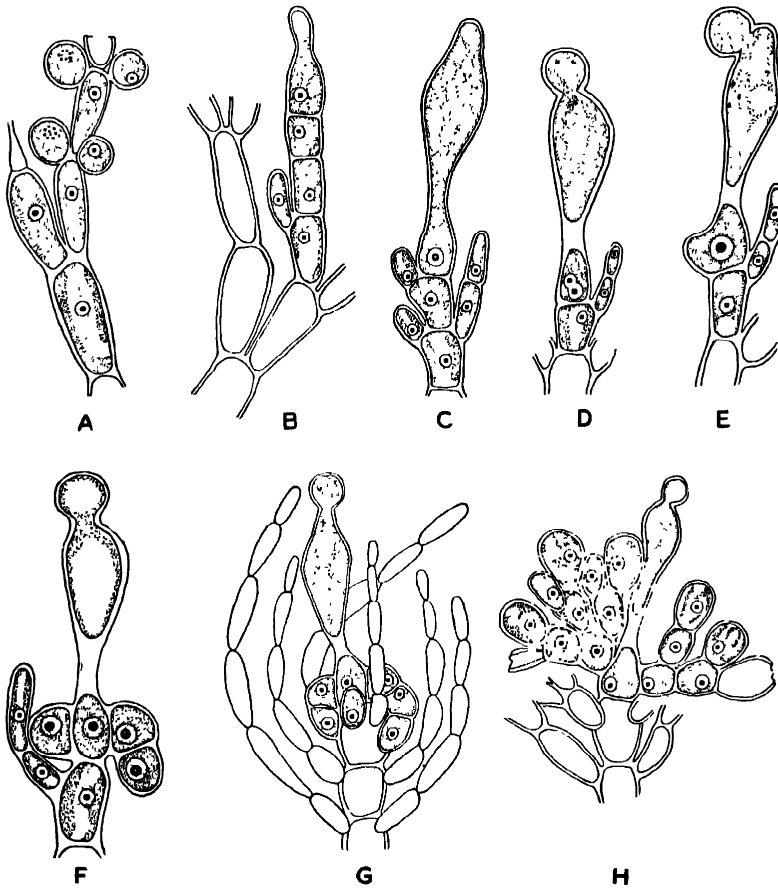



FIG. 76. *Batrachospermum.* *A*, antheridial branch with globular antheridia, one of which has liberated its protoplast; *B*, young carpogonial branch, the terminal cell forming the carpogonium and trichogyne; *C*, mature procarp with nucleated carpogonium and swollen trichogyne; *D*, later stage, showing spermatium united with trichogyne and male nucleus fusing with carpogonial nucleus; *E*, completed fusion of male and female nuclei, *F*, development of gonimoblasts from carpogonium, a sterile branch arising on the left, *G*, further development of gonimoblasts and sterile filaments; *H*, formation of carpospores; *A* to *F*, ×960; *G* and *H*, ×720. (*After Kylin.*)

axial row of elongated cells surrounded and completely covered by several rows of smaller peripheral cells that are cut off from the central cells by longitudinal divisions. Growth occurs by means of an apical cell.

The reproductive features of *Polysiphonia* are complex. Nonmotile

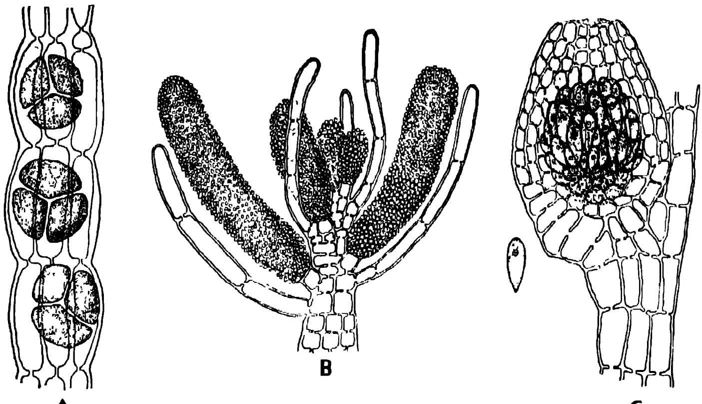



FIG. 77. *Polysiphonia* *A*, portion of plant bearing tetraspores, ×160, *B*, portion of male plant bearing clusters of antheridia, ×200; *C*, portion of female plant with cystocarp containing carpospores; also a single carpospore, ×80.

spores are formed in groups of four in a one-celled sporangium (Fig. 77*A*). They are called *tetraspores*. Chromosome reduction occurs in connection with the formation of the tetraspores, and so each is haploid. Upon germination, two tetraspores from each sporangium produce male plants and two produce female plants. These sexual plants are like the tetrasporic ones in general appearance.

The antheridia occur in dense clusters on special lateral branches of the male plants (Fig. 77*B*). In their formation, a number of cells arise laterally from the cells of the axial filament, giving rise to a simple monosiphonous branch. Each cell of this branch develops two-celled lateral branches. An oblique division of the terminal cell of each branch produces a unicellular antheridium (Fig. 78). The antheridium discharges its protoplast, which functions as a nonmotile male cell, or spermatium. Other antheridia may then be budded off the same terminal cell.

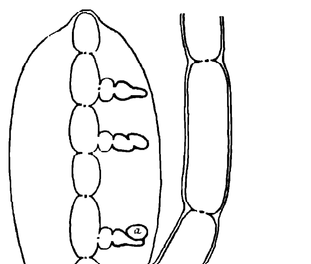



FIG. 78. Diagram of antheridial branch of *Polysiphonia*, showing three stages in the development of an antheridium (*a*), whose protoplast functions as a male cell. (*After Yamanouchi.*)

Besides the carpogonium and trichogyne, the procarp includes several other cells as well. It arises from a large *pericentral cell* that first produces a row of four cells, the terminal one becoming the carpogonium (Fig. 79*A*, *B*). The nucleus of the carpogonium divides into two nuclei, one of which passes into the trichogyne and finally disintegrates, while the other remains in the carpogonium and functions as an egg nucleus. The pericentral cell also gives rise to a group of *auxiliary cells*, one of which crowds in between the pericentral cell and the carpogonium (Fig. 79*C*). The entire structure comprises the procarp.

The free-floating spermatium, coming in contact with the trichogyne, remains uninucleate. The male nucleus enters the trichogyne, passes

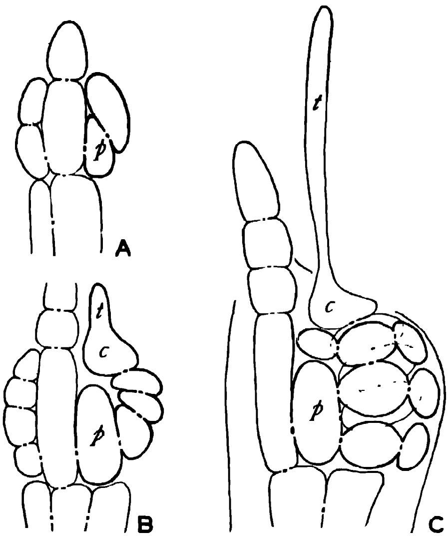



Fig. 79. Diagrams showing development of procarp of *Polysiphonia* *A*, early stage; *B*, later stage, the pericentral cell (*p*) having produced four cells, the terminal one forming the carpogonium (*c*) and trichogyne (*t*); *C*, mature stage, a group of auxiliary cells having developed from the pericentral cell. (*After Yamanouchi.*)

into the carpogonium, and fuses with the female nucleus. A passageway to the pericentral cell now is opened through the intervening auxiliary cell and the fusion nucleus passes through. Then all the cells of the procarp unite and the fusion nucleus divides to form many nuclei. Lobes into which these nuclei pass are put out from the procarp and then the carpospores are cut off. The whole structure comprises the cystocarp (Fig. 77*C*). The usual envelope of sterile cells is formed around it.

After escaping from the cystocarp, a carpospore gives rise to a tetrasporic plant. A stalked sporangium is produced laterally from an axial cell, pushing through the cortical cells. The tetraspores give rise to sexual plants. *Polysiphonia* displays an isomorphic alternation of generations. The sexual plants, with haploid cells, are gametophytes. The tetrasporic plant, with diploid cells, is a sporophyte. The sporophyte generation, however, beginning with the zygote, includes also the cystocarp and carpospores. The gametophyte generation begins with the tetraspore.

**Summary.** In the Rhodophyceae both chlorophyll, with its associated carotinoids, and a red pigment (phycoerythrin) are present in the plastids. With only a few possible exceptions, all members are multicellular, the thallus being most commonly filamentous but often plate-like. The cells contain a definite nucleus (sometimes more than one), one or more plastids, and a cell wall that is often gelatinous. Reserve food is stored chiefly as "floridean starch." Reproduction occurs by means of aplanospores and heterogametes. The female organ is a carpogonium. Carpospores arise from the zygote, either directly (in the Bangiales) or indirectly (in the other Rhodophyceae). Except in the Bangiales and Nemalionales, both carpospores and tetraspores are produced, the latter by a sporophyte. All reproductive cells are nonciliated. No resting cells are formed. A distinct alternation of generations is a feature of all red algae except the Bangiales and Nemalionales. The gametophyte and sporophyte are similar vegetatively.

## COMPARISON OF THE CLASSES OF ALGAE

The most important distinguishing characters of the ten classes of algae are as follows:

**Cyanophyceae.** Cells containing, in addition to chlorophyll and carotinoids, a blue pigment (phycocyanin) and frequently a red pigment (phycoerythrin) also. Pigments not confined to definite plastids. Reserve food stored as glycogen. Plant body unicellular, generally colonial. Cells without a well-organized nucleus. Cell walls usually forming abundant mucilage. Reproduction by fission, never by zoospores or gametes No ciliated cells.

**Euglenophyceae.** Cells with green plastids containing an excess of chlorophyll over the carotinoids; frequently colorless. Reserve food stored as paramylon. Unicellular and usually solitary; sometimes colonial. Cell walls almost always absent. Free-swimming or, when colonial, attached. Reproduction by fission, rarely by isogametes (?). Motile cells with one or two cilia attached anteriorly, equal or unequal.

**Chrysophyceae.** Cells with golden brown plastids containing chlorophyll and an excess of carotinoids; sometimes colorless. Food stored as oil or leucosin. Unicellular and often colonial, rarely multicellular. Cell walls almost always absent. Free-swimming or sometimes attached. Reproduction by fission, and sometimes by zoospores, rarely by isogametes (?). Motile cells with one or two cilia attached anteriorly, equal or unequal.

**Dinophyceae.** Cells with yellow-brown plastids containing chlorophyll and an excess of carotinoids, or colorless, storing food as starch or oil. Unicellular and mostly solitary, rarely multicellular. Sometimes naked but usually with sculptured cell walls. Nearly all free-swimming. Reproduction by fission, and sometimes by zoospores, rarely by isogametes (?). Motile cells generally with two laterally attached cilia, one lying in a transverse groove.

**Xanthophyceae.** Cells with yellow-green plastids containing a larger proportion of carotinoids than chlorophyll. Reserve food stored as oil or leucosin. Unicellular (and uninucleate), coenocytic, or multicellular. Cell walls often absent, when present usually consisting of two overlapping halves. Reproduction by fission or by spores and isogametes. Motile cells with two unequal cilia attached anteriorly.

**Bacillariophyceae.** Cells with golden-brown plastids containing an excess of carotinoids over chlorophyll and storing food mainly as oil. Unicellular and either solitary or colonial. Cell wall consisting of two overlapping valves, highly silicified. Reproduction by fission, auxospores, and isogametes. Motile cells rare.

**Chlorophyceae.** Cells with plastids containing a greater proportion of chlorophyll than carotinoids. Reserve food usually stored as starch. Unicellular (and uninucleate), coenocytic, or multicellular. Unicellular forms solitary or colonial. Reproduction by fission or by spores and either isogametes or heterogametes. Motile cells generally with two or four cilia attached anteriorly.

**Charophyceae.** Cells with plastids containing a greater proportion of chlorophyll than carotinoids; usually storing food as starch. Multicellular. Reproduction by heterogametes formed in complex multicellular sex organs of a distinctive type. Sperms with two equal cilia attached anteriorly.

**Phaeophyceae.** Cells with plastids containing chlorophyll and an excess of carotin and a brown pigment (fucoxanthin). Reserve food occurring chiefly as laminarin or oil. Multicellular. Reproduction by spores and either isogametes or heterogametes. Motile cells laterally biciliate, the cilia of unequal length.

**Rhodophyceae.** Cells with plastids containing chlorophyll, carotinoids, and a red pigment (phycoerythrin). Reserve food stored chiefly as "floridean starch." With rare exceptions multicellular. Reproduction by spores and heterogametes, these never ciliated.

## GENERAL CONCLUSIONS

The algae constitute the simplest and oldest group of green plants. Their bodies are adapted, both in structure and function, to live in water. Although knowledge is lacking concerning the nature of the first plants to have lived on the earth, they must have been aquatic and may have been similar to some of the existing blue-green algae. These plants are unicellular, have a very primitive cell structure, and reproduce by fission. Because they live in a variety of habitats, including hot springs, they may have lived on the earth before conditions were favorable for the existence of other green plants.

The algae are not a homogeneous assemblage but embrace a number of groups representing divergent lines of descent, all of which probably have had a common origin. Advanced students of the algae try to trace these lines of evolution, but we shall be concerned mainly with certain general tendencies and with the progress that the group as a whole has made.

**Development of Multicellular Bodies.** The unicellular plant body obviously represents the simplest condition of structural organization and, necessarily, also the oldest. It is characteristic of all the blue-green algae, flagellates, dinoflagellates, diatoms, and many of the green algae. Unicellular plants may be either solitary or colonial, the latter condition having arisen from the tendency of cells, following division, to remain together for a while before separating. In the evolution of the algae, close association of cells in a colony may have led to a dependence of the cells on one another, with the resultant establishment of a multicellular body. It is significant that, among the algae, no sharp distinction exists between highly organized colonies and simple multicellular plants. This intergradation strongly indicates that multicellular plants have been derived from unicellular ones through the formation of colonies.

Although the multicellular bodies of algae are very diverse in form, they may be referred to three main types: filamentous, plate-like, and massive. The filamentous type is most common, probably because it seems best adapted to aquatic life. In such a body all the cells are in direct contact with water and the absorbing surface is very large. Thus the absorption of gases is greatly facilitated. The massive type of body, as exemplified by many brown algae, is adapted to withstand the buffeting action of waves and water currents along rocky seacoasts. In the simple multicellular algae growth is intercalary, every cell having the power of division. In branching forms growth is often limited to definite regions, such as the terminal cell of each branch. In many brown and most red algae growth occurs by means of an apical cell that cuts off a series of posterior segments.

An important evolutionary tendency exhibited by the algae is for certain cells to become structurally differentiated in response to special functions. It occurs in both colonial and multicellular forms. A simple expression of this tendency is seen in those filamentous algae having the basal cell modified as a holdfast. In many branching filaments the cells of the branches are smaller than those of the main filament. The formation of sporangia and gametangia represents a specialization of certain cells for reproduction. Differentiation becomes marked among the brown algae, especially in the Laminariales and Fucales, where the body consists of distinct vegetative organs within which simple tissues may be formed. A highly differentiated vegetative body is also characteristic of the Charophyceae and many marine Siphonocladiales and Siphonales.

**Asexual Reproduction.** In reproduction, as in vegetative structure, the algae show a progressive advance. Most unicellular forms increase in number by fission, which is merely reproduction by cell division and is obviously the most primitive method in the plant kingdom. Among multicellular forms cell division results in growth and, to make reproduction possible by other means than fragmentation, cells must be liberated from the parent. The spores of algae are merely detached cells with the capacity of directly producing a new plant. They result not only in a multiplication of individuals but in their widespread distribution. Spores may be formed from a cell with or without previous division of its protoplast. The commonest kind of spores in the algae are zoospores—naked cells with cilia. Nonmotile spores with a cell wall (aplanospores and akinetes) are generally formed in response to adverse environmental conditions, to which they are very resistant. Obviously they have been derived from zoospores that have lost the power of locomotion. The same may be true of the nonmotile spores of the red algae. Fission and spores produced by a haploid plant body are a means of accomplishing vegetative or asexual reproduction because no reduction of chromosomes is involved. This is the only kind present in the blue-green algae, flagellates, dinoflagellates, many diatoms, and a few green algae.

Like vegetative spores, the spores produced by two successive divisions of a diploid cell, involving a reduction of chromosomes, are usually regarded as asexual. In reality, however, they belong to the sexual life cycle, since meiosis is always a necessary consequence of a previous gametic union. Although such spores are functionally equivalent to the zoospores and aplanospores produced by a haploid plant body, they are not homologous with them, and should be designated as *meiospores*. Meiospores are produced by the zygote in such green algae as *Ulothrix* and *Oedogonium*, and by the sporophyte in all algae with an alternation of generations.

In most green algae any ordinary vegetative cell is capable of producing spores. In nearly all the brown and red algae, however, spores are not borne in transformed vegetative cells but in sporangia, which are cells specialized for reproduction. Sporangia differ from ordinary vegetative cells in size or shape and sometimes are restricted to definite parts of the body.

**Sexual Reproduction.** Sexual reproduction is accomplished by gametes and represents a distinct advance over reproduction by vegetative spores. Its essential feature is the fusion of two cells to form a zygote. It seems certain that originally gametes were derived from vegetative zoospores that had become too small to form a new plant directly. This is shown by the fact that in *Ulothrix* and many other isogamous algae zoospores and gametes intergrade, the smaller spores often germinating but producing dwarf filaments. The derivation of gametes from zoospores is shown also by the striking similarity between them in form and in the number and arrangement of their cilia. Any peculiarity in the spores is duplicated in one or both of the gametes, as in *Oedogonium*, the brown algae, etc. With few exceptions (notably the Conjugales, Charophyceae, and Fucales), gametic reproduction has not replaced reproduction by vegetative spores but is supplementary to it. In nearly all the green algae the zygote is a resting cell, acquiring a heavy wall and carrying the plant through a period of severe conditions into the next growing season. In fact, the formation of gametes is often induced by the advent of such conditions. In the brown and red algae the zygote germinates at once.

Originally, in the evolution of the algae, both of the fusing gametes were ciliated and of the same size. This condition of isogamy is retained by the yellow-green algae, diatoms, and many of the simpler green and brown algae. In such forms as *Pandorina,* one of the pairing gametes is slightly larger and less active than the other. In *Cutleria* both gametes are ciliated, but the female gamete is considerably larger than the male. In *Dictyota* and *Fucus* the female gamete (egg) is increased in size still more and, although extruded into the water, is nonciliated, only the male gamete (sperm) being motile. Finally, in *Oedogonium* and many other algae, the large nonmotile egg is not liberated but is fertilized within the oogonium by the small motile sperm. Thus the evolution of heterogamy from isogamy has been gradual.

After sexual reproduction had become established, one gamete retained its motility and small size, while the other sacrificed its motility for an increased nutritive capacity. The advantage of heterogamy lies in the greater amount of reserve food that comes to be stored in the zygote. This advantage is reflected by the occurrence of heterogamy in many green algae, most brown algae, all stoneworts, and all red algae, as well as in all plants above the thallophyte level. It should be emphasized that heterogamy has arisen independently in the various groups of algae where it occurs.

The production of gametes in ordinary vegetative cells is characteristic of *Ulothrix*, *Oedogonium*, and most other green algae. A more advanced condition is seen in *Vaucheria,* the Charophyceae, and nearly all the brown and red algae, where the gametes are borne in gametangia or sex organs, which are specialized for reproduction, a function lost by the other cells of the body. This tendency parallels the production of spores in sporangia. The sporangia remain unicellular but the gametangia of some algae have become multicellular by the formation of cross walls, as in *Ectocarpus* and *Cutleria*. In *Dictyota* the antheridia are multicellular and the oögonia are unicellular.

**Alternation of Generations.** In nearly all the green algae the vegetative plant, of which there is but one kind, gives rise to gametes and is haploid. Here the diploid condition, which always results from fertilization, is restricted to the zygote itself, since the reduction of chromosomes takes place when it germinates. This reduction always involves the formation of four haploid nuclei. In *Oedogonium* each of the four zoospores (meiospores) coming from the zygote contains one of these nuclei. In *Spirogyra* three of the nuclei degenerate and the zygote gives rise directly to a haploid vegetative body. In *Coleochaete* four haploid cells are formed by the zygote, but each divides one, two, or three more times before zoospores are organized. In the two lower orders of red algae (Bangiales and Nemalionales) an analogous condition exists in the formation of carpospores.

In some of the algae, notably in the diatoms, *Acetabularia, Codium, Bryopsis,* and the Fucales, there is only one kind of vegetative body and it is diploid, the reduction of chromosomes occurring in connection with the formation of gametes, or in several nuclear divisions immediately preceding their formation. This is also the condition in animals.

Some botanists recognize an alternation of generations wherever there is a diploid and a haploid phase in the life history, even though one or the other is represented by only one cell—in other words, wherever there is sexual reproduction. Such a broad use of the term makes it almost meaningless. In algae displaying a true alternation of generations, a more or less prolonged growth phase intervenes between fertilization and meiosis, as well as between meiosis and fertilization. Here the life history involves two distinct and independent vegetative bodies, a haploid body (gametophyte) producing gametes and a diploid body (sporophyte) producing spores. The gametophyte arises from a spore, the sporophyte from a zygote. The reduction of chromosomes occurs when the spores are formed. A true alternation of generations is found in only a very few green algae, such as *Ulva* and *Cladophora,* in all brown algae except the Fucales, and in all red algae except the Bangiales and Nemalionales. The alternation may be isomorphic, with both generations alike vegetatively, as in *Ulva, Cladophora, Ectocarpus, Dictyota,* and *Polysiphonia,* or it may be heteromorphic, with both generations unlike vegetatively, as in *Cutleria* and *Laminaria.* In all algae possessing a true alternation of generations both gametophyte and sporophyte are free-living; one is never dependent upon the other.

