sterile cells. It gives rise to numerous small biciliate sperms, two of which arise from each sperm mother cell. The presence of swimming sperms, universal among bryophytes and pteridophytes, represents the retention of a primitive algal character.

The archegonium is a very characteristic organ of bryophytes and pteridophytes. Although corresponding to the oögonium of the algae, it is much more highly developed. The archegonium is usually stalked and flask-shaped. It is composed of an axial row of cells surrounded by a sterile jacket. The axial row consists of an egg—the basal and largest cell of the series—and a variable number of canal cells, which disorganize and become mucilaginous prior to fertilization. The fertilized egg gives rise to an embryo that develops within the archegonium, the basal portion of which enlarges to form a protective covering, the *calyptra.*

In all bryophytes the sporophyte is without differentiation into stem and leaves and is without a direct connection with the soil. In nearly all bryophytes the sporophyte consists of a basal absorbing organ (*foot*), a stalk (*seta*), and a terminal spore-producing portion (*capsule*). The capsule is a sporangium. All bryophytes are *homosporous*, the spores of a given species being alike in size and form. On germination, the spore produces either the main gametophyte directly or, more commonly, a filamentous *protonema* from which the main gametophyte sooner or later arises.

1. HEPATICAE

The liverworts are primitive land plants, most of them growing in the presence of abundant moisture on soil, rocks, and tree trunks. With very few exceptions, the gametophyte is dorsiventral. It may be thalloid, but more commonly is leafy, the leaves being nearly always without a midrib. Unicellular unbranched rhizoids maintain a connection with the substratum. The Hepaticae are widely distributed but are more numerous in the tropics than elsewhere. A few fossil forms are known from the Upper Carboniferous of England. There are about 6,000 species of liverworts, nearly all being included in four principal orders, the Marchantiales, Sphaerocarpales, Jungermanniales, and Anthocerotales.

1. Marchantiales

The Marchantiales are a well-defined order of about 30 genera and 400 species. They range from arctic to tropical regions and are well represented in the Temperate Zones. In the tropics they occur chiefly between altitudes of 900 and 1,500 m. Nearly all of them are terrestrial, growing mainly on damp soil or rocks. Some common genera of Marchantiales, all of widespread distribution, are *Riccia, Reboulia, Asterella, Conocephalum,* and *Marchantia.* The largest genus is *Riccia,* with over 100 species.

Gametophyte. The Marchantiales are characterized by a flat, dorsiventral, thalloid gametophyte—with few exceptions ribbon-like and nearly always rather fleshy. It branches either dichotomously from the apex or, less commonly, by means of adventitious outgrowths arising apically or ventrally. In *Riccia* the thallus is small and, as a result of repeated dichotomy, often grows in the form of a fan or rosette (Fig. 128). In all the Marchantiales growth takes place by means of an apical cell situated in an apical notch. It is of the *cuneate* (wedge-shaped) type, cutting off segments on four sides—above and below as well as left and right (Fig. 129*A*).

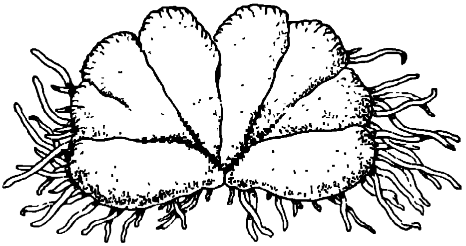

FIG. 128. Dorsal view of the gametophyte of *Riccia natans*, showing sporophytes in the grooves and scales arising from the ventral surface, ×3.

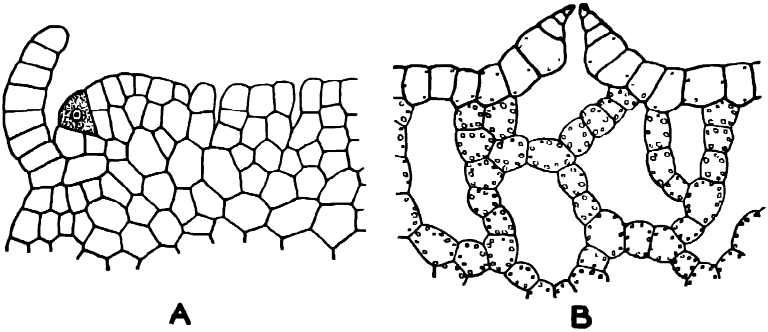

FIG. 129. *Reboulia hemisphaerica.* *A*, longitudinal section of portion of growing region of thallus with apical cell and developing air chambers, ×160; *B*, portion of upper region of thallus, showing air pore and air chambers, ×85.

The gametophyte is of simple external form but exhibits a high degree of internal differentiation, nearly always consisting of–(1) an upper epidermal layer; (2) a loose, green, dorsal region having one or more layers of air chambers; (3) a compact, colorless, ventral region. The epidermis, usually colorless or pale green and often with slightly thickened walls, nearly always contains numerous air pores that communicate with the air chambers. Air pores and air chambers are not developed in a few genera (*e.g.*, *Dumortiera* and *Monoclea*), their absence being a result of reduction.