**Interrelationships.** It is not possible to arrange the classes of algae in such a way as to indicate their true relationship. The sequence in which these groups have been presented is merely one denoting an ever-increasing complexity in vegetative and reproductive structures. It does not denote descent of one group from the one preceding it in the series, although in some cases this may be true. Each group merely stands for a different degree of progress from what was originally a primitive condition.

The most important evidence concerning the interrelationships of plant groups is derived from paleobotany. The dearth of fossils belonging to groups below the pteridophyte level is so great, however, that practically all conclusions regarding phylogeny must be based on the comparative structure and development of existing plants. This means that such conclusions, even though well substantiated, are largely speculative.

The Cyanophyceae are the most primitive group of autotrophic plants. Except for the presence of chlorophyll, they are strikingly like the bacteria. Which of these groups appeared first on the earth is very uncertain, but is unimportant in connection with the present discussion. Both groups are at a very low level of structural organization. The classes consisting mainly of flagellates show a considerable advance over the Cyanophyceae by their well-organized nuclei, definite plastids, and ciliated cells. In the absence of transitional forms, any direct connection between the Cyanophyceae and flagellates is difficult to visualize. It is easier to think of the flagellates as having arisen directly from the bacteria. A direct relationship between the Cyanophyceae and any of the higher algal classes is also unlikely, although there is some evidence of this in the case of the Rhodophyceae. Ciliated cells are not present in either group; some members of each have both phycocyanin and phycoerythrin; and a few primitive Rhodophyceae have a nuclear structure but little advanced over that of the Cyanophyceae. It is primarily the absence of ciliated cells that would seem to preclude the possibility of a relationship between either group and the flagellates.

That the Xanthophyceae and Chlorophyceae have arisen independently from a flagellate ancestry is strongly indicated by the presence of naked, free-swimming reproductive cells in the life history and by the occurrence of intermediate forms. The derivation of the Bacillariophyceae and Phaeophyceae directly from flagellate ancestors is less evident. The only connection between the diatoms and flagellates is the presence of ciliated reproductive cells in a few diatoms. The origin of the Phaeophyceae is obscure because the group is without unicellular members. Yet their motile reproductive cells suggest that they may have arisen from brown, laterally biciliate flagellates. There is also the possibility of a direct connection between the Phaeophyceae and Chlorophyceae. The Charophyceae are an isolated group, yet seem to represent a specialized offshoot from the Chlorophyceae.

# CHAPTER IV

## THALLOPHYTA: FUNGI

Fungi are dependent (heterotrophic) thallophytes. Lacking chlorophyll, they are unable to carry on photosynthesis and hence must obtain their food from an external source. Many are *saprophytes*, living on dead organic matter; others are *parasites*, obtaining nourishment from the bodies of living plants or animals, the organism attacked being the *host*. At least some of the fungi may have evolved directly from the algae through loss of power to carry on photosynthesis. Because of their relation to the decomposition of organic matter and to disease, fungi are of tremendous economic importance. The fungi comprise the five classes Schizomycetes, Myxomycetes, Phycomycetes, Ascomycetes, and Basidiomycetes. To these might be added the class Lichenes.

### 1. SCHIZOMYCETES

The Schizomycetes, or bacteria, are similar in many respects to the Cyanophyceae, differing from them chiefly in their smaller size and lack of chlorophyll. In fact the two groups are often combined into a single group, the Schizophyta. The bacteria are at once the smallest and simplest of all known organisms, unless the viruses are to be considered as living. They are also the most widely distributed, occurring under all conditions where life may exist—in fresh and salt water, in soil, in the air, and in the living and dead bodies of other organisms. Like the Cyanophyceae, they are a very ancient group and must have been among the first forms of life to have existed on the earth. The bacteria comprise about 1,500 species. Some common genera are *Streptococcus*, *Micrococcus*, *Sarcina*, *Bacterium*, *Bacillus*, *Pseudomonas*, *Microspira*, *Spirillum*, *Cladothrix*, and *Beggiatoa*.

**Structure and Reproduction.** Like the blue-green algae, bacteria are unicellular plants that reproduce by fission. Their cells are of three general types: spherical (*coccus*) forms, rod-shaped (*bacillus*) forms, and curved or spiral (*spirillum*) forms (Fig. 80). Some are nonmotile, while others bear cilia, by means of which they move rapidly. The cilia may cover the entire cell or may be restricted to one or both ends, where they occur either singly or in tufts. The rod-shaped types average about 2.5$\mu$ in length,[1] while many of the spherical forms are only about 0.5$\mu$ in diameter.

[1] The unit of microscopic measurement is the *micron*, abbreviated $\mu$. It is one-thousandth of a millimeter (0.001 mm.), approximately equivalent to 1/25,000 inch.

The cells of bacteria are so simple that they might almost be said to be structureless. A mass of homogeneous protoplasm is surrounded by a thin cell wall, generally composed chiefly of chitin, a nitrogenous substance, whereas the cell walls of green plants are composed mainly of cellulose, a carbohydrate. Commonly the cell wall becomes mucilaginous, forming a slimy sheath or capsule. There is no organized nucleus but merely some scattered granules of a chromatin-like material that can be revealed by staining. In some bacteria these granules are aggregated to form a distinct central group. Other granules may also be present; these generally represent reserve food.

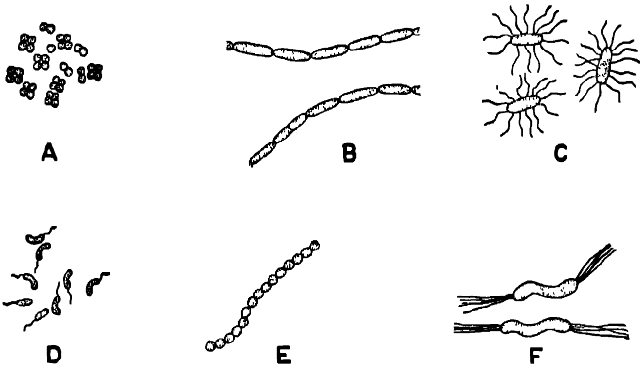



FIG. 80. Group of common bacteria, ×1,500. *A*, *Sarcina lutea*; *B*, *Bacillus subtilis*; *C*, *Bacillus typhosus*; *D*, *Spirillum cholerae*; *E*, *Streptococcus pyogenes*; *F*, *Spirillum undulatum*.

In some bacteria the two cells separate following division, while in others they remain together in colonies. Spirillum forms are nearly always solitary. In the coccus forms the colonies may be cubical, plate-like, chain-like, filamentous, or irregular. In the bacillus forms the divisions occur only in one plane, and so the colonies are always filamentous. In *Beggiatoa*, a sulphur bacterium, the filaments are as highly organized as those of *Oscillatoria*. In *Cladothrix*, an iron bacterium, the filaments exhibit false branching.

As in the Cyanophyceae, cell division takes place by the formation of an inward-growing cell wall. Under favorable circumstances, cell division in many bacteria may occur as frequently as every 20 minutes, so that, in the course of 24 hours, a single cell may give rise to billions. Such a rate of multiplication is soon checked, however, by the exhaustion of the food supply or by the accumulation of poisonous waste products of metabolism. Although all bacteria are active only in the presence of moisture and other favorable conditions, if these fail, many bacteria can pass into a resting stage and remain inactive for a long time. Bacteria on dust particles in the air are in a dormant state and can resist desiccation and great extremes of temperature. In some bacilli the resting cell becomes an *endospore*. Here the protoplast rounds up inside the cell cavity and invests itself with a new cell wall, the old wall eventually disappearing. Endospores are extremely resistant. With the return of favorable conditions, they again become active vegetative cells. Thus "spore formation" in bacteria does not result in reproduction but merely in survival during a period of stress.

Although the bacteria are said to be without sexual reproduction, there is some evidence that it may occur at least in certain bacteria, since there seems to be Mendelian segregation resulting from mixtures of different types.

**Activities.** Most bacteria are either saprophytic or parasitic and in both cases food is absorbed through the cell wall. Some can live either as saprophytes or as parasites, while a few can make their own food without the aid of chlorophyll or light. *Aerobic* bacteria require free oxygen in respiration, while *anaerobic* bacteria obtain oxygen from organic compounds.

Most diseases of animals and many diseases of plants are caused by parasitic (pathogenic) bacteria, the disease itself being merely a response on the part of the host to the presence of the parasite. A disease manifests itself by symptoms, which are abnormalities in structure or function. Well-known human diseases of bacterial origin are typhoid fever, tuberculosis, diphtheria, pneumonia, cholera, and tetanus. Some bacterial diseases of plants are pear blight, cabbage rot, cucurbit wilt, and crown gall. The disease may be caused by direct attack of the bacteria on the host tissues, by the liberation of toxins, or by both.

The decomposition of dead organic matter is accomplished chiefly by saprophytic bacteria. They break up organic compounds into simpler substances through a series of intermediate steps, a succession of different bacteria being involved. The ultimate products of decomposition are such simple substances as water, carbon dioxide, ammonia, hydrogen sulphide, etc. Bacteria of decay cause fermentation and putrefaction. They play an important part in the economy of nature by returning to the air and soil substances that may again be used by other organisms.

All plants require nitrogen in order to synthesize proteins, but only the nitrogen-fixing bacteria and a few other forms are able to use the nitrogen of the air directly. Practically all green plants are dependent for nitrogen upon its compounds, particularly nitrates. Some of the nitrogen-fixing bacteria, such as *Clostridium* and *Azotobacter*, live free in the soil and are saprophytic on organic matter, while *Rhizobium* is parasitic in the roots of various Leguminosae, such as clover, alfalfa, peas, beans, etc. These bacteria combine atmospheric nitrogen with oxygen and other elements, particularly potassium, sodium, or calcium, and form nitrates, which may later be utilized by green plants. The root of the legume responds to the presence of these parasitic bacteria by forming local enlargements called *tubercles* or *nodules*.

Nitrifying bacteria also live in the soil but form nitrates in a different way. The decomposition of organic matter by bacteria of decay yields ammonia ($NH_3$). This is oxidized, first to nitrites ($NO_2$ compounds) by *Nitrosomonas*, and then to nitrates ($NO_3$ compounds) by *Nitrobacter*. An interesting fact about these bacteria is that, although lacking chlorophyll, they are able to synthesize carbohydrate food from water and carbon dioxide (or carbonates). They derive their energy, not from sunlight, but from the oxidations that they carry on. With respect to their nutrition, these bacteria, like green plants, are autotrophic, even though they do not carry on photosynthesis. The process by which they make their own food is sometimes called *chemosynthesis*. Such autotrophic bacteria may have preceded all other forms of life on the earth. In addition to the nitrifying bacteria there are other kinds that are autotrophic. They oxidize sulphur, hydrogen sulphide, free hydrogen, methane, or iron compounds. *Beggiatoa* is a colorless filamentous form that oxidizes hydrogen sulphide ($H_2S$) to form water and sulphur, storing the sulphur as yellow granules inside its cells. It is found in sulphur springs. Certain iron bacteria oxidize ferrous iron compounds to ferric hydroxide ($Fe(OH)_3$), which accumulates to form a kind of iron ore. These bacteria are common in bogs.

Denitrifying bacteria live in the soil, especially where poorly drained. They convert nitrogen salts into gaseous nitrogen. This escapes into the air and so causes a loss of soil fertility.

**Myxobacteria.** The myxobacteria are a group of peculiar organisms that live as saprophytes on animal refuse. Their cells resemble those of true bacteria but form remarkable complex colonies held together by mucilage. Some of the myxobacteria form stalked sporangia that are often brightly colored. Some exhibit slow creeping movements. In these respects the group resembles the myxomycetes.

**Summary.** The Schizomycetes are the simplest of all plants. All of them are unicellular, the cells being either solitary or in colonies. A definite cell wall is present, generally composed of chitin rather than of cellulose, and usually breaks down to form mucilage. The protoplast shows little organization, a nucleus being represented only by scattered granules of chromatin. Reproduction occurs by fission. Some bacteria move by means of cilia, while others are nonmotile. In some species a resting cell (endospore) may form inside a vegetative cell, becoming invested with a new cell wall. The Schizomycetes are closely related to the Cyanophyceae, differing from them chiefly in the lack of chlorophyll, presence of cilia in some members, and character of the resting cell.

## 2. MYXOMYCETES

The Myxomycetes, or slime molds, are peculiar organisms that, like the flagellates, are claimed by both botanists and zoologists, the latter calling them Mycetozoa (fungus-animals). They are a widely distributed group, living in damp, shady places as saprophytes on humus, decaying wood, bark, fallen leaves, etc. All lack chlorophyll. The

FIG. 81. Plasmodium of *Didymium*, a slime mold, ×30. (*From Gilbert M. Smith.*)

Myxomycetes number over 400 species. Some of the common genera are *Lycogala*, *Stemonitis*, *Fuligo*, *Arcyria*, and *Trichia*.

**Plant Body.** The vegetative body of a myxomycete is a *plasmodium*, which is a naked mass of multinucleate protoplasm (Fig. 81). The nuclei, like those of the higher plants, are well organized. The plasmodium is without definite form and may attain a diameter of several centimeters, or even a meter in some myxomycetes. The plasmodium moves by the formation of pseudopodia and engulfs solid particles of food as it passes over them, digesting them within food vacuoles. In these respects it resembles an amoeba. It also absorbs food material in solution through the plasma membrane. Depending on the species, the plasmodium may be white or some shade of yellow, orange, red, brown, or violet. The plasmodium tends to move toward moisture but shows an avoiding reaction to light, appearing at the surface of its substratum only at night. In times of drought it retracts itself into a waxy mass and hardens, forming a *sclerotium.* In this condition the organism may remain dormant for months, or sometimes even for years, becoming active again in the presence of water.

**Reproduction.** Although the myxomycetes are animal-like in their vegetative state, their reproductive features are distinctly plant-like. When reproduction is to occur, the entire plasmodium comes to the

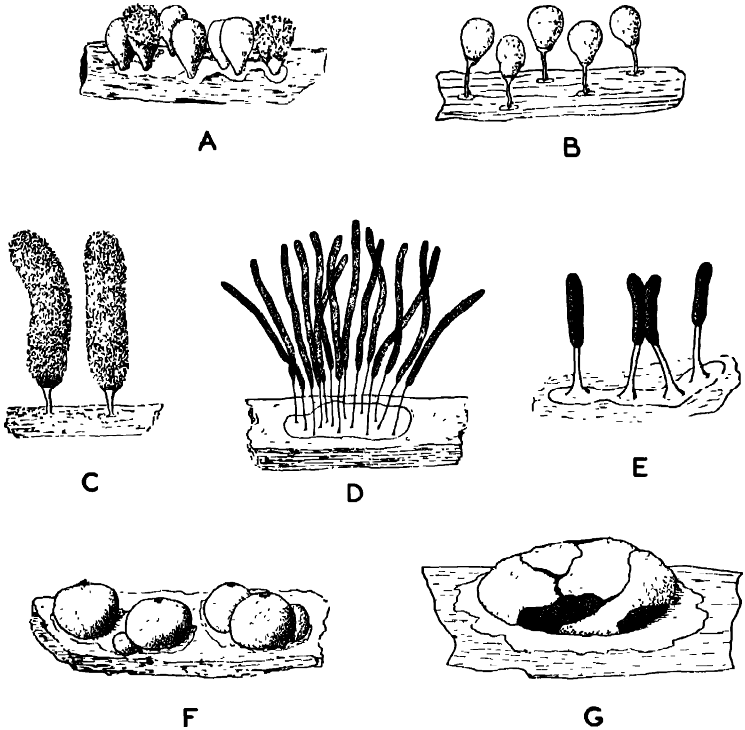



FIG. 82. Group of common slime molds, showing sporangia arising from the plasmodium. *A*, *Hemitrichia ovata*, ×10, *B*, *Craterum leucocephalum*, ×10; *C*, *Arcyria incarnata*, ×5; *D*, *Stemonitis herbatica*, ×2; *E*, *Diachea leucopoda*, ×10; *F*, *Lycogala epidendrum*, ×1; *G*, *Fuligo septica*, ×½.

surface of its substratum and contracts into a cushion-like mass. As this hardens, it forms one or more sporangia that are usually brown or yellow (Fig. 82). In some myxomycetes the entire plasmodium may be converted into a single giant sporangium, called an *aethalium*, but, more commonly, a number of small separate sporangia are formed. These may be either sessile or stalked. Throughout the various genera the sporangia exhibit much diversity in form, but are commonly spherical, oval, or cylindrical. The sporangium contains many nuclei and the remains of the plasmodium, the latter usually forming a network of tough strands known as the *capillitium* (Fig. 83). In the meshes of this network innumerable spores are formed, each one being uninucleate. The spores have cellulose walls and are scattered by the wind. In their dispersal the wall of the sporangium ruptures irregularly at the apex and the capillitium performs hygroscopic movements.

The myxomycetes display considerable variation with respect to the development of the plasmodium from a spore. Commonly the protoplast escapes from the spore wall and becomes a zoospore, developing one long cilium and one very short one, both anteriorly attached. Sometimes two to eight zoospores are produced. The zoospore may ingest food and undergo multiplication by fission. After a period of free swimming, the cilia are retracted and the protoplast becomes amoeboid. These amoeboid cells, called *myxamoebae*, may also take in food and divide repeatedly, or they may pass into a resting stage. Finally, however, they fuse in pairs. Then, instead of forming resting zygotes, a number come together to form a multinucleate plasmodium. In the fusion of the small amoeboid cells in pairs, the two nuclei unite, but there are no subsequent nuclear fusions. Consequently the nuclei of the plasmodium are diploid. They undergo repeated divisions as the plasmodium increases in size. Reduction of chromosomes to the haploid number occurs just prior to the formation of spores in the sporangium.

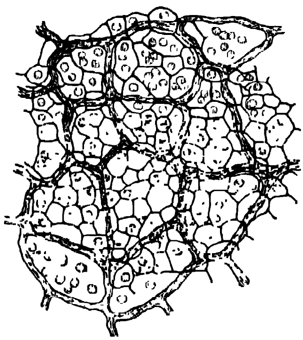


FIG. 83. Portion of capillitium of *Stemonitis* with spores in its meshes, ×250.

**Summary.** The Myxomycetes combine features found in both plants and animals. The body is a naked mass of multinucleate protoplasm (a plasmodium) that displays amoeboid movements and engulfs solid food particles. In a quiescent state it gives rise to sporangia containing numerous walled spores from which eventually, although not directly, a new plasmodium is formed. Sexual reproduction occurs by a fusion of similar amoeboid gametes. Certain aspects of the life history suggest a relationship to the flagellates. Any possible connection with the true fungi is very uncertain.

**Other Slime Fungi.** In addition to the Myxomycetes, or slime molds, there are two other groups of slime fungi that deserve some attention. These are the Acrasieae and the Labyrinthuleae. Many mycologists include all three groups in a separate assemblage, the Myxothallophyta, and place them outside and below the fungi. They have certain important characters in common: simple, naked, nucleated, amoeboid cells resembling protozoans but plant-like in their reproduction by the formation of spores. The interrelationships of the three groups of slime fungi are not well understood, but are not assumed to be close. They have probably been derived from protozoan ancestors and have evolved along independent lines.

**Acrasieae.** These simple forms are saprophytes on soil, decaying wood, and animal refuse. The vegetative body is a myxamoeba, a naked cell with a nucleus and a contractile vacuole. It reproduces by fission and in the presence of unfavorable conditions may encyst. Eventually, a number of myxamoebae come together without fusing to form a pseudoplasmodium in which each myxamoeba retains its individuality. Not

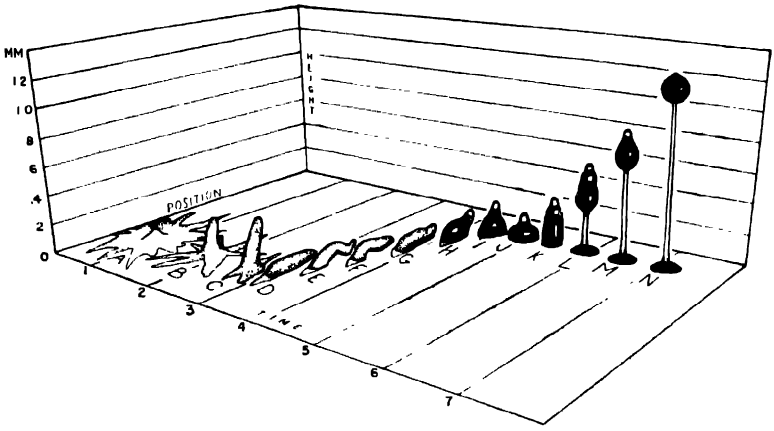



FIG 84. Three-dimensional graph showing the development of the fruiting body of *Dictyostelium discoideum* in height, time, and position *A*, aggregation of a mass of individual myxamoebae; *B* to *D*, formation of the pseudoplasmodium; *E* to *G*, migration of pseudoplasmodium, *H* to *N*, formation of fruiting body with disk, stalk, and spherical spore mass. (*From J. T. Bonner* )

only is a multinucleate plasmodium lacking, but no zoospores are produced. The pseudoplasmodium assumes a definite form, usually elongating and varying in length from several tenths of a millimeter to a millimeter or more.

The subsequent behavior of the pseudoplasmodium is remarkable in that it migrates over the substratum, apparently by a gliding of the amoebae over one another. After coming to rest, the pseudoplasmodium is transformed into a fruiting body consisting of a basal disk, a vertical stalk, and a terminal spherical region that is converted into a mass of spores (Fig. 84). In some species the fertile region consists of a series of spherical spore masses arranged at the ends of whorled branches. All these complex changes are accomplished by movements of individual myxamoebae to their proper place in the fruiting body, where each becomes the type of cell appropriate for its position, such as a disk cell. stalk cell, or spore. The spores have a cell wall. Upon germination, each spore gives rise to a myxamoeba.