In most species of *Riccia* the dorsal region is composed of erect rows of cells separated by very narrow, vertical air chambers, but in some species it is spongy, consisting of a loose network of large irregular air chambers separated by one-layered partitions that extend in all directions (Fig. 137*A*). The uppermost cells form a rather ill-defined epidermis. In *Riccia natans* simple air pores are present, but in the other species air pores are either rudimentary or wanting. Simple air pores consist of a single tier of cells surrounding a small central opening, the cells being in several concentric circles (only one circle in *Riccia natans*). Simple air pores occur on the thallus of most of the genera of Marchantiales (Fig. 129*B*). In *Marchantia* and a few related forms, however, the thallus bears compound air pores. These are barrel-shaped, consisting of four or five superimposed layers of cells and having both an upper and a lower opening (Fig. 130). *Conocephalum, Marchantia,* and many other genera have a single layer of air chambers from the floor of which special chlorophyllose filaments arise. *Reboulia* and *Asterella* have several layers of air chambers without green filaments (Fig. 129*B*). In many forms the limits of the air chambers are plainly visible on the dorsal surface of the thallus as polygonal areas, an air pore occurring in the center of each.

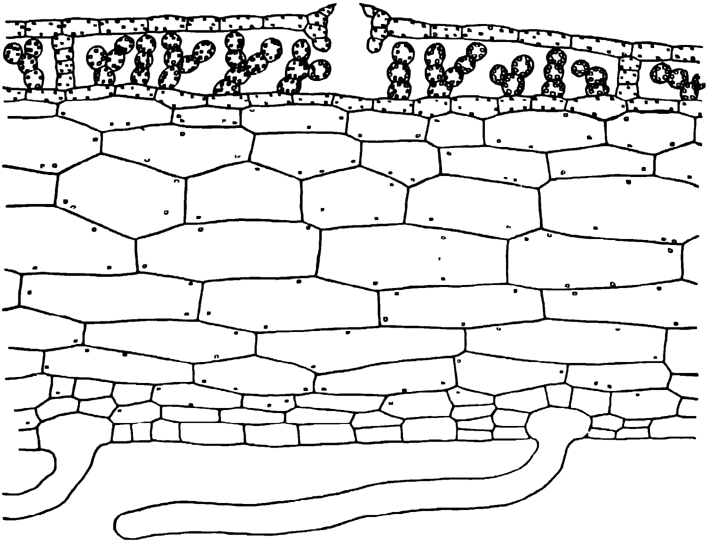

FIG. 130. Section through the thallus of *Marchantia polymorpha*, showing epidermis with an air pore that leads to an air chamber with green filaments, X200 Rhizoids are shown below.

In practically all the Marchantiales the lower surface of the thallus bears numerous rhizoids and scales. The rhizoids are of two kinds, smooth and tuberculate. The former have smooth walls, the latter peg-like thickenings that project into the lumen. In *Riccia* rhizoids are usually abundant, but frequently ventral scales are rudimentary or absent.[1] In nearly all the Marchantiales the ventral scales are arranged in two longitudinal rows; in *Marchantia* they are in four or more rows.

Throughout the order decay of the older parts of the thallus results in the isolation of branches, each of which forms a new plant. In some species vegetative propagation occurs by the formation of adventitious branches that become detached. In two genera, *Lunularia* and *Marchantia*, multicellular *gemmae* are produced. These are flat, stalked, discoid bodies that arise in groups on the dorsal side of the thallus inside *cupules*.

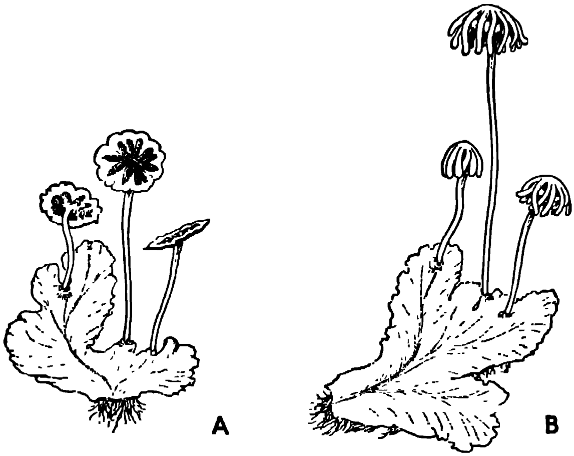

FIG. 131. Male (*A*) and female (*B*) plants of *Marchantia polymorpha*, natural size.

In *Lunularia* the cupules are crescentic, while in *Marchantia* they are cup-shaped. The gemmae arise from the floor of the cupule. Each gemma has two notches, one on either side, and in each notch is an apical cell. Upon separation from the cupule, a single gemma gives rise to two new thalli.

Sex Organs. The sex organs of the Marchantiales are invariably dorsal in origin, arising either directly on the thallus itself or on a more or less specialized receptacle. Both kinds of sex organs arise in acropetal succession from segments of an apical cell. According to the species, the antheridia and archegonia occur on the same plant or on separate plants. In *Riccia* each branch of the thallus has a median dorsal groove extending backward from the growing apex; in this groove the sex organs are borne. Although generally scattered irregularly, they sometimes tend to be segregated into separate groups. The sex organs arise singly just behind

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[1] When *Riccia natans* floats on the surface of quiet water, it has numerous large scales and few or no rhizoids. When it grows on muddy banks and flats, it has many rhizoids and few scales.

the apical cell and soon become sunken in the thallus by upgrowth of the surrounding tissues, each coming to lie in an individual pit.

In the other Marchantiales the antheridia are similarly sunken in pits but the archegonia are not. The antheridia may be borne in irregular median groups on the dorsal side of the thallus, as in some species of *Asterella*, but more commonly they occur on a definite receptacle. This may be cushion-like and sessile, as in *Reboulia* and *Conocephalum*, or raised above the thallus on a stalk, as in *Marchantia*. The antheridial receptacle of *Marchantia* has a number of marginal growing points, from each of which an acropetal series of antheridia extends toward the center, the antheridia being sunken in the upper surface of the receptacle (Figs. 131*A* and 132*A*).

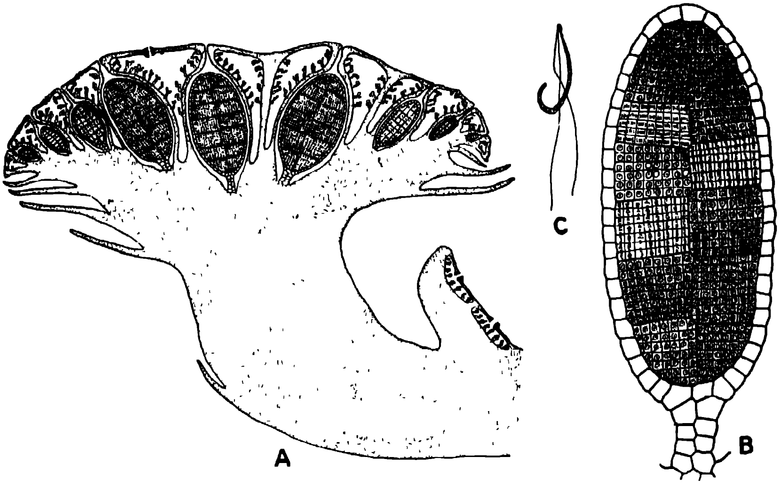

FIG. 132. Male structures of *Marchantia polymorpha*. *A*, longitudinal section through young male receptacle, showing embedded antheridia, ×40; *B*, nearly mature antheridium, ×200; *C*, a single sperm, more highly magnified.

In *Reboulia*, *Asterella*, *Conocephalum*, and many other genera the archegonia are borne on a stalked receptacle that, with few exceptions, is terminal in position and represents a specialized upright branch of the thallus. Unlike the antheridia, the archegonia are not embedded in pits. The female receptacle is commonly hemispherical or conical and more or less lobed. Each lobe represents a separate growing point back of which either one or several archegonia arise. As the receptacle grows, the archegonia are carried to a position on its lower side close to the stalk. In *Marchantia* the archegonial receptacle reaches its greatest degree of specialization. It does not have lobes, but consists of a number of rays alternating with groups of archegonia (Figs. 131*B* and 133*A*). The archegonia hang with the necks downward.

Air chambers and air pores are developed on both the male and female receptacles. In *Reboulia* and *Asterella* the air pores on the female receptacle are compound, while those occurring elsewhere on the plant are simple. In *Conocephalum* the air pores are compound on both the male and female receptacles, but are simple on the thallus. In *Marchantia* the air pores are everywhere compound.