**Labyrinthuleae.** In this little-known group the vegetative cell is spindle-shaped with tufts of pseudopodia at the ends. When the cells come in contact, their pseudopodia generally fuse, the union of numerous cells producing a net-like structure called a net-plasmodium. The individual cells, retaining their identity, appear to glide along the threads of the net in limited movements. During this stage they feed, increase in size, and undergo repeated division. In dividing, the cells become constricted at the middle and then separate, but are held together by a protoplasmic strand. At the close of the vegetative stage, the cells collect into sessile or stalked masses and become encysted. In some species the spores have cell walls, in others not. Later the spores germinate, freeing one to four spindle-shaped cells with polar pseudopodia.

## 3. PHYCOMYCETES

The Phycomycetes, or alga-like fungi, comprise the first group of "true fungi" (Eumycetes), as the higher fungi are often called in contrast to the bacteria and myxomycetes. All the true fungi have a definite nucleus and nearly all have a characteristic plant body called a *mycelium*. This is composed of branching filaments, each branch being a *hypha*. The hyphae may be either loosely or compactly interwoven. With few exceptions, the Phycomycetes are characterized by an absence of cross walls in the mycelium, and so, as in *Vaucheria*, the plant body is a coenocyte. Their spores are borne in indefinite numbers within a sporangium. The origin of the Phycomycetes is not clear. They may have evolved either from colorless flagellates or, through loss of chlorophyll, from the Chlorophyceae, a group which they resemble in both vegetative and reproductive features. A number of Phycomycetes cause diseases of economic plants, such as cranberry gall, brown rot of lemon, downy mildew of grape, and late blight of potato. The group is a relatively small one, numbering about 1,000 species. These are included in seven main orders: Chytridiales, Monoblepharidales, Plasmodiophorales, Saprolegniales, Peronosporales, Mucorales, and Entomophthorales.

### 1. Chytridiales

The Chytridiales are the simplest of the Phycomycetes. Nearly all of them are parasitic, many living on fresh-water algae and others attacking seed plants growing in moist situations. The order includes about 65 genera and 300 species, the best-known forms being *Chytridium*, *Olpidium*, and *Synchytrium*.

**Chytridium.** A common species of *Chytridium* attacks the green alga, *Oedogonium*. A uniciliate zoospore comes in contact with an oögonium of the host, loses its cilium, and sends into the host cell a tube through which food is absorbed. This tube represents a weakly developed mycelium. The external part of the fungus then becomes transformed into a sporangium, its protoplast undergoing cleavage into many zoospores (Fig. 85*A*). A zoospore may penetrate a zygote of the host and, by the secretion of a thick wall, become a resting spore. When the zygote germinates, the resting spore of the fungus sends out tubes that give rise to terminal sporangia.

**Olpidium.** This fungus grows on many different hosts, some of which are fresh-water algae. One species, *Olpidium brassicae*, attacks young

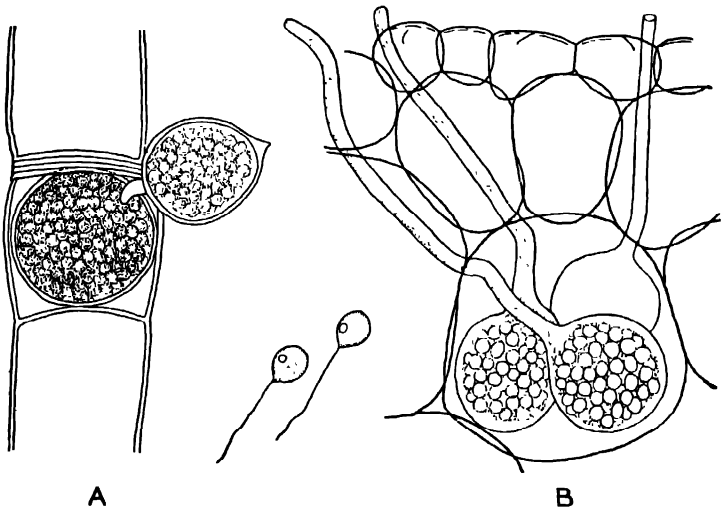



FIG. 85. Chytridiales. *A*, sporangium of *Chytridium olla* attached to zygote of *Oedogonium; B*, sporangia of *Olpidium brassicae* in root of cabbage seedling; also two zoospores of same to the left. (*A, after Campbell; B, after Woronin.*)

cabbage plants. A uniciliate zoospore comes to rest on the host, withdraws its cilium, and secretes a cell wall. It sends a short tube into the host and the protoplast enters one of the cells. At first the protoplast is naked and amoeboid. It enlarges and becomes multinucleate, finally occupying the whole cell cavity. Then it forms a cell wall and becomes a sporangium. A tube is sent to the surface of the host and numerous uniciliate zoospores escape through it (Fig. 85*B*). Sexual reproduction occurs by means of isogametes that are formed like the zoospores but escape and fuse in pairs. The zygote sends a short tube into a host cell, after which its protoplast enters, enlarges, and secretes a thick wall. After resting over the winter, it gives rise to a number of uniciliate zoospores.

**Synchytrium.** This form attacks the epidermal cells of various seed plants, such as cranberry, primrose, hog peanut, filaree, and many others. A disease called cranberry gall is caused by *Synchytrium vaccinii*, while the destructive black wart of the potato is caused by *Synchytrium endobioticum*. A uniciliate zoospore comes in contact with a young epidermal cell of the host and enters it. Without forming a cell wall, the protoplast of the fungus enlarges and lives symbiotically with the protoplast of the epidermal cell, not killing it but causing it and the adjacent cells of the

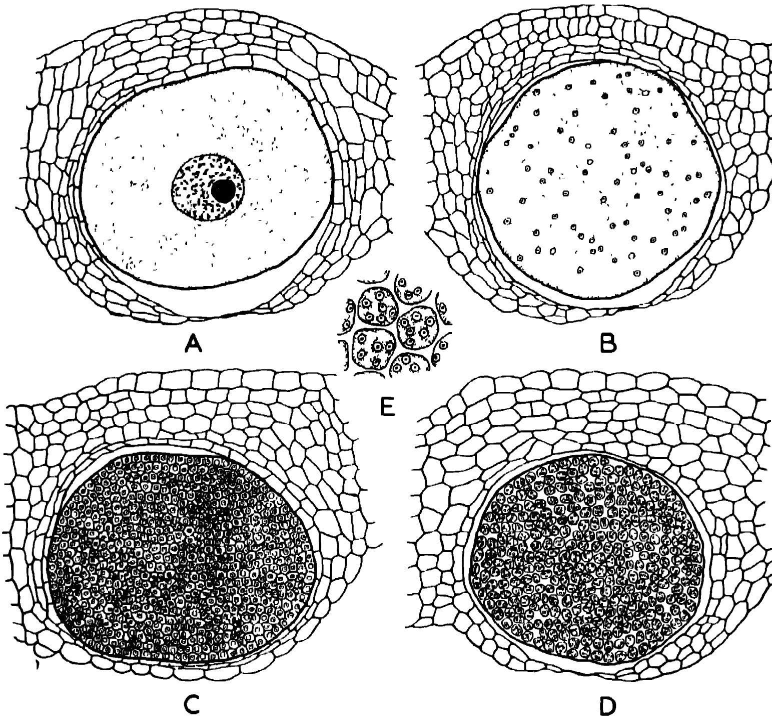



FIG. 86. Stages in the development of the sporangia of *Synchytrium decipiens*. *A*, greatly enlarged fungous protoplast in leaf of host after having destroyed one of its epidermal cells; *B*, division of large nucleus of fungus to form many small free nuclei; *C*, cleavage of protoplast into many small uninucleate cells, *D*, separation of small cells to form sporangia, each of which has become multinucleate, *E*, enlarged portion of same; *A* to *D*, ×125; *E*, ×500.

host to enlarge. A small gall or blister forms on the surface of the host, this serving as a means by which an infected plant can be recognized. Blisters usually appear both on the leaves and stems.

Finally, the infected epidermal cell dies. Then the fungus secretes a wall about itself and goes into a resting stage (Fig. 86*A*). Later its nucleus undergoes repeated divisions and progressive cleavage of the cytoplasm from the surface inward results in the formation of many protoplasts, each of which secretes a wall (Fig. 86*B*, *C*). These cells may be multinucleate when formed but, if uninucleate, they soon become multinucleate by additional free-nuclear divisions (Fig. 86*D*, *E*). Each of these cells becomes a sporangium and, when conditions are favorable, gives rise to a number of naked zoospores (usually 8 to 12) that escape. Frequently, however, the resting cell arising from a vegetative protoplast divides to form a number of gametangia rather than sporangia. Each of these produces many isogametes that, after escaping, fuse in pairs The zygote invades a host cell and then goes into a resting stage, forming a thick wall. Later it gives rise to many zoospores. Both the zoospores and gametes of *Synchytrium* are uniciliate.

**Summary.** Most of the Chytridiales are unicellular fungi with either no mycelium or a very poorly developed one. Generally all or most of the vegetative body develops into a sporangium or gametangium. Reproduction occurs by uniciliate zoospores or isogametes. Because they possess the simplest type of sexual reproduction known among the fungi, the Chytridiales are regarded by some mycologists as primitive forms, while others consider them to be degenerate Phycomycetes.

## 2. Monoblepharidales

The Monoblepharidales are a very small order containing 2 genera: *Monoblepharis*, with 6 species, and *Monoblepharella*, with 2 species

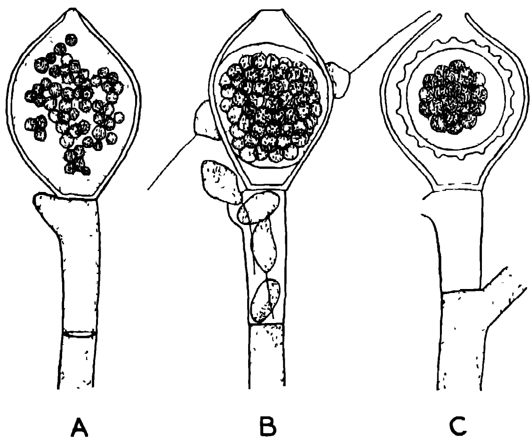



FIG. 87. *Monoblepharis sphaerica.* *A*, end of hypha with young oögonium and a young antheridium just below it, *B*, sperms escaping and approaching the matuie oogonium with its single egg; *C*, zygote with empty antheridium below it. (*After Cornu.*)

*Monoblepharis* is a saprophyte on decaying aquatic vegetation. It has a well-developed mycelium that produces sporangia and sex organs. The sporangia are terminal club-shaped cells containing many uniciliate zoospores. Sexual reproduction is heterogamous. The oögonium is a globular cell, cut off by a wall commonly at the end of a hypha (Fig. 87). Its protoplast rounds up and becomes a large uninucleate egg. The antheridium usually arises immediately below the oögonium as a short slender branch that is cut off by a basal wall. It gives rise to a number of uniciliate sperms that escape and swim in the water. A sperm enters the oögonium through a terminal pore and unites with the egg. The Monoblepharidales are remarkable in being the only fungi with swimming sperms. According to the species, the zygote may mature either inside or outside the oogonium. It becomes a thick-walled resting cell, later producing a new mycelium.

### 3. Plasmodiophorales

This order comprises 8 genera and 23 species, of which the best known is *Plasmodiophora brassicae*, a parasite attacking cabbages and other crucifers and causing a disease known as clubroot. Another member of the group, *Spongospora subterranea*, is responsible for a disease of potatoes

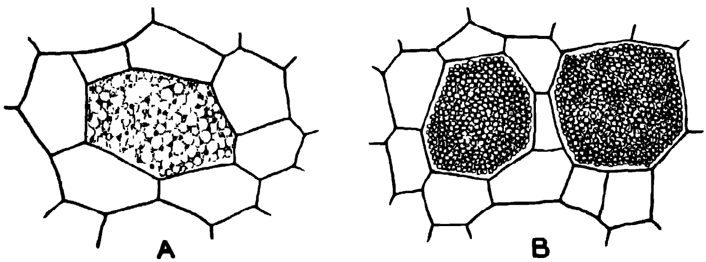



FIG. 88. Section of a portion of a cabbage root, showing two stages in the development of *Plasmodiophora brassicae* within the cells, ×250. *A*, plasmodium completely filling a cell; *B*, spore formation

called powdery scab. The Plasmodiophorales, once regarded as parasitic myxomycetes, are now generally considered to belong to the lower phycomycetes.

When cabbages are attacked by *Plasmodiophora*, the root undergoes a marked enlargement. The cells of the root are invaded by biciliate zoospores. The cilia, attached anteriorly, are of unequal length.[1] The zoospores lose their cilia and become amoeboid, migrating directly through the cell walls of the host. An amoeboid cell (myxamoeba) gives rise to a multinucleate plasmodium (Fig. 88*A*). This soon undergoes cleavage into many uninucleate, walled cells, each of which is said to form four or eight biciliate isogametes that pair and fuse. The amoeboid zygote enlarges, becomes multinucleate, and migrates into another cell of the root, which it finally fills. The diploid nuclei of the young plasmodium continue to divide until the two reduction divisions have occurred. Then a number of small spores are formed, each with a cell

[1] Until recently it was thought that the zoospores were uniciliate and, chiefly on this basis, *Plasmodiophora* and related forms were classified as a family under the Chytridiales.

wall (Fig. 88*B*). These are liberated by decay of the host. Upon germination, each gives rise to a zoospore.

## 4. Saprolegniales

The Saprolegniales, or water molds, are an order of aquatic fungi, usually occurring in ponds and streams. Most of them are saprophytic on plant or animal remains lying in the water, while a few are parasitic. Many also occur on damp soil. The order includes 20 genera and about 120 species, representative members being *Saprolegnia* and *Achlya*.

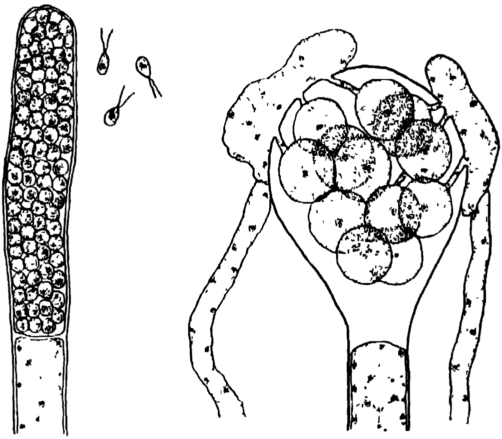



FIG. 89. *Saprolegnia* *A*, a sporangium and three escaped zoospores, ×350, *B*, an oögonium with many eggs and with two antheridia in contact with it, ×350.

**Saprolegnia.** This common water mold usually lives on dead insects, fishes, tadpoles, and other aquatic animals. Sometimes it attacks living fishes and fish eggs. The vegetative body consists of a delicate, branching, coenocytic mycelium that penetrates the food supply. Some of the hyphae form terminal sporangia, each of which is a slender elongated cell, cut off by a basal wall, and giving rise to many uninucleate zoospores (Fig. 89*A*). These are developed by progressive cleavage of the cytoplasm within the sporangium. The zoospores escape singly into the water through a terminal pore in the sporangial wall. In *Achlya* they escape as a mass.

The zoospores of *Saprolegnia* are oval and have two equal cilia attached apically. After swimming for a while, they become quiescent, form a cell wall, and go into a dormant stage. After about 24 hours, the protoplasts escape and again become motile, but this time the spores are kidney-shaped and laterally biciliate. Finally they settle down and, on a suitable substratum, each produces a new mycelium. The occurrence of two types of zoospores is very puzzling and its significance has never been satisfactorily explained.

*Saprolegnia* is heterogamous, forming sex organs on special branches of the mycelium (Fig. 89*B*). The oögonium is a spherical cell that produces several eggs, sometimes many, rarely only one. At first they are multinucleate but, by degeneration of the extra nuclei, become uninucleate. The antheridium is a slender curved tube that arises just below the oögonium or, in most species, from an adjacent hypha. Each oögonium may be surrounded by several antheridia. Both kinds of sex organs are cut off from the vegetative mycelium by a basal wall. No sperms are organized. Instead, the tip of the antheridium comes in contact with the oögonium and sends into one or more of the eggs a fertilization tube through which some of the cytoplasm and a male nucleus pass. This nucleus unites with the egg nucleus, resulting in fertilization. The zygote secretes a heavy wall and usually remains dormant for several months, finally producing a new mycelium In *Achlya* it has been shown that the reduction of chromosomes occurs when the zygote germinates. In some species of *Saprolegnia* the antheridia are nonfunctional, while in others antheridia are not even formed. Nevertheless the eggs become thick-walled and later germinate, thus developing by parthenogenesis.

In *Achlya,* which is dioecious, the appearance of sex organs is caused by hormone-like substances. These are secreted into the water by the male and female plants and stimulate production of sex organs of the opposite sex. A hormone produced by the male plants causes oögonia to appear on the female plants, while a hormone produced by the female plants results in the appearance of antheridia on the male plants.

**Summary.** The Saprolegniales are chiefly saprophytes. They are aquatic fungi with a well-developed mycelium. They produce biciliate zoospores in persistent sporangia. All of them are heterogamous. The oögonium contains one or more eggs that are fertilized by a male nucleus coming from the antheridium through a fertilization tube. In most members the entire oögonial protoplast enters into the formation of eggs. The absence of swimming sperms in an exclusively aquatic order is a noteworthy feature.

### 5. Peronosporales

The Peronosporales, or downy mildews, are mostly parasites that attack various seed plants, the mycelium living within the intercellular spaces of the host. The order includes about 12 genera and 150 species, representative members being *Pythium, Albugo, Phytophthora, Plasmopara,* and *Peronospora.*

**Albugo.** This fungus lives as a parasite on a number of different seed plants. A common species, *Albugo candida,* attacks various members of the Cruciferae, such as radish, turnip, mustard, and shepherd's-purse, causing a disease known as white rust of crucifers. The mycelium, which may live in almost any part of the host, ramifies throughout the intercellular spaces and sends short button-like haustoria into the living cells. Here and there beneath the epidermis the mycelium gives rise to compact clusters of erect sporangiophores from the ends of which thin-walled,

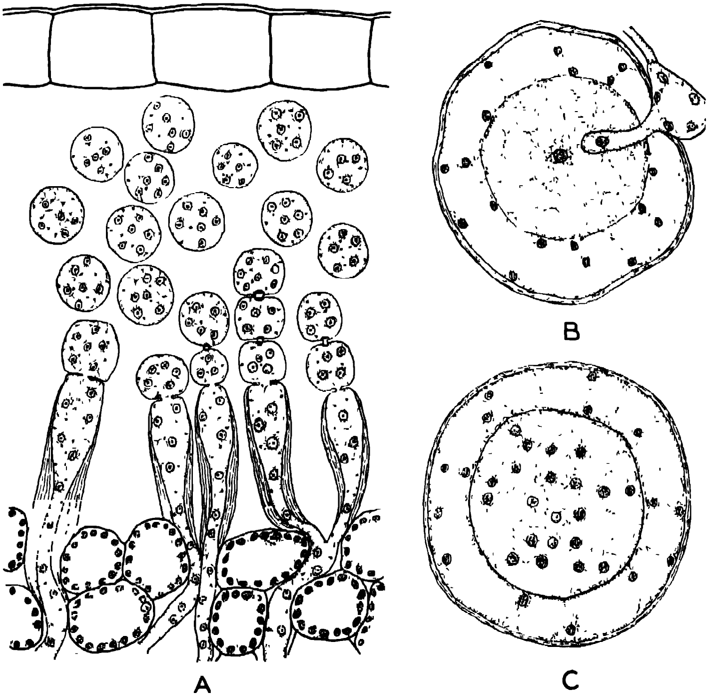



FIG. 90. Sporangia and sex organs of *Albugo*. *A*, cross section of a small portion of the stem of shepherd's-purse, showing sporangiophores of *Albugo candida* arising beneath the epidermis and giving rise to multinucleate sporangia, ×600, *B*, sex organs of *Albugo candida*, a fertilizing tube from an antheridium penetrating an oogonium with a single nucleus in the ooplasm, ×750; *C*, oogonium of *Albugo portulacae* with multinucleate ooplasm, ×500.

globular, multinucleate sporangia are cut off in chains (Fig. 90*A*). These push up the epidermis and form a white blister on the surface of the host. These blisters may appear on the leaves, stems, floral parts, or fruits. Finally, the epidermis is ruptured and the sporangia are carried by the wind to uninfected hosts. Here they give rise to 12 or more laterally biciliate zoospores that escape, swim about for a while, encyst, and finally produce new mycelia. When a spore germinates, it produces a hypha that enters the host through a stoma.

The sex organs of *Albugo candida*, appearing later in the season than the sporangia, are formed on the mycelium deep within the host tissues.

The oögonium is a globular multinucleate cell, cut off by a cross wall from the swollen end of a hypha (Fig. 90*B*). The cytoplasm becomes differentiated into a peripheral zone, the *periplasm*, and a central denser region, the *oöplasm*, which becomes the egg. At first both regions are multinucleate, but later all nuclei degenerate except a single nucleus in the oöplasm. The antheridium, appearing on a separate hypha, is a slender multinucleate cell. After coming in contact with the oögonium, it sends into it a fertilizing tube that extends into the egg, where a male nucleus and a small amount of cytoplasm are discharged. Following fusion of the male and female nuclei, the periplasm is used up in the formation of a heavy wall around the zygote. The zygote is finally freed by decay of the host tissues and, after undergoing a period of rest, gives rise to more than one hundred biciliate zoospores, each of which may, under appropriate conditions, produce a new mycelium.

*Albugo bliti*, a species common on the pigweed (*Amaranthus*), differs from *Albugo candida* in several respects. Periplasm and oöplasm are differentiated but the latter remains multinucleate. The entire contents of the antheridium are discharged into the egg and each male nucleus fuses with a female nucleus. In *Albugo portulacae*, which lives on the common purslane (*Portulaca*), multinucleate pairing and fusing also occur (Fig. 90*C*).

**Other Downy Mildews.** The Peronosporales include genera that bear sex organs like those of *Albugo*, but differ in the way their sporangia and spores are formed. Some of these are of considerable economic importance. A species of *Pythium* is frequently the cause of a disease of seedlings known as damping-off. It is particularly common in greenhouses and other warm, moist places. *Pythium* is intermediate between the Saprolegniales and Peronosporales in that it produces zoospores in both permanent and detachable sporangia.

*Phytophthora infestans* causes a serious potato disease called late blight, while another species, *Phytophthora citrophthora*, is responsible for the brown rot of lemon. *Plasmopara viticola* causes downy mildew of the grape, a very destructive disease. In both *Phytophthora* and *Plasmopara* the internal mycelium sends erect sporangiophores to the surface of the host (Fig. 91). Instead of forming blisters, as in *Albugo*, the sporangiophores push out through the stomata and bear solitary terminal sporangia on branches. The sporangia, which are shed without opening, are carried by the wind to uninfected hosts, where each produces several biciliate zoospores. These form a new mycelium within the leaf.

*Peronospora* is a large genus of about 60 species, some of which are parasitic on various garden vegetables, such as cabbage, spinach, onion, pea, etc. It is of interest in that, in many species, no zoospores are produced, the detachable sporangia giving rise to new mycelia directly.

**Summary.** The Peronosporales are almost all internal parasites on seed plants. They have a well-developed mycelium and small multinucleate sporangia that, with few exceptions, are borne on erect sporangiophores. The sporangia are almost always detachable and, after dispersal by the wind, give rise to biciliate zoospores or, in some cases, to a new mycelium directly. All members are heterogamous. The oögonium produces only one egg, in the formation of which the outer portion of the oögonial protoplast is not included. The male nucleus reaches the egg through a fertilization tube developed by the antheridium.

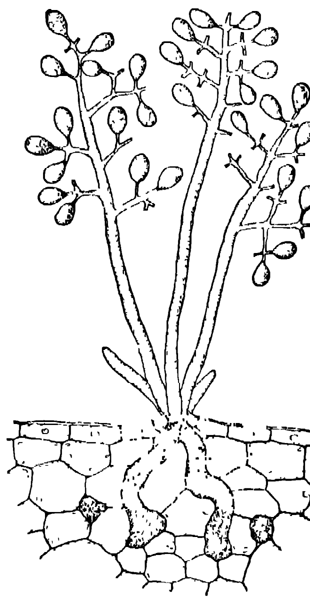


FIG. 91. *Plasmopara viticola* on the stem of grape. Sporangiophores bearing numerous sporangia are emerging through a stoma. ×200.

## 6. Mucorales

The Mucorales are the black molds, most of which are terrestrial saprophytes living on decaying vegetable and animal matter. There are about 30 genera and 400 species, common representatives of the group being *Rhizopus*, *Mucor*, and *Pilobolus*. The largest genus is *Mucor*, with about 50 species.

**Rhizopus.** The common black mold that grows on moist stale bread is *Rhizopus nigricans*. It also occurs on fruits, vegetables, jelly, and other decaying organic matter. The mycelium consists of a white fluffy mass of profusely branched coenocytic hyphae. These grow horizontally over the substratum, sending into it tufts of short root-like haustoria through which food is absorbed (Fig. 92*A*). Erect unbranched sporangiophores arise in clusters from the mycelium at places where the haustoria are formed. Each sporangiophore produces a large, globular, terminal sporangium. In its development, the tip of the sporangiophore enlarges as additional cytoplasm and nuclei pass into it (Fig. 93*A*). Soon the peripheral part of the enlarging sporangium becomes denser than the central portion and a line of vacuoles appears between them (Fig. 93*B*). These two regions are then separated by a cleavage furrow, arising from below, and finally by a dome-shaped wall. This projects into the sporangium to form a *columella* (Fig. 92*B*).

The portion of the sporangium lying between the columella and the outer wall now undergoes a process of progressive cleavage, whereby it becomes divided into numerous small, multinucleate protoplasts by furrows that start at the surface and grow inward (Fig. 93*C–E*). Finally, each protoplast secretes a cell wall and becomes a minute, black, multinucleate spore (Fig. 93*F*). The spores, produced in enormous numbers, are liberated into the air by rupture of the sporangial wall. Upon reaching a suitable supply of food, they give rise to new mycelia. The replacement of zoospores by aerial spores is a notable feature of the Mucorales.

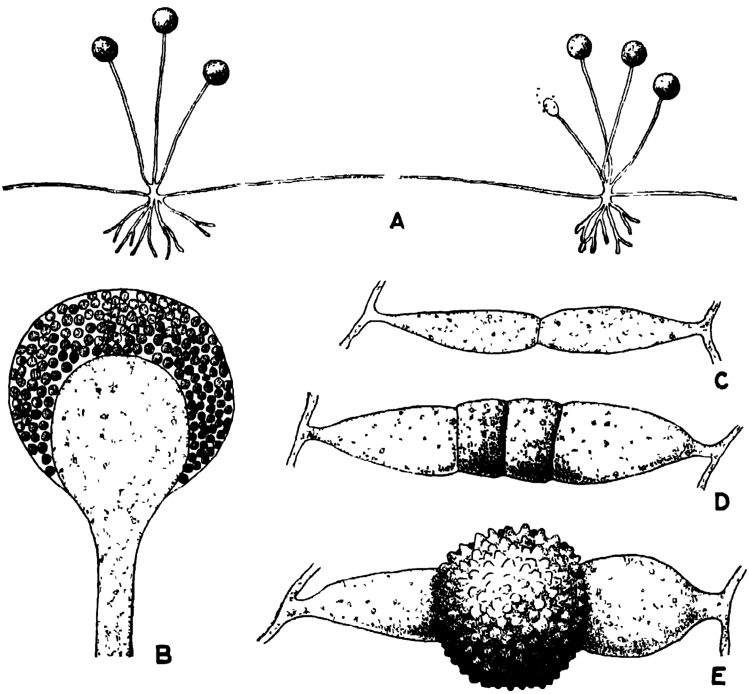



FIG. 92. *Rhizopus nigricans.* *A*, horizontal branch of mycelium producing haustoria and sporangia, ×15; *B*, a mature sporangium, showing central columella, ×150; *C*, *D*, *E*, stages in sexual reproduction, resulting in the formation of a heavy-walled zygote, ×150.

Sexual reproduction occurs in *Rhizopus* only under special conditions (Fig. 92*C–E*). A short lateral branch is put out by each of two hyphae lying parallel to each other. Their tips come in contact, enlarge, and from each a multinucleate cell is cut off by a cell wall. Although ordinarily of the same size, often one cell is slightly larger than the other. Finally, the wall between the cells is dissolved and their contents fuse to form a zygote. Many of the nuclei become associated in pairs and fuse, the others disintegrating. The zygote enlarges and becomes a thick-walled resting cell. The two conjugating cells are usually interpreted as gametangia and their contents as large compound isogametes. It has been observed in other Mucorales, but not in *Rhizopus*, that the zygote,

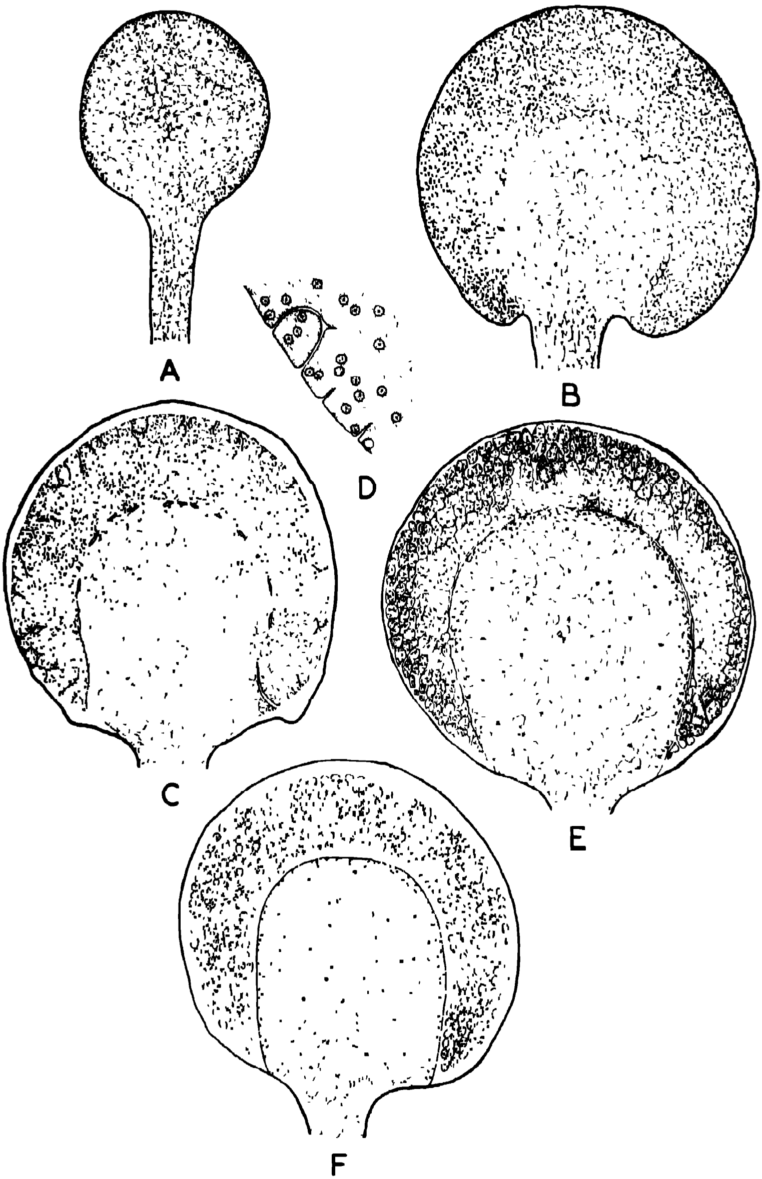



FIG. 93 Development of the sporangium of *Rhizopus nigricans* *A*, young sporangium; *B*, appearance of small vacuoles between outer and inner parts of sporangium; *C*, enlargement and fusion of vacuoles to form columella cleft, appearance of cleavage furrows at outer surface; *D*, enlarged view, showing early cleavage furrows and scattered nuclei and vacuoles; *E*, sporangium completely cut off from columella; cleavage further advanced, *F*, mature sporangium. (*After Swingle.*)

upon germination, gives rise to a short hypha bearing a terminal sporangium. This contains many aerial spores. Meiosis occurs during the first two divisions of the fusion nucleus in the zygote.

Although all the mycelia of *Rhizopus* appear to be alike, gametic reproduction does not take place unless two sexually differentiated mycelia, designated as plus and minus strains, come together. This may happen very infrequently for, when a mycelium produces spores, all the resulting mycelia belong to the same strain and conjugation does not take place between them. Molds with sexually differentiated strains are said to be *heterothallic*, while those without such differentiation are *homothallic*. In homothallic species conjugation may take place between any two hyphae, even those of the same mycelium. In some of the heterothallic Mucorales, when a sporangium is formed at the end of a hypha arising from the zygote, a segregation of strains occurs, so that some of the spores in the sporangium produce plus mycelia and others minus mycelia. In other heterothallic species this sporangium contains spores of one kind or the other, but not both kinds In *Rhizopus nigricans* it is not known where the segregation of strains takes place.

*Pilobolus*, which lives on barnyard refuse, is an interesting mold with a peculiar method of spore dispersal. As the sporangium ripens, the portion of the sporangiophore just below it enlarges and becomes very turgid. Finally it bursts suddenly, shooting out the entire sporangium with considerable force, sometimes to a distance of 2 m., and always toward the brightest source of light.

**Summary.** The Mucorales are largely saprophytic fungi with a well-developed mycelium. They produce no zoospores, asexual reproduction occurring by aerial spores borne in sporangia. Sexual reproduction is isogamous, conjugation occurring between the entire contents of two multinucleate gametangia.

### 7. Entomophthorales

The Entomophthorales constitute a small group of fungi, most of which are parasitic on insects. The order includes 6 genera and about 50 species, the best-known genera being *Empusa* and *Entomophthora*. A common species, *Empusa muscae*, attacks the housefly. The mycelium, which is feebly developed, penetrates the body of the host and eventually kills it. Then it sends out numerous sporangiophores, from each of which a single multinucleate sporangium is cut off (Fig. 94). This is forcibly discharged into the air and, upon coming in contact with an uninfected fly, produces a new mycelium. Although it becomes detached and functions directly as a spore, the sporangium of *Empusa* corresponds to the sporangium of the Mucorales. In *Entomophthora* the sporangiophores are branched and the sporangia uninucleate. Sexual reproduction seems to be absent in *Empusa muscae* but, in several other species, as in the Mucorales, it occurs by the conjugation of multinucleate protoplasts, each representing the whole contents of a gametangium.

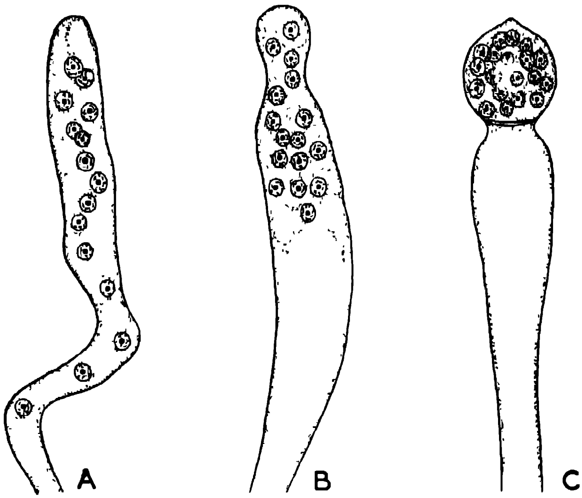



FIG. 94. Development of the sporangium of *Empusa muscae*, ×600. *A*, hyphal body elongating to form a sporangiophore; *B*, migration of nuclei to apex; *C*, formation of multinucleate sporangium at tip of sporangiophore.

## 4. ASCOMYCETES

The Ascomycetes, or sac fungi, constitute the largest group of fungi. They differ from the Phycomycetes in having a septate mycelium, that is, one divided by cross walls into cells. They are also characterized by the production of spores in a sac-like structure called an *ascus*. This is a cell that at first contains two nuclei. These fuse and the fusion nucleus typically gives rise to eight nuclei by three successive divisions, the first two of which are reductional. From these haploid nuclei, eight walled *ascospores* are then organized. In all except the lowest orders, the asci are enclosed by a definite fruiting body, the *ascocarp*, composed of interwoven hyphae. The relationships of the Ascomycetes are obscure. They may have been derived either from the Phycomycetes or from the Rhodophyceae. The group is of immense economic interest, many members causing serious plant diseases, such as peach leaf curl, brown rot of stone fruits, black knot of plum, apple scab, and bitter rot of apple. There are about 25,000 species of Ascomycetes. These are included in nine main orders: Protoascales, Protodiscales, Plectascales, Perisporiales, Pezizales, Helvellales, Tuberales, Pyrenomycetales, and Laboulbeniales.

## 1. Protoascales

The Protoascales include the yeasts and other simple forms, most of which are regarded as degenerate Ascomycetes. They number about 500 species. These are mainly saprophytes but some are parasites on animals. A few of the saprophytic forms have a mycelium. In the yeasts, which are unicellular fungi, a mycelium ordinarily is not developed. Yeasts are of economic value in breadmaking and in the preparation of alcoholic beverages. The best-known genus is *Saccharomyces*. Some yeasts reproduce by fission but most of them reproduce by budding (Fig. 95). A bud

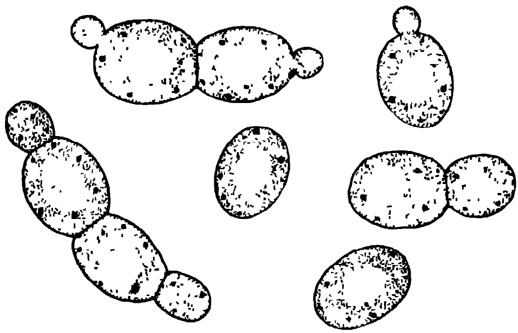


FIG. 95. *Saccharomyces cerevisiae*. Cells in the living condition, showing reproduction by budding, ×1,500

arises as a small outgrowth, usually at one end of the cell. The nucleus divides to form two nuclei, one of which goes into the bud. The bud enlarges and becomes abstricted from the parent cell. It may either separate at once or remain attached and produce another bud. In this way short chains may be formed.

In many yeasts, under conditions unfavorable for vegetative activity, the contents of any cell may divide to form four or, in some species, eight thick-walled spores, thus becoming a simple ascus. In some yeasts a conjugation of two cells precedes the formation of ascospores. The development of an ascus directly from the zygote is a feature occurring only in the Protoascales.

There is considerable variation in the life history of different yeasts, and even in the same yeast under different environmental conditions. Thus the ascospores may enlarge to form vegetative cells that undergo a long period of multiplication, or they may conjugate at once. The zygote may become an ascus directly, or may give rise to vegetative cells that later become asci. Under unfavorable conditions, vegetative multiplication may be omitted. If no conjugation occurs, the ascospores are formed by parthenogenesis.

Yeasts present three different types of life cycles. The first may be illustrated by *Schizosaccharomyces octosporus*, a fission yeast. Here the vegetative cells are haploid, and eight spores arise in the cell formed by the conjugation of two cells (Fig. 96). The zygote is the only diploid cell in the life history, meiosis occurring when its nucleus divides. In the second type of life cycle, the vegetative cells are diploid. Two ascospores unite and the zygote, without undergoing meiosis, gives rise to vegetative cells that multiply and finally produce ascospores. Meiosis occurs when the spores are formed, and so they are the only haploid cells in the life history.

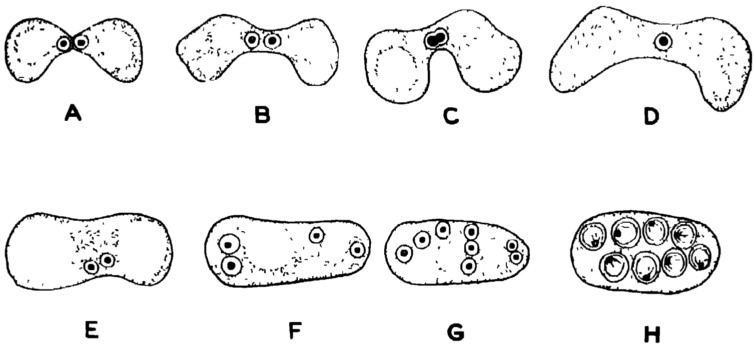



FIG 96 *Schizosaccharomyces octosporus*. *A* to *D*, conjugation of two cells, the two nuclei uniting to form a single nucleus, *E* to *G*, three successive divisions of the fusion nucleus to form eight nuclei, *H*, formation of eight ascospores (*After Guilliermond*)

The third type of life cycle, represented by *Saccharomyces cerevisiae*, is more complicated. Here the vegetative cells are either haploid or diploid. When two haploid cells conjugate, the zygote gives rise to a large number of diploid vegetative cells by budding. Meiosis occurs when one of these cells forms four ascospores. The spores give rise to haploid vegetative cells that multiply by budding. These are smaller than the diploid vegetative cells.

Yeasts live in sugar solutions and are the principal agents in causing alcoholic fermentation. They use as food only a small part of the sugar that they absorb. The rest is broken down into carbon dioxide, ethyl alcohol, and small amounts of other substances. This process of fermentation is accomplished by the production of an enzyme called *zymase*. It is most active in the absence of free oxygen and serves as a means of releasing energy when the ordinary type of respiration cannot be carried on.

## 2. Protodiscales

The Protodiscales, numbering less than 100 species, are internal parasites attacking seed plants, especially trees. The only genus is *Taphrina*. A common species, *Taphrina deformans*, causes a disease of peaches known as peach leaf curl, while *Taphrina pruni* produces a disease of the domestic plum called plum pockets, in which the fruit becomes shriveled. *Taphrina cerasi* attacks branches of the cherry, causing brush-like deformities known as witches'-brooms.

The mycelium of *Taphrina* grows in the intercellular spaces of the host and sends to the surface groups of asci that arise just beneath the cuticle (Fig. 97). Each ascus contains eight ascospores. The asci are crowded to form a layer, called the *hymenium*, but are without accompanying sterile hyphae. Moreover, an ascocarp is not developed and

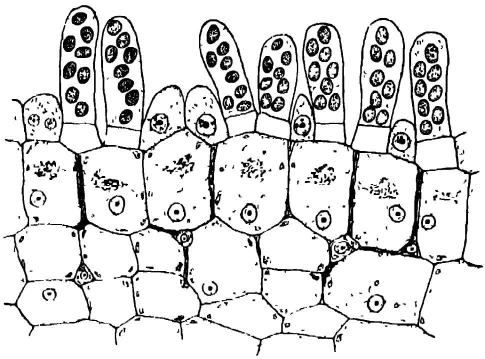


FIG. 97 *Taphrina deformans* Cross section of portion of peach leaf, showing layer of asci and ascogenous cells on the surface, ×500

there is no formation of sex organs. The cells of the mycelium are binucleate. The two nuclei in the young ascus fuse, three successive divisions result in the formation of eight free nuclei, and from these the eight ascospores are organized. Upon germination, the ascospores, which are haploid, may give rise to one or more uninucleate cells by a process that resembles budding in yeasts. In some species these cells, which are called *conidia*, are formed while the ascospores are still within the asci. The ascospores, or the conidia produced by them, infect new host plants, a hypha penetrating the cuticle and pushing its way between the epidermal cells. The germinating spore may become binucleate by division of its nucleus, or a pair of ascospores or conidia may conjugate, a nucleus passing from one to the other. The binucleate condition is then transmitted to the cells of the vegetative mycelium.

### 3. Plectascales

The Plectascales include the blue and green molds, saprophytes that are abundant everywhere, occurring on bread, cheese, jelly, fruits, vegetables, meat, leather, etc. The order includes over 30 genera and 800 species. The two commonest genera are *Aspergillus* and *Penicillium*, the latter numbering over 500 species. One species, *Penicillium notatum*, produces a substance, called *penicillin*, that has remarkable germicidal properties. It has recently come into prominence as a valuable agent in the treatment of many infections and diseases caused by certain bacteria, particularly cocci. Its great advantage over many other drugs lies

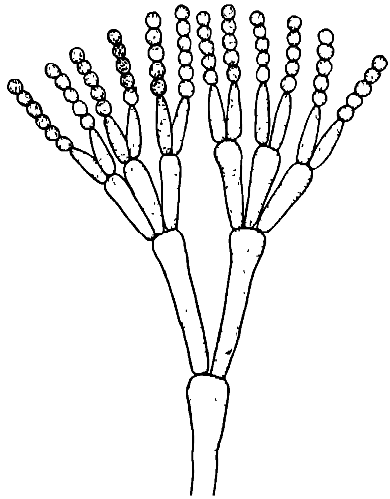


FIG. 98. Branching conidiophores of *Penicillium* producing chains of conidia, ×800.