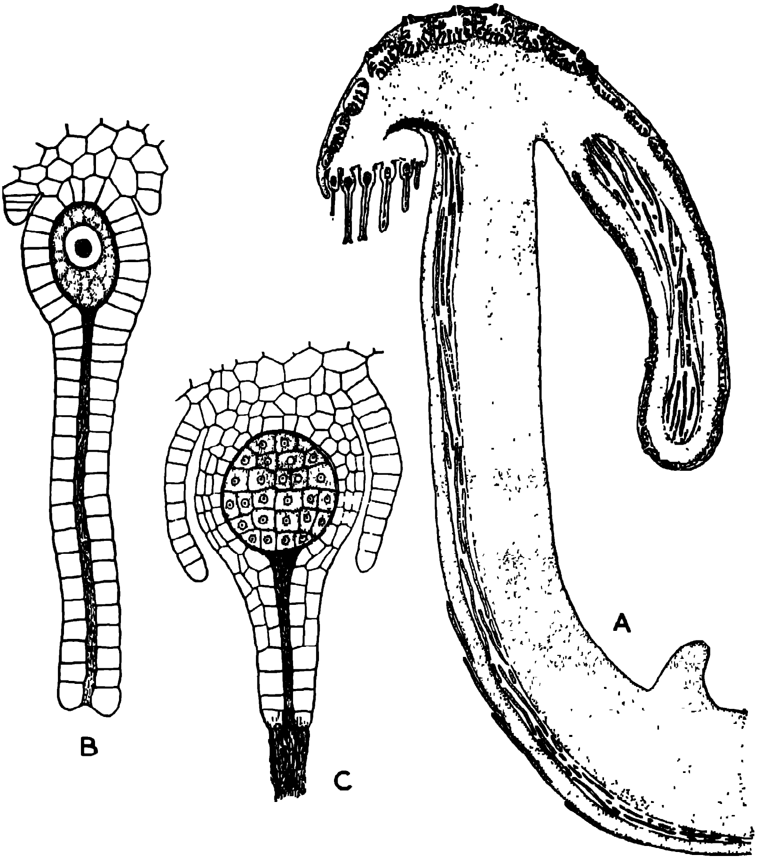

FIG. 133. Female structures of *Marchantia polymorpha*. *A*, longitudinal section through young female receptacle, showing a row of archegonia, ×40; *B*, mature archegonium with egg ready for fertilization, ×300; *C*, young embryo lying within the archegonium, ×300.

The mature antheridia of the Marchantiales are club-shaped structures with a short stalk (Fig. 132*B*). The chamber in which each lies communicates with the surface of the thallus or receptacle by a pore through which the sperms escape. The antheridium arises from a single superficial initial cell that becomes papillate and then divides transversely (Fig. 134*A*). The outer segment undergoes several additional transverse divisions, resulting in the formation of about four superimposed cells (Fig. 134*B*-*D*). In each of these vertical walls appear at right angles to each other and later, by the formation of periclinal walls in the upper part of the antheridium, an outer layer of sterile cells is cut off from a central group of spermatogenous cells (Fig. 134*E*-*H*). The lower portion of the antheridium forms the stalk. By continued division, the spermatogenous cells give rise to many small, cubical, sperm mother cells, each of which produces two biciliate sperms (Fig. 132*B*, *C*).

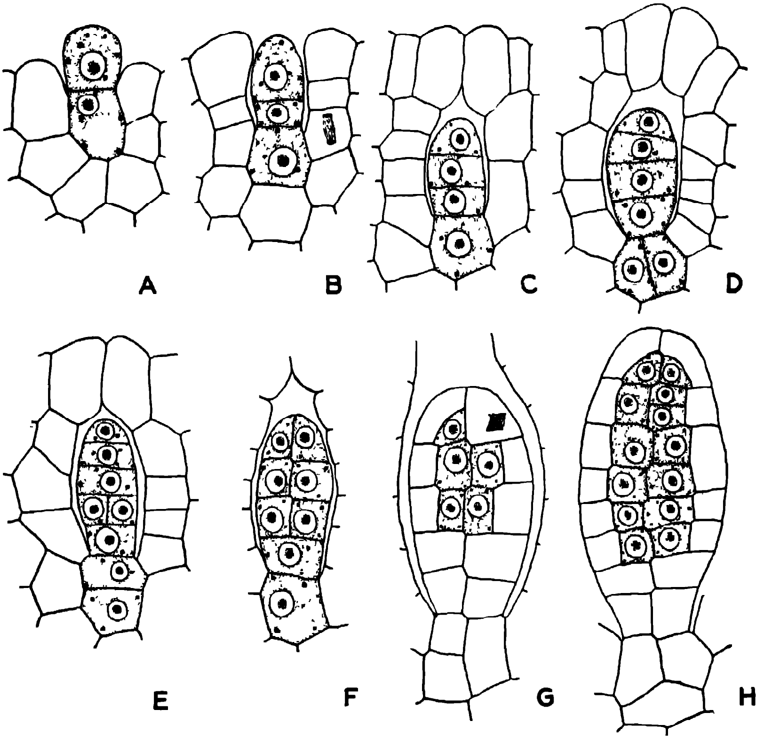

FIG. 134. Early stages in the development of the antheridium of *Marchantia polymorpha*, ×750. *A*, division of initial into an inner and outer cell, *B*, *C*, *D*, formation of a filament of four cells from the outer cell; *E* and *F*, appearance of vertical walls, *G*, appearance of periclinal walls; *H*, later stage, showing sterile jacket surrounding spermatogenous cells, with stalk below.