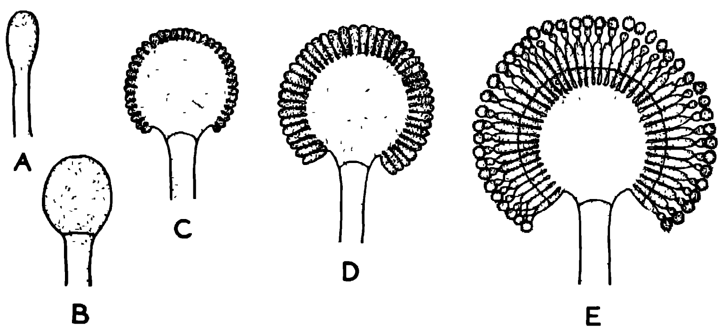



FIG 99. *Aspergillus niger*. *A* to *E*, successive stages in the development of a conidiophore and its conidia, as seen in optical section, ×400.

in its almost complete nontoxicity to the human body. Substances like penicillin are called *antibiotics*.[1]

The mycelium of the Plectascales produces special branches, called *conidiophores*, that cut off chains of spores, or *conidia*, enormous numbers

[1] Most antibiotics, including streptomycin, aureomycin, and chloromycetin, are derived from actinomycetes, a group of organisms of which some are mold-like and others bacteria-like. They are variously classified with the Fungi Imperfecti, the bacteria, or as a distinct group of fungi. Some are parasites but most are saprophytes prevalent in the soil.

of which are liberated into the air. Upon coming in contact with a suitable food supply, the conidia produce new mycelia. In *Penicillium* the conidia arise from the ends of branched conidiophores (Fig. 98). In *Aspergillus* the conidia are abstricted from the ends of short hyphae that radiate from the enlarged tip of a conidiophore (Fig. 99).

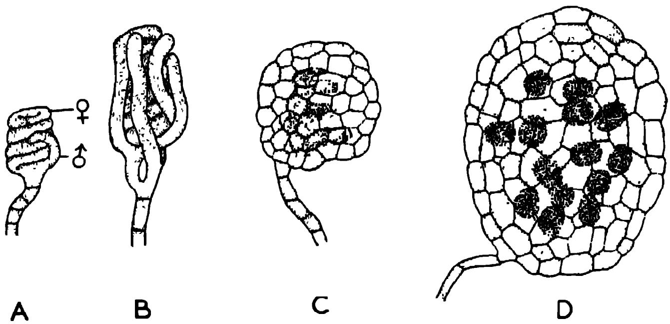



FIG. 100. Development of the ascocarp of *Aspergillus*. *A*, sex organs; *B*, sterile hyphae enclosing the sex organs; *C* and *D*, later stages, showing the development of asci. (*From a Turtox classroom chart.*)

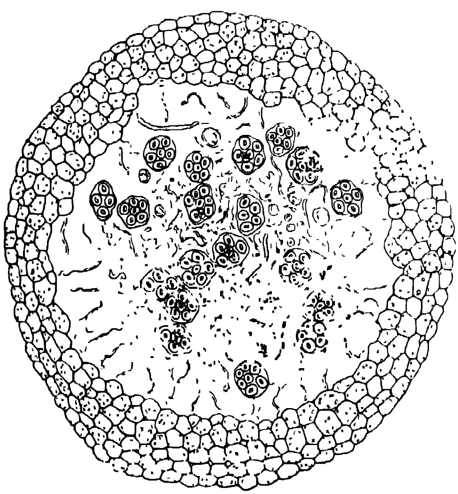


FIG. 101. Section through a mature ascocarp of *Aspergillus*, showing the completely enclosed asci, ×500.

The sex organs are represented by two short, spirally twisted filaments, the contents of which appear to fuse (Fig. 100). Then *ascogenous hyphae*, bearing numerous small asci, arise from one of the filaments. These are intermixed with and surrounded by sterile hyphae, those on the outside forming a minute, globular, closed ascocarp. A fruiting body of this type is known as a *cleistothecium*. There is no definite hymenium in the

Plectascales, the asci being irregularly scattered throughout the mass of sterile hyphae (Fig. 101).

### 4. Perisporiales

The Perisporiales, or powdery mildews, are superficial parasites attacking many kinds of seed plants, such as grape, lilac, willow, rose, squash, bean, pea, apple, grasses, and numerous others. They number about 500 species. Common genera are *Sphaerotheca*, *Erysiphe*, *Uncinula*, *Podosphaera*, *Microsphaera*, and *Phyllactinia*. The mycelium lives on

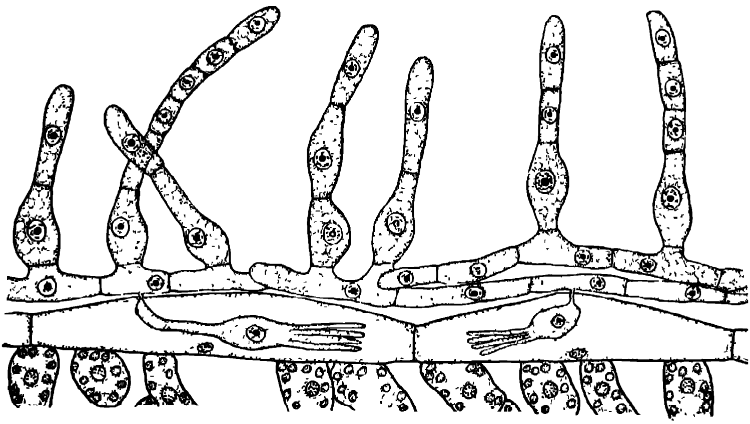


FIG. 102. *Erysiphe graminis* growing on surface of grass leaf, showing haustoria in epidermis of host and conidia in various stages of development. ×500.

the surface of the leaves, forming whitish patches. Short haustorial branches are sent into the epidermal cells and through them food is absorbed. During the summer the mycelium produces erect conidiophores, which give rise to chains of conidia (Fig. 102). These are very abundant and result in a rapid spread of the fungus to uninfected hosts. In the autumn closed ascocarps (cleistothecia) appear. They are minute, spherical, dark brown or black bodies with long appendages that, in some genera, are branched at the tip (Fig. 103). Inside the ascocarps are the asci, each usually with eight ascospores. The ascocarps, scattered by the wind, survive the winter. During the next season the ascospores produce new mycelia.

The character of the appendages produced by the ascocarps is important in distinguishing genera from one another. Thus in *Sphaerotheca* and *Erysiphe* the tips of the appendages are undivided, while in *Podosphaera* and *Microsphaera* they are dichotomously divided. In *Uncinula* the tips of the appendages are hooked or curved, while in *Phyllactinia* they are straight but the appendages are swollen at the base so as to form an enlarged plate.

The sex organs arise from uninucleate cells formed at the tips of special branches of the mycelium, all the cells of which are uninucleate (Fig. 104). The antheridium, slightly smaller than the oögonium (ascogonium), comes in contact with it. The intervening cell wall is dissolved and the male nucleus passes over to fuse with the female nucleus. Sterile hyphae, arising from the cell beneath the oögonium, form a closed ascocarp. Following fertilization, the fusion nucleus gives rise to three

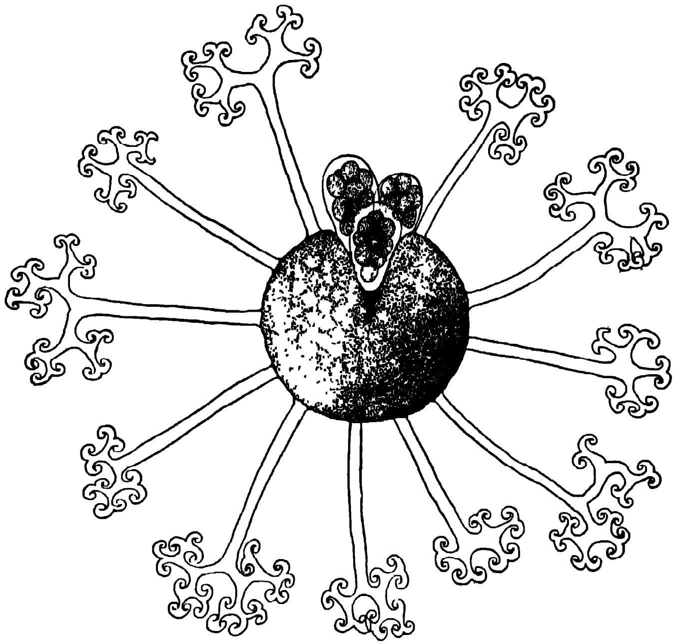


FIG. 103. Ascocarp of *Microsphaera alni* with characteristic appendages, crushed slightly so that three asci, each with eight ascospores, have appeared, ×250.

to five (often more) free nuclei and then transverse walls come in, forming a short row of cells. All of these are uninucleate except the penultimate cell, which is binucleate. In *Sphaerotheca* and *Podosphaera* this cell directly forms a solitary ascus in which the two nuclei fuse, while in the other genera it gives rise either to a row of cells, each of which becomes an ascus, or to ascogenous hyphae that, in turn, produce the asci. Although in *Sphaerotheca* and *Podosphaera* the ascocarp has only one ascus, in the other genera it contains a basal layer of several parallel asci. The development of the ascus takes place in the regular way, except that it frequently contains less than eight ascospores. Eight nuclei are formed as usual, but some are not organized into spores. The asci are generally not intermixed with sterile hyphae.

If the male and female nuclei actually fuse in the oögonium, the fusion in the young ascus involves two diploid nuclei, necessitating a double reduction of chromosomes in the two meiotic divisions that immediately follow. This behavior has been disputed by some investigators, who assert that the only nuclear fusion occurs in the young ascus and involves haploid nuclei, some claiming that the male and female nuclei remain

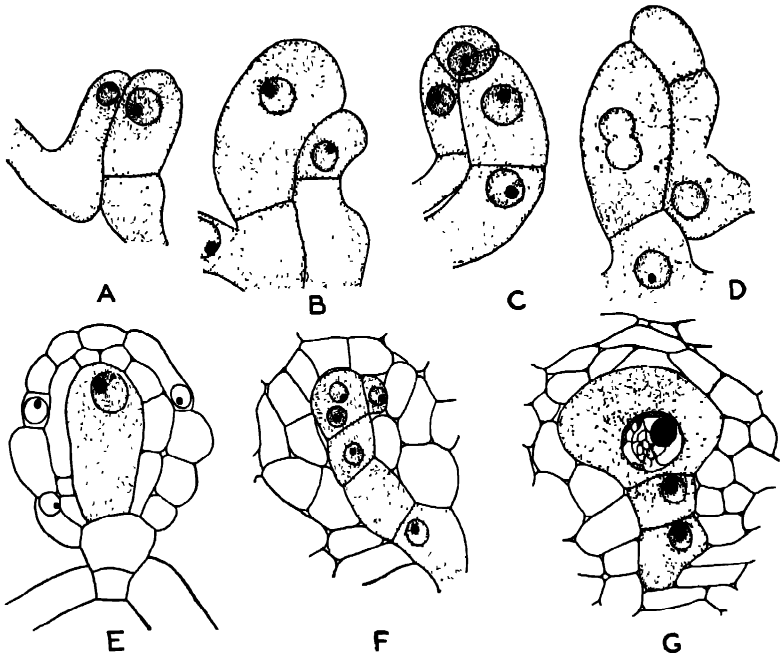



FIG. 104. *Sphaerotheca castagnei.* *A*, antheridial and oogonial branches in contact; *B*, antheridial branch cut off by a wall; *C*, antheridial cell separated from stalk cell; *D*, union of male and female nuclei in oogonium; *E*, oogonium with zygote nucleus and two layers of investing hyphae derived from cell just below; *F*, multicellular ascogonium, the penultimate cell, with two nuclei, becoming the ascus; *G*, young ascus with fusion nucleus and two ascogonial cells below it. (*After Harper.*)

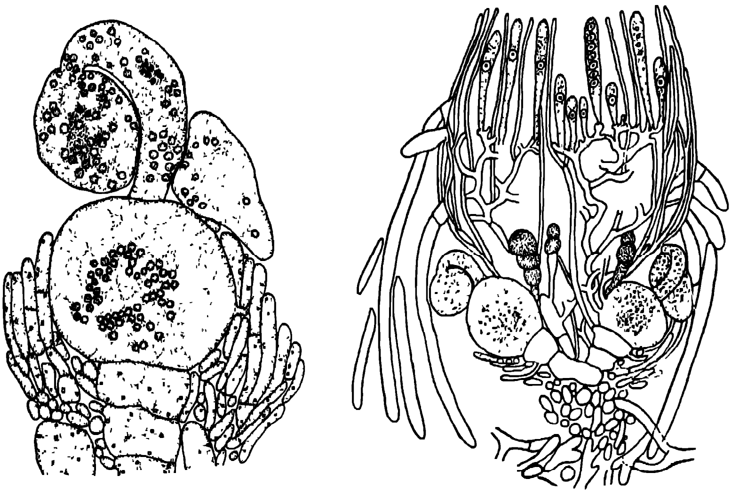
distinct in the oögonium, others that the antheridium is nonfunctional and a male nucleus does not enter the oögonium. If these views are correct, the fusion nucleus in the young ascus is diploid and divides meiotically in the usual way.

## 5. Pezizales

The Pezizales, or cup fungi, grow mostly on decaying wood or humus, but some are parasitic on seed plants. They are a large order of approximately 5,000 species. The principal genera include *Pyronema, Peziza, Ascobolus, Lachnea,* and *Sclerotinia.*

**Pyronema.** This is a saprophyte on soil, especially where it has been burned over. The mycelium grows as a white fluffy layer on the surface.

It bears well-developed sex organs. The female organ resembles the procarp of *Nemalion*. It consists of a globular, multinucleate basal portion, the *ascogonium*, and an elongated curved cell, the *trichogyne*, arising from its upper end (Fig. 105*A*). The antheridium, which is terminal, club-shaped, and multinucleate, arises from an adjacent hypha. It comes in contact with the tip of the trichogyne, whose nuclei degenerate, and discharges its contents into it. The wall at the base of the trichogyne



A B

FIG. 105. *Pyronema confluens*. *A*, ascogonium and trichogyne with antheridium in contact with its tip and discharging nuclei into it. Antheridium is curved around trichogyne and appears in section to be cut in two *B*, somewhat diagrammatic section of a young ascocarp, involving two ascogonia from which ascogenous hyphae and paraphyses have arisen. Asci are shown in various stages of development. (*After Harper*.)

disappears and the male nuclei migrate into the ascogonium, where multinucleate pairing of male and female nuclei occurs. The nuclei do not fuse, however, until an ascus is formed.

Following fertilization, the ascogonium is cut off from the trichogyne by a new wall and branching ascogenous hyphae arise from it (Fig. 105*B*). These give rise to asci. Sterile hyphae (paraphyses) grow up from the mycelium and intermingle with the asci, the entire group of fertile and sterile hyphae becoming surrounded by a fleshy ascocarp. Ordinarily several sets of sex organs enter into the formation of a single ascocarp. The ascocarp of *Pyronema* is disk-shaped, red or yellow, and only 2 or 3 mm. in diameter. The asci and paraphyses form a definite layer, the *hymenium*, that covers its upper surface. A broadly open ascocarp is called an *apothecium*, a type of fruiting body that is characteristic of the Pezizales.

The origin of the asci is somewhat complex (Fig. 106). The paired nuclei of the ascogonium pass into the ascogenous hyphae, where they multiply. The members of each pair remain together as walls are formed. The terminal cell of a branch that is to become an ascus bends back to form a hook and its two nuclei divide simultaneously. Three

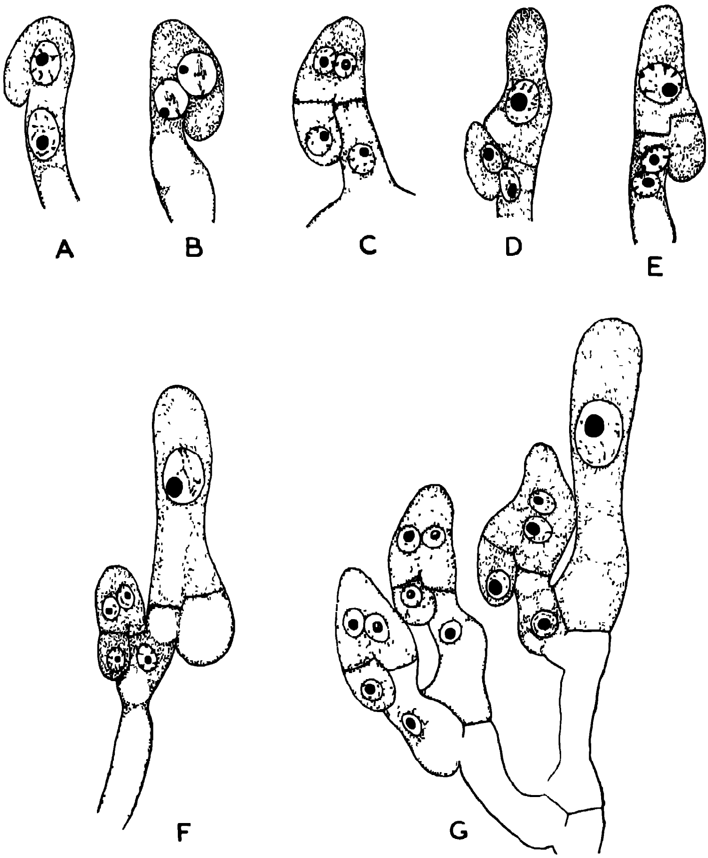



FIG. 106. Origin of the ascus in *Pyronema confluens*. *A*, hook formation at tip of ascogenous hypha, *B*, simultaneous division of nuclei; *C*, formation of uninucleate terminal and basal cells and of binucleate penultimate cell; *D*, fusion of nuclei in penultimate cell to form an ascus; also migration of nucleus of basal cell into terminal cell; *E*, same stage except that nucleus of terminal cell has migrated into basal cell; *F*, later stage showing development of hook from basal cell; *G*, development of three hooks and an ascus from binucleate tip of an ascogenous hypha. (*After Claussen.*)

cells are now cut off by walls. The terminal and basal cells are uninucleate but the middle one (the penultimate cell) has two nuclei of opposite sex, these being the descendants of a male and female nucleus that came from the fertilized ascogonium. The two nuclei may now fuse and the middle cell become an ascus, or the nucleus from the terminal cell may migrate into the basal cell and another hook may be formed. This behavior may be repeated a number of times. Each cell in which a nuclear fusion occurs may become an ascus, the fusion nucleus under-

FIG. 107. Ascocarps of *Peziza* growing on decaying wood, natural size.

going the usual three successive divisions to produce eight ascospore nuclei. The significance of hook formation, which occurs in many Ascomycetes, is a puzzle.

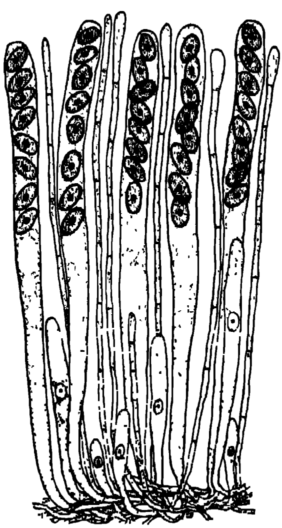


FIG. 108. Several mature asci of *Peziza*, each with eight ascospores, intermixed with paraphyses, ×250. Some young asci are arising below.

**Peziza.** *Peziza* is one of the best-known cup fungi, including about 150 species. It is a common saprophyte on rich humus or on decaying wood. The mycelium, which is extensive and much branched, penetrates the substratum and gives rise on the surface to smooth, fleshy, cup-like ascocarps 1 to 5 cm. or more in diameter (Fig. 107). These are generally bright red, brown, or gray. As in *Pyronema*, the ascocarp is lined with a layer of parallel asci and paraphyses, these constituting the hymenium (Fig. 108). Each ascus contains eight ascospores. Upon germination, these produce new mycelia. In *Peziza* the ascocarp apparently arises directly from the mycelium without any formation of sex organs.

**Sclerotinia.** A parasitic cup fungus, *Sclerotinia fructicola*, attacks plums and peaches, causing a disease known as brown rot of stone fruits. The twigs, flowers, and fruits become infected with the mycelium. As the fruit turns brown and decays, great numbers of conidia are formed on the surface. These are cut off in chains from the ends of short conidiophores. The conidia carry the fungus to uninfected trees. The fungus is usually carried over the winter on dried diseased fruits, called "mummies," that remain on the tree and furnish a fresh source of conidia the following spring. Brown cup-like ascocarps, which are rare, resemble those of *Peziza* and may be formed early in the season on mummified fruits lying on the ground.

**Summary.** The Pezizales are mostly saprophytes but some are parasites. All have a well-developed mycelium. The asci, accompanied by paraphyses, form a hymenial layer that lines an open, disk-like or cup-like ascocarp, the apothecium. This may be fleshy or leathery and sessile or stalked. Some members have well-developed sex organs, the asci arising from the fertilized ascogonium. In other members the asci arise directly from the mycelium, sex organs being absent.

### 6. Helvellales

The Helvellales are related to the Pezizales, being distinguished from them mainly by the form of the ascocarp, which is also an apothecium but

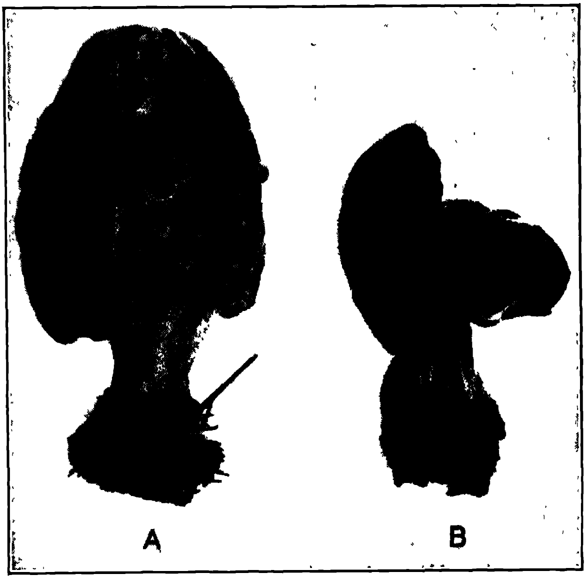


FIG. 109. Ascocarps of *Morchella* (*A*) and *Helvella* (*B*), natural size.

is more highly differentiated. The Helvellales are saprophytes that grow chiefly on humus. They number about 300 species. The best-known genera are *Morchella* and *Helvella*.

**Morchella.** The common edible morel (*Morchella esculenta*) has a much-branched mycelium growing in rich humus soil. On it are formed compact masses of hyphae that develop into fleshy ascocarps of characteristic form. These come to the surface of the soil, where they often attain a height of 15 to 20 cm. A mature ascocarp of *Morchella* is differentiated into a thick hollow stalk and a conical cap (Fig. 109*A*). The surface of the cap contains numerous depressions lined with a hymenium consisting of parallel asci and paraphyses.

**Helvella.** The mycelium is subterranean and composed of hyphae with multinucleate cells. It gives rise to fleshy ascocarps that push upward to the surface of the ground, there reaching a height of about 5 cm. These are differentiated into a stout stalk and a saddle-shaped cap, the outer surface of which is covered with a hymenium consisting of parallel asci and paraphyses (Fig. 109*B*). The asci contain eight ascospores and discharge them into the air with considerable force.

### 7. Tuberales

The Tuberales are the well-known truffles, esteemed as a gastronomic delicacy. There are nearly 300 species, the representative genus being *Tuber*. The mycelium is subterranean, especially in woods, some forming the mycorrhiza of forest trees. Truffles occur in California and in various parts of southern and central Europe. Their life history is incompletely known. The ascocarp is fleshy and matures underground. It is more or less globular, its diameter rarely exceeding 8 cm. It is usually open when young but later nearly or completely encloses the asci. The ascocarp is thus a modified apothecium. The hymenium may surround a large central cavity or it may form irregular folds that divide the cavity into chambers.

### 8. Pyrenomycetales

The Pyrenomycetales, or black fungi, are a large order of about 450 genera and 14,000 species that are generally segregated into three smaller orders, the Hypocreales, Dothideales, and Sphaeriales. They include saprophytes that live on decaying wood, humus, etc., and parasites that attack various seed plants. Some representative genera are *Nectria, Claviceps, Plowrightia, Venturia, Xylaria* and *Neurospora.*

**Nectria.** This large genus of about 250 species grows on living or dead wood. It is responsible for several important fungous diseases. One of the most destructive of these, canker of woody plants, is caused by *Nectria cinnabarina* and *Nectria galligena.* They attack a great variety of shrubs and trees, but not conifers. The fungus gains entrance through wounds in the stem. The cortex becomes infected and its cells are immediately killed. This results in a wound that gradually enlarges. Sometimes enough cork tissue is developed around the infected area to close the wound, but usually this is not possible and the trunk is finally girdled. During the summer the mycelium produces large, pinkish, disk-like masses, or *stromata*, that break through the bark and give rise to large numbers of conidiophores, the conidia being carried by the wind to new hosts. Later in the season small, red, flask-shaped ascocarps, called *perithecia*, are developed on the stromata (Fig. 110).

**Claviceps.** The common ergot disease of rye and other grasses is caused by *Claviceps purpurea*. Its damage to the rye is usually slight, but the eating of diseased grain by animals results in a paralysis and other serious conditions. A drug derived from the fruiting bodies of this fungus, called *ergotine*, has important uses in medicine. The ovaries of the rye are infected by ascospores in the early summer and become hypertrophied, a

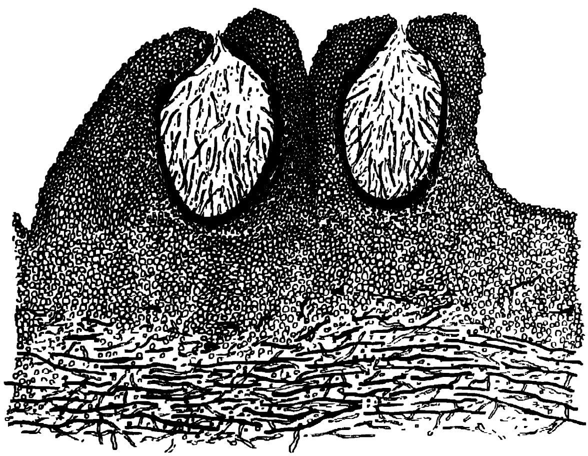


FIG. 110. Stroma of *Nectria cinnabarina* on bark of *Ribes*, showing two perithecia with young asci and paraphyses. ×75.

mycelium developing within. The formation of conidia soon follows. The conidia are minute cells abstricted from the tips of short conidiophores. As they are formed, a sweet liquid is exuded from the spikelet. This attracts insects, which carry the conidia to uninfected flowers. Later the mycelium hardens to form a compact *sclerotium*, which replaces the ovary of the flower. The sclerotia are elongated, slightly curved, purplish bodies that project from the ears of the rye. Many of them eventually fall to the ground, where they pass the winter. In the spring the sclerotium produces several or many globular, stalked *stromata*, which are compact mycelial masses containing numerous flask-shaped, deeply embedded perithecia (Fig. 111). The entire stroma is cream-colored at first, becoming grayish violet. Each perithecium is lined with a hymenium consisting of many asci and paraphyses. The ascospores, which are needle-shaped, are discharged forcibly and dispersed by the wind.

The sex organs of *Claviceps* are borne on hyphae lying below the surface of the stroma. The ascogonium is broader than the antheridium and both are multinucleate. The contents of the antheridium enters the ascogonium, which then gives rise to ascogenous hyphae. As in *Pyronema*, the asci arise as a result of hook formation at the tips of the ascogenous hyphae. Their development occurs in the typical manner.

**Plowrightia.** This is another parasitic genus, its best-known species, *Plowrightia morbosa*, causing a destructive disease of the plum and cherry known as black knot. The mycelium passes the winter under the bark of

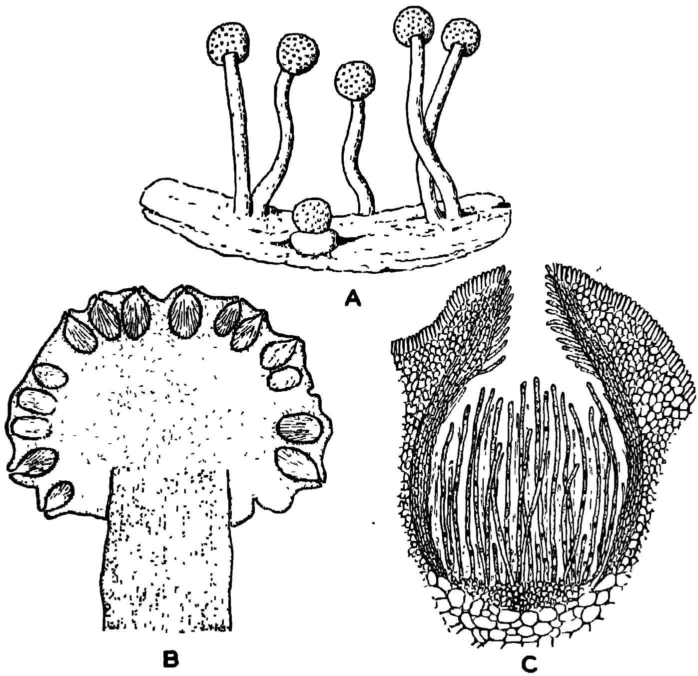



FIG. 111. *Claviceps purpurea.* *A*, stalked stromata arising from a sclerotium, ×4; *B*, longitudinal section through a stroma, showing the embedded perithecia, ×30; *C*, a perithecium with young asci and paraphyses, ×250.

a branch or twig. In the spring it breaks out on the surface to form an elongated gall or knot consisting of both mycelium and hypertrophied host tissue (Fig. 112). Leaves and fruits are not attacked. The elongated knots, often reaching a length of 12 cm. or more, are developed mostly on one side of the stem, which becomes more or less deformed. In early summer the mycelium within the knot gives rise to innumerable short conidiophores that form a velvety layer on the surface. The conidia, distributed by the wind, spread the fungus to other hosts. Later in the season conidium formation ceases and the knot becomes hard and black, forming a stroma in which hundreds of perithecia appear (Fig. 113). These are small flask-shaped organs, embedded in the stroma, and lined with a hymenium consisting of asci and paraphyses. The ascospores mature and are liberated during the following spring. Like the conidia, they directly infect new hosts.

**Venturia.** *Venturia inaequalis* is the cause of an apple disease known as apple scab. It affects chiefly the leaves and fruits, producing brown spots that become scaly as a result of cork formation. The mycelium grows between the cuticle and the epidermis. It forms large numbers of

FIG. 112. Galls produced on cherry twigs by the black-knot fungus, *Plowrightia morbosa*, natural size.

conidiophores that break through to the surface (Fig. 114*A*). Conidia, abstricted from their tips, spread the fungus during the summer to other apple trees. In the autumn, after the infected leaves fall to the ground, the mycelium becomes saprophytic and produces perithecia in the following spring (Fig. 114*B*). These appear on the lower side deeply embedded within the leaf tissues. Sex organs are produced, but the ascocarp begins to develop before fertilization has occurred. The ascogonium is long, coiled, and multinucleate. It has a trichogyne with which the antheridium comes in contact. Following fertilization, the ascogonium gives rise to ascogenous hyphae from which asci are developed as a result of hook formation at their tips. The ascocarps (perithecia) are dark brown and flask-shaped when mature, discharging the ascospores forcibly.

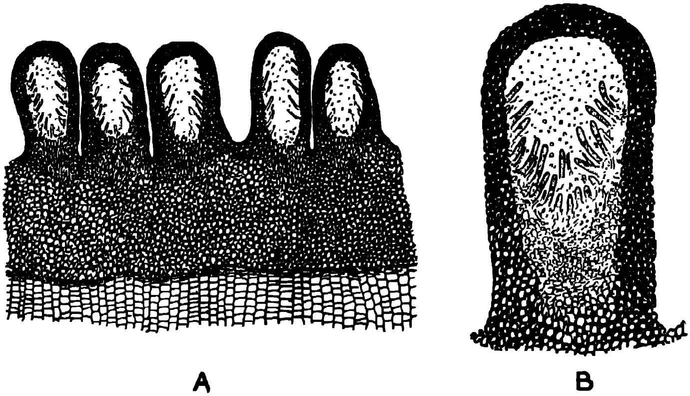



FIG. 113. *Plowrightia morbosa.* *A*, section of stroma bearing young perithecia, $\times 50$; *B*, a single perithecium with young asci and paraphyses, $\times 150$.

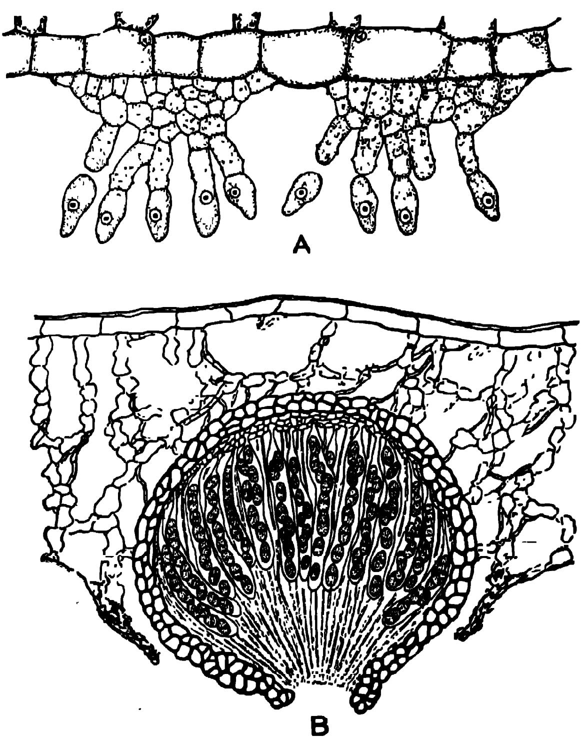



FIG. 114. *Venturia inaequalis.* *A*, conidiophores arising on lower side of apple leaf, $\times 600$; *B*, section of mature perithecium on old apple leaf, $\times 250$.

**Xylaria.** *Xylaria* is a large genus of about 200 species. It is a common saprophyte, the mycelium living in decaying wood. It produces sclerotia from which black, club-shaped, often branched stromata arise. At first these are covered with a mass of white conidiophores from which small oval conidia are abstricted. Later the stromata produce numerous embedded, flask-shaped perithecia lined with a hymenium (Fig. 115).

**Neurospora.** This is the pink bread mold, a form much used experimentally in genetics. The mycelium produces conidia in branched chains. Perithecia are rarely formed. They are dark-colored, pear-shaped, and without paraphyses. Like *Rhizopus*, *Neurospora* is heterothallic and sexual reproduction occurs only when a plus and a minus strain come together. The young perithecium contains a coiled ascogonium from which trichogynal hyphae grow out. If these come in contact with spermatia, conidia, or hyphae of the opposite strain, the perithecia mature and asci are produced. Two nuclei of opposite sex fuse in the young ascus, the fusion nucleus undergoes three divisions of which the first two are meiotic, and eight ascospores are formed in the usual way. Experiments have shown that sexual differentiation occurs in connection with ascospore formation, usually during the first meiotic division but sometimes during the second. As a result, four ascospores in each ascus will produce plus mycelia and four minus mycelia. Other genetic characters behave similarly.

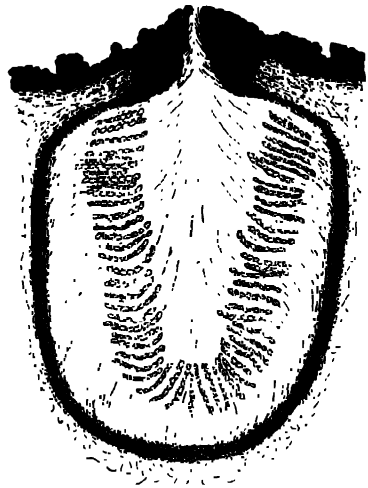


FIG. 115. Longitudinal section through a perithecium of *Xylaria*, showing asci arising from the hymenium, ×100.

**Summary.** The Pyrenomycetales include both saprophytes and parasites. They are characterized by a flask-shaped ascocarp (a perithecium) with a small opening at the top. It is lined with a hymenium composed of parallel asci and paraphyses. The perithecia may arise singly on the mycelium, in small groups, or may be embedded in a compact mycelial mass, the stroma. Sex organs are present in some members.

Differences in the character of the perithecia and stromata provide a basis for splitting up this large order into three smaller orders.

1. *Hypocreales.* These forms have soft, bright-colored perithecia with a definite wall. The perithecia may occur singly or in a stroma, which is also bright-colored. They include *Nectria* and *Claviceps*.

2. *Dothideales.* Members of this group have black stromata in which

the perithecia, lacking independent walls, are developed as stromatal cavities. *Plowrightia* belongs here.

3. *Sphaeriales.* The Sphaeriales have dark-colored perithecia with a distinct wall. The perithecia may be free or embedded in the substratum or in stromata that are firm, leathery or brittle, and dark-colored. Here belong *Venturia*, *Xylaria*, and *Neurospora.*

### 9. Laboulbeniales

The Laboulbeniales comprise an order of about 50 genera and 1,200 species. They are parasitic on insects, especially aquatic ones. As a rule the mycelium grows on the surface of the host and is very small, usually less than 1 mm. in length. The Laboulbeniales are of particular interest because their sex organs are remarkably like those of the red algae. The antheridium is unicellular and produces a nonmotile male cell, the spermatium. The ascogonium has a trichogyne and auxiliary cells. Ascogynous hyphae arise from the fertilized ascogonium, small perithecia are formed, and the asci bud out from the auxiliary cells. The whole process resembles cystocarp formation in the red algae.

## 5. BASIDIOMYCETES

The Basidiomycetes, or club fungi, comprise the highest group of fungi. They resemble the Ascomycetes in having a mycelium with cross walls. They are characterized by the production of spores externally on a club-like structure known as a *basidium.* This arises from the swollen end of a hypha and may consist of either four cells or one. Four slender branches (sterigmata) arise from the basidium, each forming a *basidiospore* at its tip. The young basidium contains a nucleus derived from the fusion of two nuclei. Two successive divisions, which are reductional, result in the formation of four haploid nuclei, each passing into one of the basidiospores. In the higher members the basidia are borne on a distinct fruiting body, the *basidiocarp,* composed of interwoven hyphae. The Basidiomycetes are related to the Ascomycetes and are generally regarded as having been derived from them. Some are of great economic importance, particularly the smuts, rusts, and mushrooms. The Basidiomycetes number about 20,000 species. They embrace seven principal orders: Ustilaginales, Uredinales, Auriculariales, Tremellales, Exobasidiales, Hymenomycetales, and Gasteromycetales.

### 1. Ustilaginales

The Ustilaginales, or smuts, are parasites that live on various herbaceous seed plants. They attack chiefly floral organs, particularly those of grasses. They are most destructive to oats, less so to wheat and corn. The smuts number about 500 species. The principal genera are *Ustilago* and *Tilletia.*

**Ustilago.** The life history of the corn smut (*Ustilago zeae*) will be described. The mycelium ramifies throughout the stem and leaves of the corn plant and in its vegetative condition does not seem to do much damage. It lives in the intercellular spaces, sending short haustoria into the host cells. When flowers appear, some of the ovaries become packed with the mycelium and, as a consequence, become greatly swollen and distorted. Swellings may also appear in other parts of the plant. Later the mycelium divides up into countless numbers of black spores, called

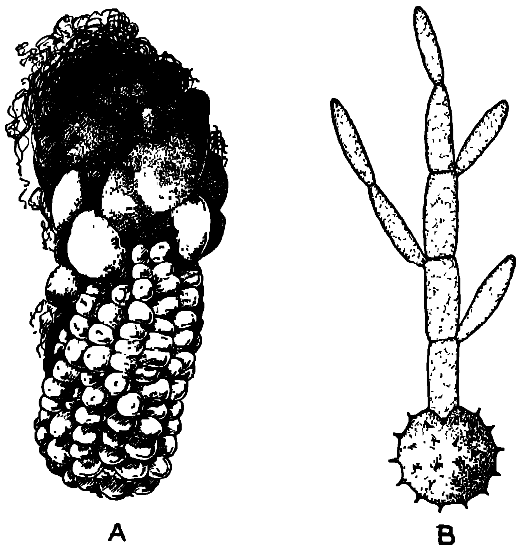



FIG. 116. *Ustilago zeae.* *A*, an ear of corn infected with smut, some of the grains of which are greatly enlarged and filled with chlamydospores, one-half natural size; *B*, a germinating chlamydospore, the four-celled basidium producing basidiospores, ×1,400.

*chlamydospores*, which form large powdery masses (Fig. 116*A*). A chlamydospore is a heavy-walled cell representing merely a transformed cell of the vegetative mycelium.

A chlamydospore may germinate at once but, as a rule, falls to the ground and remains dormant until the following spring. Then it sends out a short filament of three or four cells that lives saprophytically on organic matter in the soil (Fig. 116*B*). Thin-walled basidiospores are budded off each cell of the filament, often in great numbers. This filament is a basidium but, because of the large number of spores produced, is not a typical one. In some smuts, however, only one spore is budded off each of the four cells of the basidium. The basidiospores infect young corn plants in the spring.

The cells of the vegetative mycelium are binucleate, as are the young chlamydospores. But before the chlamydospore is mature the two nuclei fuse, thus establishing the diploid condition. The fusion nucleus divides reductionally in the young basidium and four cells are formed by the appearance of transverse walls, thus separating the four haploid nuclei. When a basidiospore is budded off, two nuclei are formed, one of which passes into the spore while the other remains in the basidium. The latter may divide again, if another spore is budded off, and this may be repeated many times. These haploid basidiospores produce on the young corn plant mycelia of limited extent and with uninucleate cells. When two mycelia of opposite sex come together within the host, a union of cells takes place without a fusion of nuclei. The binucleate cells formed in this way give rise to a mycelium that spreads throughout the host, eventually producing chlamydospores.

## 2. Uredinales

The Uredinales, or rusts, are destructive parasites. They attack a great variety of vascular plants, including ferns, conifers, and angiosperms, being especially common on grasses. The mycelium lives in the intercellular spaces, particularly of the leaves. There are about 3,000 species of rusts, the most important genera being *Puccinia*, *Uromyces*,

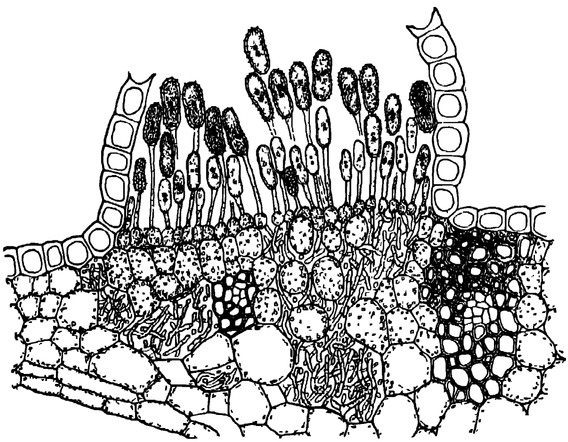


FIG 117. *Puccinia graminis*. Section through a uredinium on a leaf sheath of wheat, showing uredospores in various stages of development, ×200.