The archegonium also arises from a single superficial initial that becomes papillate and divides transversely (Fig. 135*A*). Three vertical walls now appear in the outer segment, these being arranged in such a way that a middle cell and three peripheral cells are formed (Fig. 135*B*, *H*). The middle cell is the *primary axial cell*, the peripheral ones the *primary wall cells*. The primary axial cell, by a transverse division, gives rise to a *cover cell* and a *central cell* (Fig. 135*C*). The archegonium now grows in length, the central cell dividing to form a *primary neck canal cell* and a *primary ventral cell* (Fig. 135*D*). As a result of additional transverse divisions, the primary neck canal cell gives rise to a vertical row of neck canal cells, most commonly either four or eight in number, while the primary ventral cell divides transversely to form the *ventral canal cell* and *egg* (Fig. 135*E*–*G*).

By this time the archegonium has become distinctly flask-shaped, the slender *neck* being sharply marked off from the bulbous *venter*. In all the Marchantiales the neck consists of six vertical rows of jacket cells surrounding the canal (Fig. 135*I*). The canal cells disorganize, forming a mass of mucilage through which the sperms can swim (Fig. 133*B*). The egg is fertilized within the venter of the archegonium, which enlarges to form the *calyptra*, the embryo developing within (Fig. 133*C*). In all the Marchantiales except *Riccia*, an *involucre* arises around the archegonia. In *Asterella*, *Marchantia*, and several other genera an additional envelope, the *pseudoperianth*, arises after fertilization and generally becomes very conspicuous (Fig. 139).

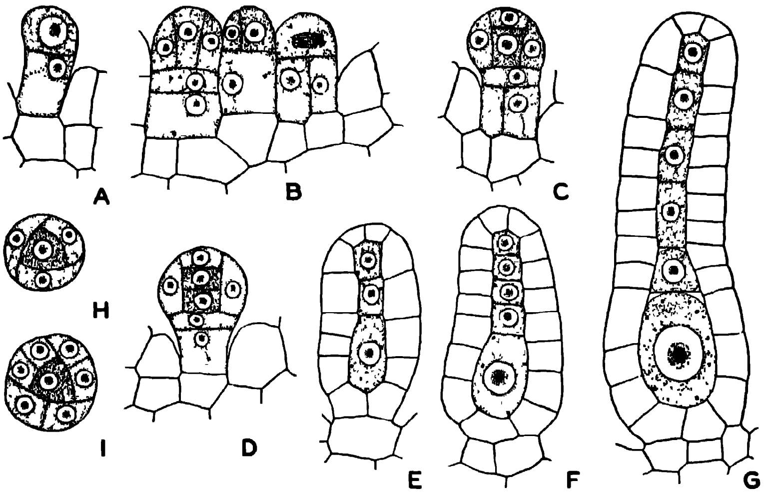

FIG. 135. Development of the archegonium of *Marchantia polymorpha*, ×600. *A*, division of initial into an inner and outer cell; *B*, appearance of three vertical walls in the outer cell; *C*, formation of cover cell and central cell from the primary axial cell; *D*, formation of primary neck canal cell and primary ventral cell from the central cell; *E* and *F*, later stages, with two and four neck canal cells; *G*, nearly mature archegonium, with egg and ventral canal cell derived from the primary ventral cell; *H*, cross section of very young archegonium, showing primary axial cell surrounded by primary wall cells; *I*, later stage, showing six neck cells surrounding a neck canal cell.

Sporophyte. *Riccia* displays the simplest sporophyte among the Bryophyta. In its development, the fertilized egg divides by a transverse wall, resulting in two cells approximately equal in size (Fig. 136).

Each of these now divides by a vertical wall, followed by another at right angles to it. Additional divisions, without definite sequence, take place in all three planes. Then periclinal walls cut off an outer layer, the *amphithecium*, from a central group of cells, the *endothecium*. As the embryo continues to grow, the entire central group becomes sporogenous, while the outer layer remains sterile. After the sporogenous cells have divided for the last time, they separate and round off to become *spore mother cells* (Fig. 137). Each of these then enlarges and undergoes two consecutive divisions during which the number of chromosomes is reduced one-half, and a *tetrad* of cells is formed. The walls thicken and the four members of the tetrad separate as mature spores. During the early development of the sporophyte, the venter of the archegonium becomes two-layered and forms the calyptra (Fig. 136). The sterile jacket of the sporophyte and the inner layer of the calyptra break down before the spores have ripened, leaving them enclosed within the outer layer of the calyptra. *Riccia* has no spore-dispersing mechanism, the spores being liberated by progressive decay of the thallus.

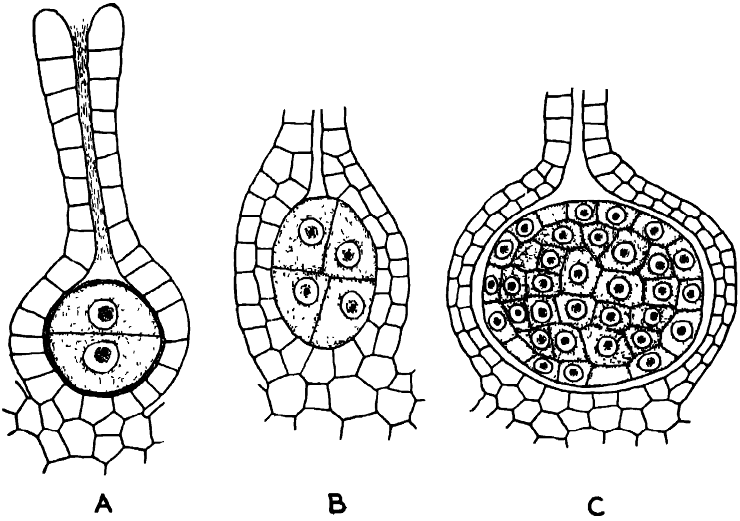

FIG. 136 Development of the embryo of *Riccia natans*, ×400. *A*, two-celled stage; *B*, four-celled stage; *C*, later stage, showing differentiation into amphithecium and endothecium.

In practically all the other Marchantiales the sporophyte consists of a *foot*, *seta*, and a *capsule* containing both spores and elaters. As in *Riccia*, the first division of the fertilized egg is transverse. In some genera, such as *Reboulia*, *Asterella*, *Conocephalum*, and others, the next two divisions are also transverse, resulting in a filament of four superimposed cells (Fig. 138). Then vertical walls come in and, with the formation of

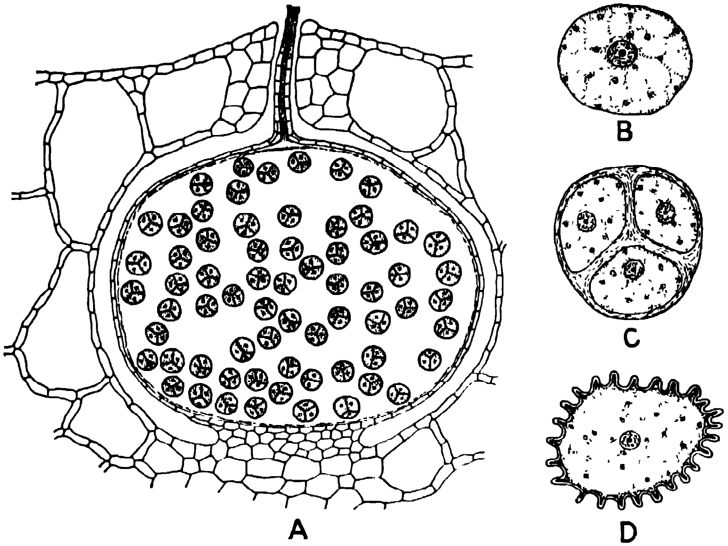

FIG. 137. Sporophyte of *Riccia natans*. *A*, longitudinal section of nearly mature sporophyte embedded in the gametophyte, showing spore tetrads enclosed within the calyptra *B*, spore mother cell; *C*, tetrad; *D*, mature spore, *A*, ×100; *B*, *C*, *D*, ×500.

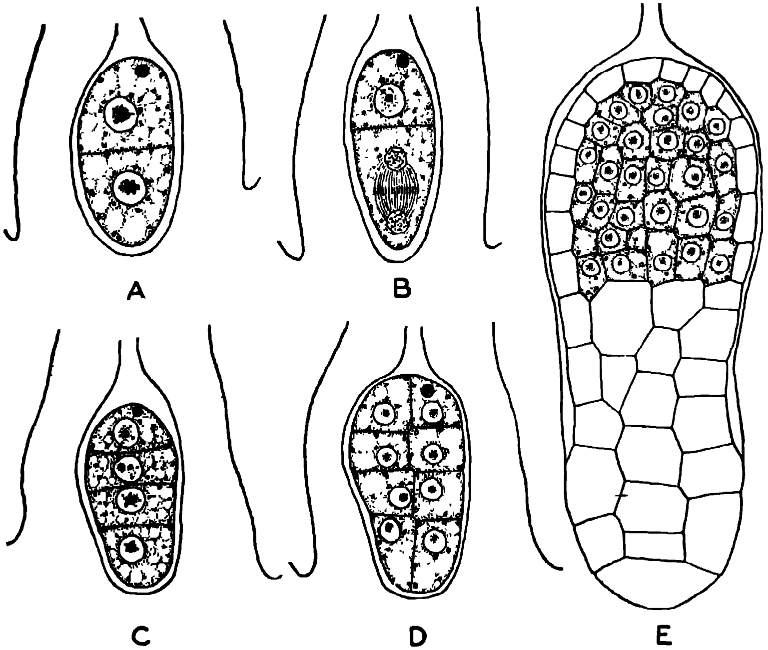

FIG. 138. Development of the embryo of *Cryptomitrium tenerum*, ×400. *A*, two-celled stage; *B*, division of lower cell; *C*, four-celled stage, the two lower cells giving rise to the foot and seta, the two upper cells to the capsule; *D*, eight-celled stage; *E*, older stage, showing differentiation of sporogenous tissue in the capsule. (*After Haupt.*)

additional walls in the upper part of the embryo, the foot, seta, and capsule are differentiated. In other genera, such as *Marchantia*, the first division of the fertilized egg is followed by the appearance of two vertical walls at right angles to each other in both the upper and lower segments, thus forming octants, as in *Riccia*. Additional walls in all three planes produce a globular embryo rather than an elongated one (Fig. 139).