*Gymnosporangium*, *Phragmidium*, *Cronartium*, *Coleosporium*, and *Melampsora*. The largest genus, *Puccinia*, has about 700 species.

**Puccinia.** The common wheat rust (*Puccinia graminis*) is the best-known member of the order. Its life history is very complicated, involving two different hosts and several kinds of mycelia and spores, all with a definite relation to one another.

The mycelium that lives on the wheat is an internal parasite, extending throughout the entire body of the host. It does not directly kill the host cells, but lives on their food materials, which it absorbs by means of haustoria. During the late spring and early summer numerous spores are produced. They break through the epidermis of the leaves, groups of them, known as *uredinia,* appearing on the surface as reddish brown streaks or lines (Fig. 117). These spores are called *uredospores.* Each consists of a stalked binucleate cell with a rather thick cell wall. They are scattered by the wind, directly infecting other wheat plants, and are chiefly responsible for the rapid spread of the disease, especially during a wet season. Successive crops of uredospores may be produced throughout the summer.

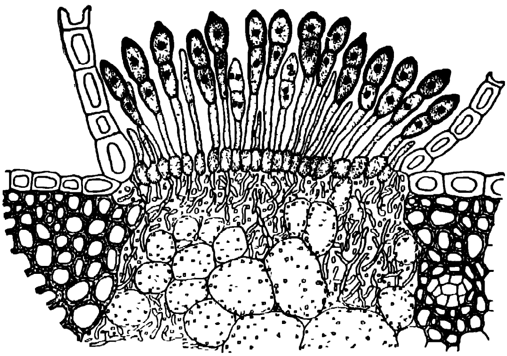


FIG. 118. *Puccinia graminis.* Section through a telium on a leaf sheath of wheat, showing teliospores in various stages of development, ×200

Later in the season, at harvest time or thereabouts, the same mycelium that produced the uredospores earlier now gives rise to elongated groups of black spores called *teliospores.* These groups, known as *telia,* appear chiefly on the stems and leaf sheaths (Fig. 118). The teliospores are also stalked but are two-celled and heavy-walled. At first each cell has two nuclei, but the members of each pair fuse as the spore matures. The teliospores do not germinate until the next spring, thus carrying the fungus over the winter. Upon germination, one or both cells of the teliospore gives rise to a short filament. This filament is the basidium (Fig. 119*A*). It consists of four cells, each of which sends out a short branch, called a *sterigma,* bearing a small terminal basidiospore. The basidiospores cannot infect wheat plants. They are carried by the wind to leaves of the common barberry (*Berberis vulgaris*), where they germinate and produce an extensive internally parasitic mycelium. It is mainly this species that is susceptible to infection by the basidiospores of wheat rust. Most other barberries are immune.

The mycelium produced by the basidiospores on the barberry develops *spermogonia* (pycnidia), small flask-shaped organs appearing on the upper side of the leaves (Fig. 119*E*). In these organs small cells, called *spermatia* (pycnospores), are formed by abstriction from the ends of slender hyphae. The spermatia are exuded from the spermogonia in drops of a sweet liquid. This attracts insects that aid in their dissemination. Soon

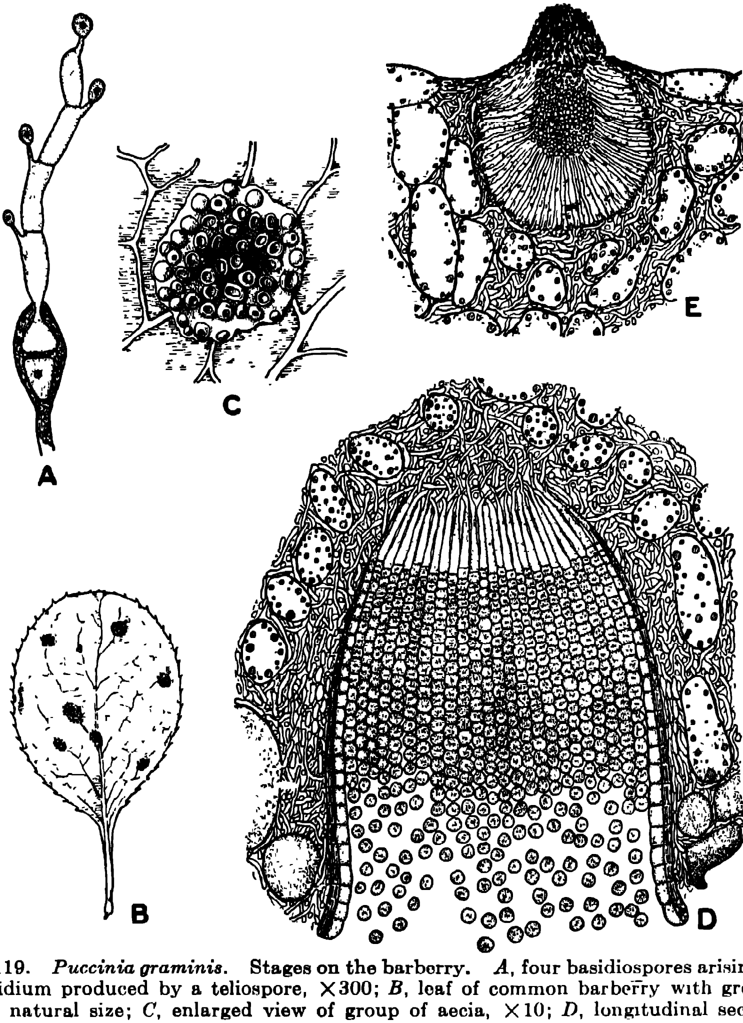



FIG. 119. *Puccinia graminis.* Stages on the barberry. *A*, four basidiospores arising from a basidium produced by a teliospore, ×300; *B*, leaf of common barberry with groups of aecia, natural size; *C*, enlarged view of group of aecia, ×10; *D*, longitudinal section of aecium with numerous aeciospores arising in chains, ×200; *E*, longitudinal section of spermogonium producing numerous small spermatia, ×200. (*A*, *after Chamberlain.*)

after the appearance of the spermogonia, the mycelium on the barberry produces larger, cup-like structures that appear in clusters on the lower side of the leaves (Fig. 119*B* and *C*). These *aecia*, or cluster cups, contain large numbers of *aeciospores*, which arise in chains from the bottom of the cup (Fig. 119*D*). The chains consist of alternating spores and sterile cells, the latter disintegrating. The aeciospores cannot infect the barberry. Instead, carried by the wind, they infect wheat plants during the late spring and summer, thus completing the life cycle.

The cells of the mycelium produced by the basidiospores on the barberry, as well as the spermatia, are uninucleate, but the aeciospores are binucleate. The binucleate condition appears to arise by the spermatia coming in contact with special receptive hyphae of the opposite sex. These extend from the basal cells of the young aecium to the orifice of the spermogonium, through which they project. A spermatium enters a receptive hypha and passes down into the basal cell, which then becomes binucleate. Each binucleate basal cell gives rise by repeated division to a chain of aeciospores. The binucleate condition is carried over by the aeciospores to the mycelium on the wheat and to the uredospores and young teliospores produced by it.

The fusion of the two nuclei in each cell of the teliospore introduces the uninucleate condition. When the teliospore germinates, the diploid nucleus in each of its cells undergoes two successive meiotic divisions that result in the formation of four haploid nuclei. Each of the four cells in the basidium receives one of these nuclei, which then passes into a basidiospore. The uninucleate basidiospores, being haploid, produce a haploid mycelium on the barberry. Thus, although there is an alternating haploid and diploid phase in the life history of *Puccinia*, the latter is not initiated by a nuclear fusion, as in most plants, but by the coming together in the same cell of two nuclei that retain their identity throughout a large number of cell divisions. Eventually the nuclear fusion occurs, but is then followed by the reduction divisions, which mark the beginning of the haploid phase.

**Other Rusts.** The wheat plant is attacked not only by *Puccinia graminis*, its most destructive rust, but by several related species. One of these is *Puccinia coronata*, whose alternate host is the buckthorn (*Rhamnus*); another is *Puccinia rubigo-vera*, which produces the aecial stage on blueweed (*Echium*) and other Boraginaceae. All three species may attack other grasses than wheat, such as barley, oats, rye, and various meadow grasses, producing the same morphological type of mycelium and spores on each kind of grass but a different physiological strain.

Many rusts have a shorter life cycle than *Puccinia graminis*. All rusts produce teliospores and these always give rise to basidia and basidiospores, but one or more of the other spore forms may be missing. Thus the aecia may be omitted, the uredospores, the aecia and spermatia, or the aecia, spermatia, and uredospores. If a rust requires two different and unrelated hosts to complete its life cycle, it is said to be *heteroecious*;

if all stages are passed on the same host, or on closely related hosts, it is *autoecious*. *Gymnosporangium juniperi-virginianae*, a heteroecious rust, has no uredospores. It develops the telial stage on the red cedar (*Juniperus virginiana*), or related species, and the aecial-spermogonial stage on the apple, pear, and quince (*Pyrus*). A heteroecious rust of great economic importance is *Cronartium ribicola*, the white pine blister rust. Its uredospore-teliospore stage is passed on various species of currants and gooseberries (*Ribes*), its aecial-spermogonial stage on the white pine (*Pinus strobus*) and related species. The damage to white pines has been so great that it has resulted in their virtual extinction in many parts of the country. *Puccinia asparagi* is an autoecious rust, producing uredospores, teliospores, aeciospores, and spermatia on the asparagus. *Puccinia malvacearum*, another autoecious rust, has a very short life cycle, producing only teliospores on the hollyhock and other Malvaceae.

### 3. Auriculariales

The Auriculariales are the ear fungi, an order of about 15 genera and over 100 species. They are chiefly saprophytes growing on bark and decaying wood. The representative genus is *Auricularia*. The mycelium produces brightly colored, gelatinous, ear-shaped bodies, each being a *basidiocarp*. When dry, the basidiocarps become wrinkled and hairy. The inner surface is lined with a hymenium consisting of basidia intermixed with paraphyses. As in the Uredinales, the basidia are four-celled and have sterigmata. Each basidium produces four basidiospores. This order may be regarded as transitional between the lower and higher Basidiomycetes.

### 4. Tremellales

The Tremellales, or trembling fungi, are somewhat similar to the Auriculariales. They include 18 genera and nearly 100 species, the best-known genus being *Tremella*. The mycelium lives in decaying wood and bark, producing gelatinous basidiocarps. These are indefinite in form and more or less wavy or folded. The hymenium occurs on the upper surface. The basidia are characteristic, being longitudinally divided into four cells instead of transversely divided. Each basidium bears four basidiospores on long sterigmata.

### 5. Exobasidiales

The Exobasidiales are internal parasites attacking particularly members of the Ericaceae, such as blueberries, cranberries, huckleberries, azaleas, etc. There are about 30 species, nearly all belonging to the genus *Exobasidium*. Galls composed of mycelium and host tissue are produced on stem tips, leaves, and floral organs. The basidia are formed under the epidermis and, when they break through, cover the host with a whitish bloom. There is no formation of basidiocarps, the basidia arising directly from the mycelium. In this and succeeding orders the basidium is one-celled. The young basidium has two nuclei that fuse, two successive nuclear divisions follow, and four basidiospores are developed, each at the end of a sterigma.

### 6. Hymenomycetales

This large order of approximately 15,000 species is usually split up into several smaller orders, but here will be regarded as one homogeneous group. Most of the members are saprophytic on humus, bark, decaying wood, etc. Some are parasitic on trees, often causing considerable damage. The Hymenomycetales have complex basidiocarps with basidia in a definite hymenial layer that becomes freely exposed. The basidia are one-celled and bear four basidiospores, each at the end of a slender sterigma.

FIG. 120. A coral fungus (*Clavaria*), natural size.

**Families.** The families of Hymenomycetales are distinguished from one another on the basis of the form of the basidiocarp and the position of the hymenium. The principal families are as follows:

1. *Thelephoraceae.* These forms produce simple basidiocarps appearing on tree trunks. Some resemble leathery incrustations with the hymenium on the smooth upper surface, while some are bracket-like with the hymenium on the lower surface. Others have the hymenium on the outside of a funnel-like basidiocarp. The representative genus is *Thelephora,* with about 150 species.

2. *Clavariaceae.* The coral fungi produce erect, fleshy basidiocarps that are usually branched like coral, the hymenium covering the surface of the branches (Fig. 120). They are commonly white or yellowish, but sometimes are more brightly colored. In some forms the basidiocarps are club-shaped and unbranched, with a complete hymenial covering. The principal genus is *Clavaria,* with about 250 species.

3. *Hydnaceae.* These are the tooth fungi, the hymenium being borne on tooth-like or spine-like processes that generally point downward. The simpler forms occur as rounded masses or thin sheets of indefinite form. Some are more or less branched. Others have a stalk and an umbrella-like pileus that bears teeth on its lower side. The main genus is *Hydnum,* with about 150 species.

4. *Polyporaceae.* The pore fungi bear a number of tubes or grooves lined with a hymenium. The basidiocarp may be crustaceous, the tubes

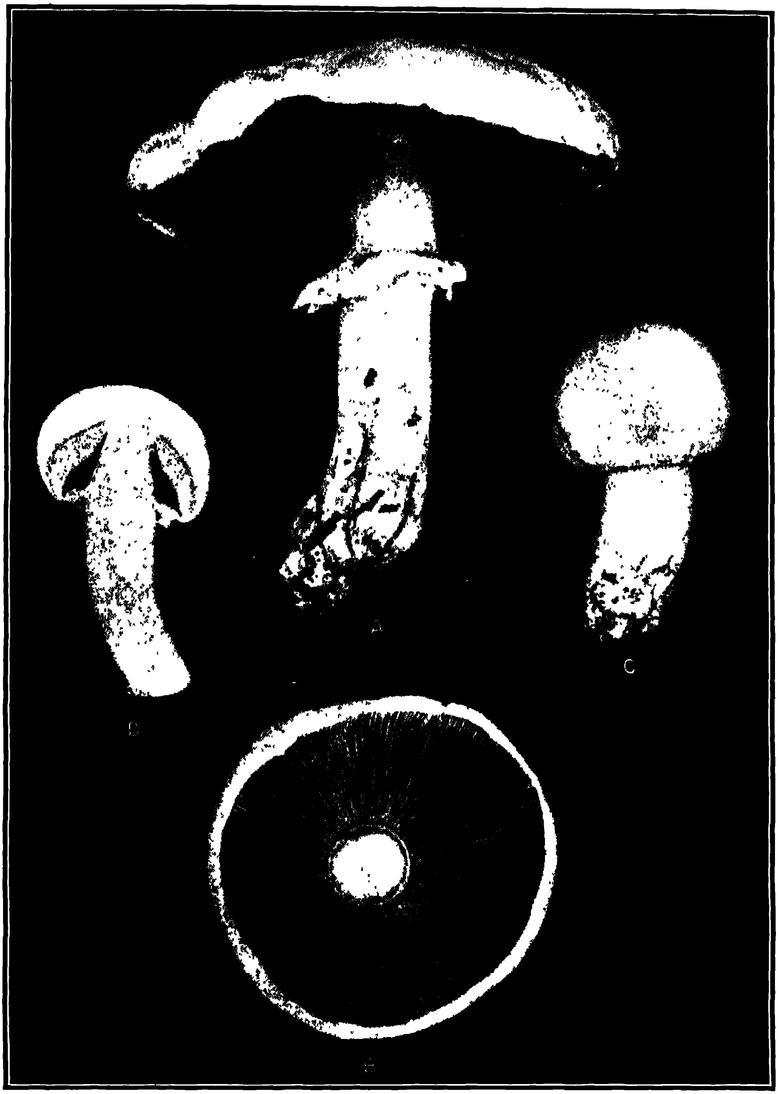


FIG. 121. *Agaricus campestris*, four-fifths natural size. *A*, mature basidiocarp, showing pileus, stipe, and annulus; *B*, view of underside of pileus with stipe removed, showing the radiating gills; *C*, young basidiocarp before the pileus has expanded; *D*, young basidiocarp cut in half, showing velum attached to stipe.

opening on its upper side. Ordinarily, however, the basidiocarp is bracket-like or umbrella-like, the tubes opening on its lower side. The texture of the basidiocarp may be leathery, fleshy, or hard and woody. Some of the largest genera are *Merulius*, *Poria*, *Fomes*, *Polyporus*, *Polystichus*, and *Boletus*. *Polyporus*, the largest genus, has about 500 species.

*Merulius lacrymans* is the dry-rot fungus, a species attacking woodwork and structural timbers. It often causes great destruction to wooden buildings.

5. *Agaricaceae.* This is the large family of gill fungi, a group to which the common mushrooms and toadstools belong. The basidiocarp may be bracket-like but more commonly is umbrella-like. It is usually fleshy, rarely leathery in texture. In this family the hymenium covers blade-like radiating plates known as *gills.* Of the numerous genera, a few common ones are *Coprinus, Agaricus, Amanita, Lepiota, Hypholoma, Russula,* and *Marasmius.* The largest genus is *Marasmius,* with about 450 species.

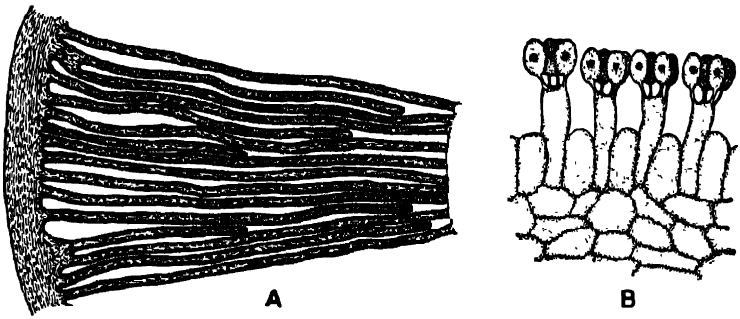



FIG. 122. *Coprinus micaceus.* *A*, cross section through a few of the gills, ×10; *B*, enlarged portion of same, showing four basidia arising from surface of gill, each with four stalked basidiospores, ×750.

**Agaricus and Other Mushrooms.** The common field mushroom (*Agaricus campestris*) grows in lawns, fields, and along roadsides. It is the principal species used for food and practically the only one that is cultivated. The mycelium lives on organic matter in the soil. The fleshy basidiocarp arises just below the surface as a "button" composed of interwoven hyphae. Soon a stalk or *stipe* and a cap-like *pileus* become differentiated. The gills, which develop on the lower side of the pileus, are covered by a membrane called the *velum.* This extends from the margin of the pileus to the stipe, becoming ruptured as the pileus expands. In *Agaricus* and many other mushrooms a portion of the velum remains attached to the stipe, forming an *annulus* around it (Fig. 121). In *Amanita,* a genus of poisonous mushrooms, the young basidiocarp is completely enclosed by an outer membrane that ruptures as the stipe elongates, forming a cup or sheath, called the *volva,* at the base of the stipe.

The hymenium of the Agaricaceae, covering the surface of the gills, consists of innumerable basidia, each of which typically bears four basidiospores on slender sterigmata (Fig. 122). The cells of the vegetative mycelium are typically binucleate and there are two nuclei in the young basidium. These fuse, two successive divisions take place, and the four resulting nuclei pass through the sterigmata into the basidiospores (Fig. 123*E-G*). The reduction of chromosomes occurs when the fusion nucleus divides. The cultivated variety of *Agaricus campestris* is exceptional in that only two basidiospores are borne on a basidium, each of which

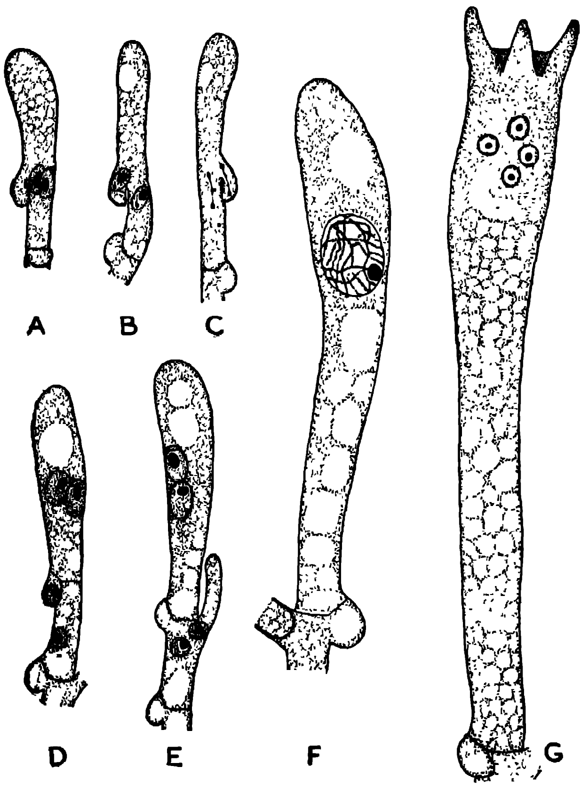



FIG. 123. Clamp formation and development of the basidium in *Armillaria mucida*. *A*, beginning of clamp formation in binucleate terminal cell; *B*, one nucleus passing into the clamp; *C*, conjugate division of the two nuclei; *D*, appearance of walls cutting off uninucleate clamp and basal cells from young binucleate basidium; *E*, fusion of clamp and basal cells, the latter sending out another branch; *F*, basidium with diploid fusion nucleus; *G*, basidium with four haploid nuclei and the developing sterigmata. (*After Kniep*.)

receives two of the four haploid nuclei. The mycelium of both the wild and cultivated form is multinucleate and probably unisexual (homothallic).

In most mushrooms the basidiospores, upon germination, give rise to mycelia of two different sexes. These have uninucleate cells. When two mycelia of opposite sex come together, fusions take place between vegetative cells, resulting in the formation of a binucleate mycelium. Upon this the basidiocarps are produced.