An early formation of periclinal walls in the capsular region cuts off the amphithecium from the endothecium, the former forming the capsule wall and the latter the sporogenous tissue (Fig. 138*E*). In *Riccia* the sporogenous tissue is derived equally from both halves of the embryo. In practically all the other genera, whether the embryo is of the filamentous or of the octant type, apparently only the upper half contributes to the sporogenous tissue, the lower half giving rise to the foot and seta. The foot anchors the sporophyte and absorbs nourishment. The seta elongates, especially after the spores ripen, pushing the capsule through the calyptra.

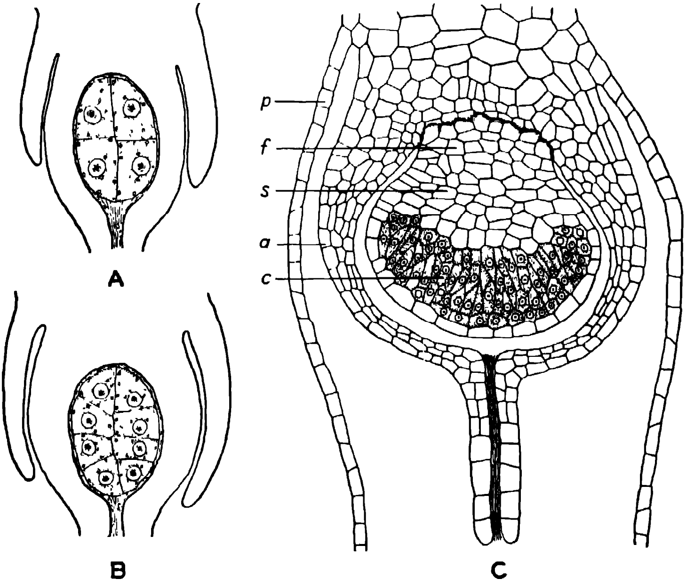

Fig. 139. Development of the embryo of *Marchantia polymorpha*. *A*, four-celled stage, ×320; *B*, slightly later stage, ×320; *C*, older embryo, showing the foot (*f*), seta (*s*), capsule (*c*) with sporogenous tissue differentiated, pseudoperianth (*p*), and calyptra (*a*), ×200.

In most genera, except *Riccia*, some of the potentially sporogenous cells of the young capsule give rise to *elaters*, while the others directly become spore mother cells. In *Marchantia*, however, the sporogenous cells greatly elongate, some remaining undivided to form elaters, the others dividing transversely a number of times to form vertical rows of spore mother cells (Fig. 140). As in *Riccia*, tetrads are formed and the walls of the spores thicken. The elaters are long, slender cells, pointed at each end, their walls developing spiral thickenings as the protoplasm disappears (Fig. 140*D*). Elaters are hygroscopic and perform squirming movements that assist in the liberation of the spores. The capsule wall is one layer of cells thick except in the apical region. In *Reboulia*, *Asterella*, and related forms local thickenings are not formed on the cells of the capsule wall and dehiscence takes place by means of an apical lid. In nearly all the other genera, however, the cells of the capsule wall bear annular thickenings, dehiscence occurring by irregular clefts.