Following the formation of a binucleate cell by the fusion of two uninucleate cells, a short branch arises into which the two nuclei pass. A hook-like lateral outgrowth, pointing toward the base of the cell, then appears at a point directly opposite the two nuclei (Fig. 123*A*, *B*). After both of these divide, one of the daughter nuclei passes into the hook and a cross wall forms at its base, another wall continuing across the branch (Fig. 123*C*, *D*). Thus two nuclei of opposite sex are in the terminal cell, one nucleus being in the lower cell and one in the hook. The tip of the hook now fuses with the lower cell to form a "clamp connection." The nucleus in the hook passes into the lower cell, which thereby becomes binucleate (Fig. 123*E*). The terminal cell continues to grow and, at each cell division, a new clamp connection is formed.

A mycelium with clamp connections is characteristic of many Basidiomycetes, occurring in at least some members of all the orders except the Uredinales. Clamp formation in the Basidiomycetes is thought to correspond to hook formation in the Ascomycetes where, however, it is limited to the ascogenous hyphae. It must be remembered that in both groups there are many members without any such formations, the ascus or basidium developing directly from the terminal cell of a hypha. Clamp connections are not present on the mycelium of *Agaricus campestris* or its cultivated variety.

### 7. Gasteromycetales

Like the Hymenomycetales, the Gasteromycetales are often broken up into several smaller orders. Nearly all its members are saprophytic on humus, but a few grow on decaying wood. There are about 1,000 species. The very complex basidiocarp entirely encloses the hymenium, remaining closed or opening only after the spores are mature. The basidiocarp is composed of an outer *peridium* and a central *gleba*, the latter generally containing many chambers. In the lower forms the chambers are filled with hyphae bearing terminal basidia; in the higher forms the chambers are lined with a definite hymenium. The basidia are one-celled and bear four terminal basidiospores, each at the end of a sterigma.

**Families.** The principal families of Gasteromycetales, distinguished from one another by the character of the peridium and gleba, are as follows:

1. *Hymenogastraceae.* This family is intermediate between the Hymenomycetales and the Gasteromycetales. The peridium is simple, being one-layered and rupturing irregularly. The glebal chambers are lined with basidia borne at the ends of lateral branches of the glebal hyphae. Because the basidiocarps are subterranean, these forms are not commonly seen. The chief genera are *Hymenogaster* and *Rhizopogon.*

2. *Sclerodermaceae.* In this family the basidiocarp is nearly spherical, with a thick, leathery, one-layered peridium that ruptures at the apex. The gleba is indistinctly chambered. The basidia are borne on lateral branches of the glebal hyphae. There are no sterigmata, the basidiospores being sessile. The representative genus is *Scleroderma.*

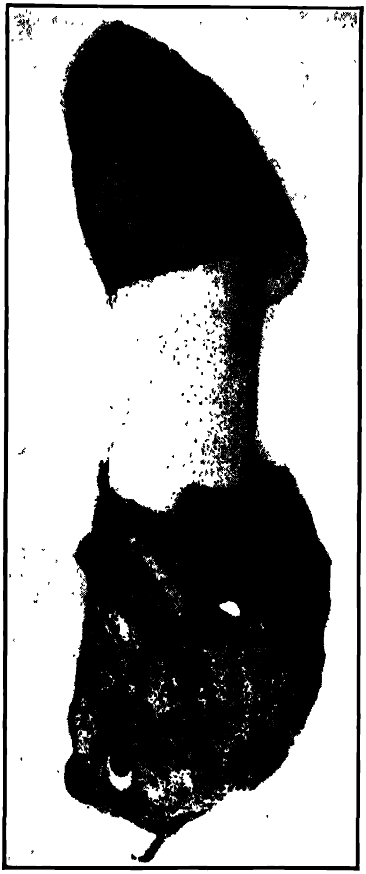


FIG. 124. A stinkhorn fungus, *Phallus impudicus*, natural size.

3. *Lycoperdaceae.* These are the familiar puffballs. The globular basidiocarps are usually less than 8 cm. in diameter but sometimes reach 50 cm. or more. The peridium is two-layered and has no definite dehiscence. In *Lycoperdon* the outer layer flakes off, the inner one bursting at the apex to liberate the spores. In *Geaster* the outer layer splits into stellate segments that spread out on the ground, the inner one dehiscing by a terminal pore. In this family the gleba is distinctly chambered. It is lined with a hymenium and contains a capillitium consisting of fibrous interwoven hyphae that aid in spore dispersal.

4. *Nidulariaceae.* The bird's-nest fungi resemble the puffballs in their younger stages, but at maturity the peridium opens and becomes cup-shaped. The separate glebal chambers, with much-thickened walls, lie at the bottom of the cup like eggs in a nest. The two chief genera are *Nidularia* and *Cyathus.*

5. *Phallaceae.* The stinkhorn fungi are the highest of the Basidiomycetes. Their basidiocarps are extremely complex (Fig. 124). At first they are white and egg-shaped. The peridium is two-layered but the tissue within is differentiated into a hollow sterile axis and an investing, dome-like, chambered gleba. When the basidiocarp is mature, these become the stipe and pileus, respectively. The gleba becomes mucilaginous and foul-smelling, attracting carrion flies that distribute the spores. The principal genera are *Phallus, Mutinus,* and *Dictyophora.* In *Dictyophora* there is a conspicuous net-like veil that hangs down beneath the pileus and spreads out around the stipe like a skirt.

## FUNGI IMPERFECTI

The Fungi Imperfecti constitute a large assemblage of forms that, because of an incomplete knowledge of their life histories, cannot be assigned to any of the three natural classes of true fungi: the Phycomycetes, Ascomycetes, and Basidiomycetes. Generally the only known method of reproduction is by conidia. Zygotes, ascospores, or basidiospores are unknown. In many cases the unknown stage has apparently been lost from the life history. When a member of this artificial group is found to possess any reproductive stage previously not reported, it is transferred to its proper genus, family, order, and class. Meanwhile it is placed in a "form genus." Many of the imperfect fungi cause important plant diseases, such as potato scab, early blight of potato, flax wilt, and various anthracnose and leaf-spot diseases. Practically all the fungi that cause such human diseases as ringworm and athlete's foot are imperfect fungi.

## LICHENES

A lichen is a plant consisting of a unicellular alga and a fungus living together in symbiotic relationship. This association, resulting in a body having a distinctive form and structure, suggests a single plant rather than a composite one. Lichens are commonly regarded as constituting an autonomous group of thallophytes, the Lichenes, which are either made coordinate with the Algae and Fungi, or included with the latter as a distinct class. By those who consider lichens to be merely fungi parasitic upon algae, they are sometimes broken up and distributed among the fungous groups that they most closely resemble.

Lichens are commonly seen growing on rocks, tree trunks, dead wood, and on the ground. They are a widely distributed group of which about 400 genera and 15,000 species are known. A few of the largest genera are *Lecidia*, *Buellia*, *Lecanora*, *Parmelia*, *Physcia*, *Collema*, *Sticta*, *Cladonia*, *Ramalina*, and *Usnea*. Lichens are mostly gray or grayish green, but some are more conspicuously colored. Based on their external form, three general types are recognized: (1) *crustose* lichens, which occur as incrustations on rocks and bark; (2) *foliose* lichens, which are flat, leaf-like, and only partially attached to the substratum; and (3) *fruticose* lichens, branching forms that hang from trees or grow either erect or prostrate on the ground (Fig. 125).

The greater part of a lichen is composed of a compact mass of tangled fungous hyphae, among which are numerous algal cells, either scattered irregularly or in a definite layer (Fig. 126). The body is usually differentiated into a compact cortical region and a lower region of looser texture, in either of which the algal cells may occur. In some lichens the algae live on the surface of the mycelium, closely covering it. With only a few rare exceptions, lichen-forming fungi are ascomycetes belonging either to the Pezizales or to the Pyrenomycetales. In three genera of lichens the fungus is a basidiomycete, the best-known species being *Cora pavonia*, which is widely distributed throughout Central and South America. The lichen-forming algae are members either of the Cyanophyceae or Chlorophyceae, most of the latter belonging to the Chlorococcales.

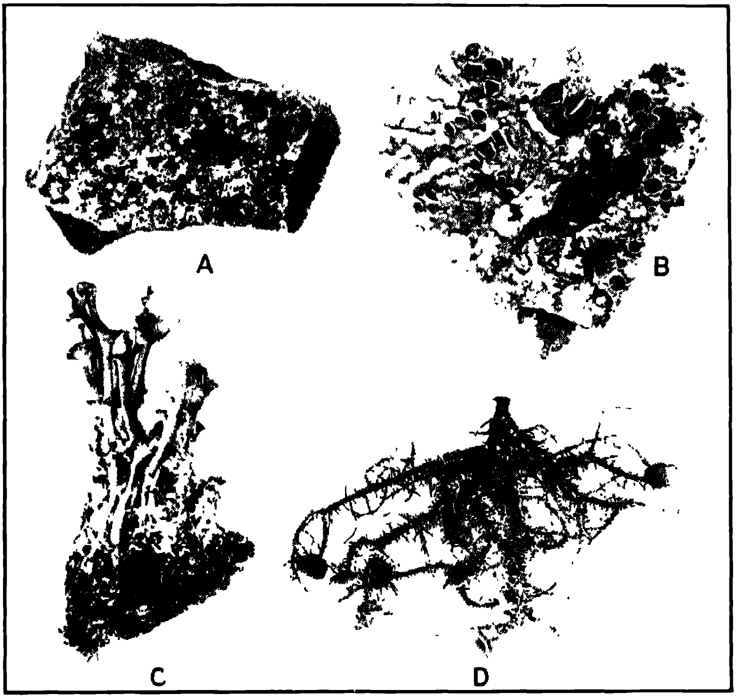



FIG. 125. Group of common lichens, natural size. *A*, a crustose form (*Placodium*) growing on rock; *B*, a foliose form (*Parmelia*) growing on bark; *C*, a fruticose lichen (*Cladonia*) which grows erect on the ground; *D*, a branching form (*Usnea*) that hangs from the limbs of trees.

Lichens were once regarded as single plants. In 1868, their dual nature was demonstrated. In 1889, lichens were first synthesized by sowing spores from the fungous element of a lichen among appropriate free-living algae. The developing mycelium was seen to enclose the algae and develop into a lichen. Although the algal symbionts are forms that may exist independently, the fungi are known only as constituents of lichens.

Vegetative reproduction takes place mainly by *soredia*, globular or scale-like bodies composed of a few hyphae closely investing one or more algal cells. They arise as buds on the upper surface of the thallus, become detached, and are scattered by the wind. The algal components multiply by fission within the lichen body. The fungous components produce ascocarps, generally in abundance (Fig. 127). These are either apothecia or perithecia. Sex organs have been observed in many lichens. The ascogonium is a spirally coiled multicellular filament commonly terminating in a trichogyne. The male cells, or spermatia, are borne on branching hyphae arising within a flask-like chamber, or spermogonium. After

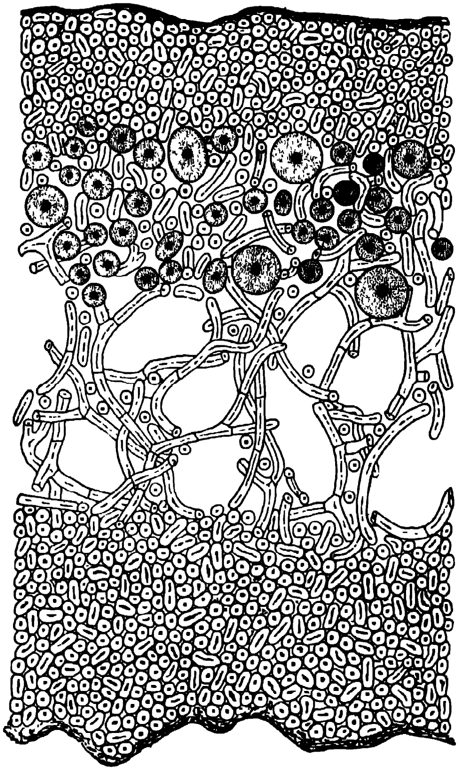


FIG. 126. Cross section through the body of a lichen (*Physcia*), showing cells of the alga (shaded) surrounded by a mass of interlacing fungous hyphae, ×500.

fertilization, which may not always take place, the ascogonium gives rise to many ascogenous hyphae and paraphyses (Fig. 127*B*). At the tips of the ascogenous hyphae typical asci with eight ascospores are formed. An ascospore, in germination, produces hyphae that die unless they come in contact with a suitable alga.

The relation of the two lichen components to each other is important to understand. The fungus lives on the alga as a parasite but does not kill it. In fact, the alga seems to be only slightly injured, merely sacrificing some of the food that it makes. At the same time, however, the alga is benefited in that the fungous body readily absorbs and retains moisture, without which the alga could not live. The fungus derives food from the alga, while the alga obtains moisture from the fungus. This reciprocal relation makes it possible for many lichens to live in dry exposed situations where neither the alga nor the fungus could live alone. Thus the relation between the two lichen components is one of mutual advantage.

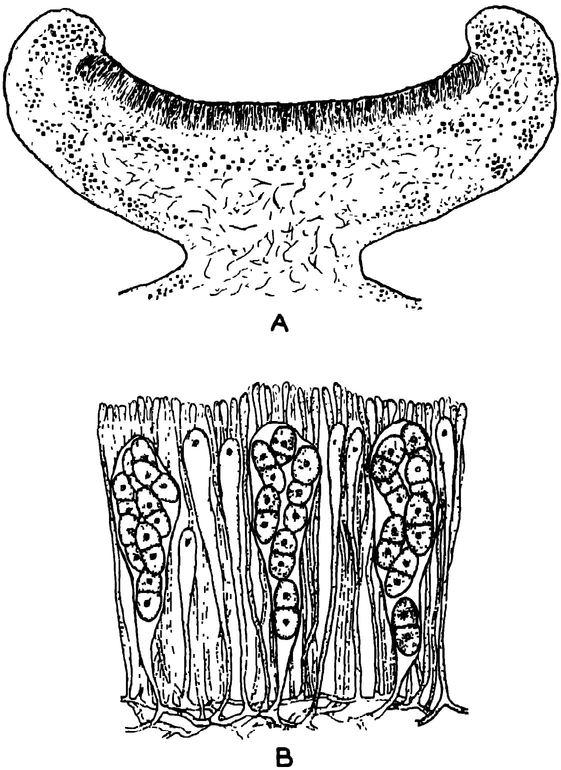



FIG. 127 *A*, longitudinal section through an apothecium of *Physcia*, showing hymenium and embedded algal cells, ×60; *B*, enlarged view of hymenium, showing asci and paraphyses, ×500.

### COMPARISON OF THE CLASSES OF FUNGI

The chief distinguishing characters of the five classes of fungi are as follows:

**Schizomycetes.** Plant body unicellular, solitary or colonial, ciliated or nonciliated. Cells without a definite nucleus. Cell walls usually forming mucilage. Reproduction by fission.

**Myxomycetes.** Plant body a naked amoeboid mass of multinucleate protoplasm (a plasmodium). Asexual reproduction by small uninucleate spores, each with a cell wall and usually borne within sporangia of definite form. Sexual reproduction by amoeboid isogametes.

**Phycomycetes.** Plant body typically a nonseptate multinucleate mycelium. Asexual reproduction by spores formed by cleavage and borne in indefinite numbers in sporangia. Lower members with zoospores, higher members with aerial spores. Sexual reproduction isogamous or heterogamous. Heterogamous forms with well-developed sex organs.

**Ascomycetes.** Plant body typically a septate mycelium. Spores borne usually in groups of eight in a sac-like structure, the ascus, their nuclei arising by three successive divisions of a fusion nucleus. Zoospores wanting. Sex organs reduced, obscure, or entirely absent.

**Basidiomycetes.** Plant body a septate mycelium. Spores borne usually in groups of four on a club-like structure, the basidium, their nuclei arising by two successive divisions of a fusion nucleus. Zoospores wanting. Sex organs not present.

## GENERAL CONCLUSIONS

The fungi are a heterogeneous assemblage of thallophytes of diverse origin held together by a physiological character—the absence of chlorophyll. Two classes, the Schizomycetes and Myxomycetes, stand apart from each other and from the three classes of "true fungi" (Eumycetes). In their unicellular organization, cell structure, and reproduction the Schizomycetes resemble the Cyanophyceae much more closely than they resemble any of the other fungi. The Myxomycetes, with their naked plasmodia, highly developed sporangia, and amoeboid isogametes, exhibit similarities to some of the Protozoa, on the one hand, and to some of the lower Phycomycetes (Plasmodiophorales) on the other.

Some botanists believe that the "true fungi" are a monophyletic group that have arisen from colorless flagellates and have subsequently differentiated into the three existing classes of Phycomycetes, Ascomycetes, and Basidiomycetes. According to this theory, no direct relationship exists between the algae and fungi, their resemblances being a result of parallel evolution along two independent lines. Other botanists believe that the "true fungi" have been derived from the algae through loss of chlorophyll, their origin having been either monophyletic or polyphyletic. According to this theory, the Phycomycetes have evolved from the Chlorophyceae, the Ascomycetes from either the Phycomycetes or the Rhodophyceae, and the Basidiomycetes from the Ascomycetes.

**Vegetative Body.** The characteristic plant body of the fungi[1] is a mycelium, made up of branching hyphae that may be either nonseptate and coenocytic (Phycomycetes) or septate (Ascomycetes and Basidiomycetes). Only a few forms are unicellular. The hyphae elongate by apical

[1] In the following discussion the term *fungi* will be limited to the three classes of "true fungi."

growth. They may be either loosely or compactly arranged. Sometimes they are aggregated to form root-like strands or a compact resting body (sclerotium). In the development of fruit bodies in the higher fungi —ascocarps and basidiocarps—masses of hyphae become interwoven to form a pseudoparenchymatous structure, but no tissue is formed by cells dividing in three planes. In the lower Phycomycetes the cell wall consists largely of cellulose, but in the other fungi its composition is altered by the presence of chitin and other substances, such as fatty acids. Within the cells of the mycelium are one, two, or many nuclei embedded in the cytoplasm. Sugars and glycogen represent the reserve carbohydrates, no starch being present. Varying amount of fats may also occur.

**Spore Reproduction.** The Phycomycetes produce spores in sporangia, either zoospores in the lower orders or aerial spores in the higher orders. The spores are formed in indefinite numbers by cleavage. After escaping, they germinate into a mycelium. The entire sporangium may be persistent, as in the Saprolegniales and Mucorales, or detachable, as in most of the Peronosporales. In many of the Ascomycetes and Basidiomycetes the detachable sporangia are replaced by conidia, which function as spores and produce a new mycelium directly. Many conidia, as well as certain other spores, multiply by budding, like the vegetative cells of the yeasts.

Many fungi produce resting spores that are thick-walled and resistant to adverse conditions. Often the same species has two or more different kinds of spores, as in the rusts. Ascospores, which are characteristic of the Ascomycetes, arise by free-cell formation. They are borne internally in an ascus, usually in groups of eight, while basidiospores, characteristic of the Basidiomycetes, are produced externally on a basidium, usually in fours. The formation of ascospores and basidiospores is related to the sexual process.

**Gametic Reproduction.** In the Phycomycetes sexual reproduction is alga-like. The Chytridiales and Plasmodiophorales produce free-swimming isogametes that fuse in pairs to produce a zygote. Among the heterogamous Phycomycetes (Monoblepharidales, Saprolegniales, and Peronosporales), all of which have well-developed antheridia and oögonia, only the Monoblepharidales have swimming sperms; in the two other orders a male nucleus reaches the egg by passing through a fertilization tube. The gametes are nearly always formed within special cells, the gametangia or sex organs. In the higher Phycomycetes (Mucorales and Entomophthorales) the gametangia are not differentiated as antheridia and oögonia, but the entire contents of two gametangia conjugate to form a zygote.

The Ascomycetes show various stages in the degeneration of the sex organs. Where these are well developed, the oögonium (ascogonium) often resembles that of the red algae. The zygote may develop directly into an ascus or, more commonly, may give rise to many ascogenous hyphae that, in turn, produce the asci. The Basidiomycetes have no sex organs (unless the spermogonia of the rusts are so regarded), but fusions between vegetative cells are common. In the Ascomycetes and Basidiomycetes the sexual nuclei come together without immediately fusing. The nuclear fusion, which takes place in the ascus or basidium, is followed at once by the production of ascospores or basidiospores, respectively.

# CHAPTER V

## BRYOPHYTA

The bryophytes, numbering about 20,000 species, form a well-defined division comprising the two classes Hepaticae (liverworts) and Musci (mosses). They are small, rather inconspicuous, green plants nearly all of which live on land in moist, shaded places. The bryophytes doubtless have been derived from aquatic ancestors, probably from some group of green algae, but it is uncertain whether they have given rise to any of the higher plant groups. Nevertheless, the bryophytes represent a general condition of structural organization through which the higher plants may have passed in the course of their evolution. Although abundant moisture is necessary for vigorous vegetative growth, some forms live in dry situations and endure considerable desiccation during long rainless periods. A few liverworts and mosses live in fresh water, but the aquatic habit in the bryophytes, as in the higher groups, has undoubtedly been secondarily acquired.

A well-defined alternation of generations is an established feature of all bryophytes, the gametophyte and sporophyte always being morphologically dissimilar. The gametophyte, arising from the spore, is the haploid generation, producing sperms and eggs. The sporophyte, arising from the zygote, is the diploid generation. It produces spores, the reduction in chromosome number taking place in connection with their formation, as in all the higher plants. Swimming spores are entirely eliminated. In the green algae the zygote is liberated into the water and is nearly always a resting cell, while in the bryophytes and all higher groups it germinates at once, without escaping, to produce an embryo sporophyte.

In the bryophytes the gametophyte, or haploid generation, is always an independent individual, while the sporophyte, or diploid generation, is entirely or largely dependent on it for its nutrition. Although the gametophyte is thalloid in some of the liverworts, in most bryophytes it is differentiated into stem and leaves. Growth takes place through the activity of an apical cell. The sex organs, antheridia and archegonia, are always multicellular and provided with an outer sterile jacket. Throughout the algae the gametangia are prevailingly unicellular but, where multicellular, all their cells produce gametes (except in the Charophyceae). The antheridium is a stalked, spherical or club-shaped organ consisting of a mass of spermatogenous tissue enclosed by a jacket of