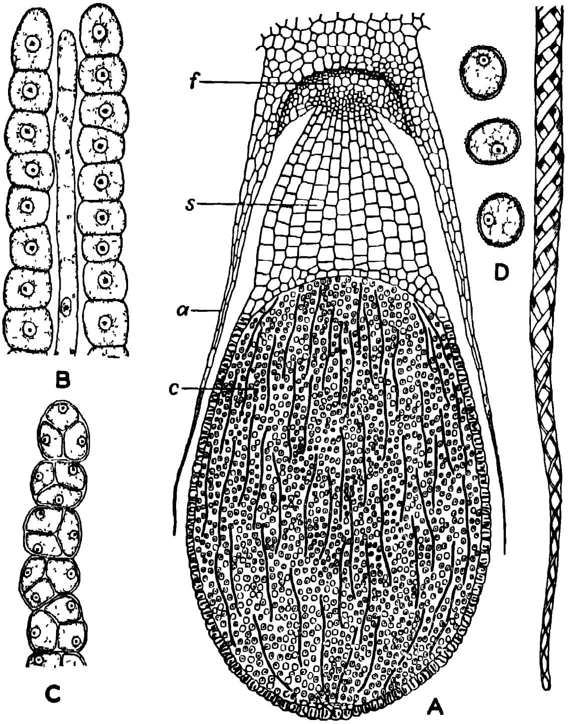

Fig. 140. Sporophyte of *Marchantia polymorpha*. *A*, longitudinal section of nearly mature sporophyte, showing the foot (*f*), seta (*s*), capsule (*c*), and ruptured calyptra (*a*); *B*, two rows of spore mother cells and portion of an undeveloped elater; *C*, a row of spore tetrads; *D*, three mature spores and the end of an elater; *A*, ×60; *B*, *C*, *D*, ×600.

Summary. The Marchantiales are a group in which the gametophyte, while remaining simple in form, has achieved a high degree of structural complexity. In all members of the order the gametophyte is thalloid and grows by means of a cuneate apical cell. It is nearly always differentiated into an upper epidermis with air pores, a dorsal photosynthetic region with air chambers, and a compact, colorless ventral region. The gametophyte reaches an extreme of complexity in forms with compound air pores and air chambers having green filaments. It bears both smooth and tuberculate rhizoids. In the lower members the sex organs are borne directly on the thallus, sunken in the dorsal surface, but throughout the group there is a marked tendency to restrict and specialize the regions producing sex organs, resulting in the development of complex receptacles. The female receptacles, and sometimes the male as well, are stalked. The antheridia, when mature, are elongated organs lying in a deep chamber. Their early development is characterized by a series of transverse divisions. The neck of the archegonium shows six cells in cross section.

In the lower members the sporophyte is a spherical, undifferentiated spore case, all the inner cells forming spores. In the higher members the sporophyte is elongated and differentiated into a foot, seta, and capsule. The capsule contains both spores and sterile cells, the latter practically always developed as elaters. Thus, throughout the group, there is a marked tendency to divert potentially sporogenous tissue to functions other than spore production. The seta is comparatively short. The capsule is spherical or nearly so, its wall being composed of a single layer of cells (the apex usually thicker). Dehiscence, lacking in *Riccia*, nearly always occurs by irregular clefts or an apical lid. The Marchantiales are a group in which a complex gametophyte is combined with a relatively simple sporophyte.

2. Sphaerocarpales

The Sphaerocarpales comprise a small order of 3 genera and 25 species. *Sphaerocarpus* is a widely distributed genus but *Geothallus*, represented by a single species, has been found only near San Diego, California. Both of these forms grow on moist earth. *Riella* is an aquatic form occurring in Europe, Africa, California, and western Texas.

Gametophyte. The gametophyte of the Sphaerocarpales displays none of the internal differentiation seen in the Marchantiales. It consists of a simple plate-like thallus that differs somewhat among the three genera. In *Sphaerocarpus* the thallus is small, flat, and often orbicular, with an entire or more or less lobed margin. It has a broad indistinct midrib, several layers of cells in thickness, that merges gradually into the one-layered wings (Fig. 141). In *Geothallus* the thallus is larger and consists of an elongated thickened axis giving rise to crowded leaf-like outgrowths on either side, these mostly one layer of cells thick. A large portion of the axis becomes converted into a fleshy tuber that lives over into the next growing season. In both *Sphaerocarpus* and *Geothallus* the thallus may be either simple or dichotomously branched. The lower surface lacks scales but bears numerous colorless rhizoids of the smooth-walled type. Growth of the thallus results from the activity of a cuneate apical cell.

In general appearance *Riella* is unlike any other liverwort. It is a submerged aquatic, usually growing erect in standing water. It has a stem-like axis that bears a dorsal leaf-like wing or, in the Algerian *Riella bialata*, two wings. The wing is mostly one layer of cells thick. It is frequently undulate and sometimes spirally twisted. The axis is commonly several times dichotomous. It produces rhizoids near the base.

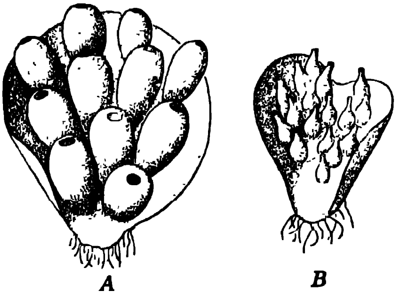

FIG. 141. Female (*A*) and male (*B*) gametophytes of *Sphaerocarpus californicus*, ×6. (*From Gilbert M. Smith.*)

Sex Organs. The antheridia and archegonia are borne directly on the thallus, each enclosed in a special involucre that is open above. They arise in acropetal succession from dorsal segments of the apical cell. In *Riella* both kinds of sex organs may occur on the same plant, although generally, as in *Sphaerocarpus* and *Geothallus*, they are borne on separate plants.

In *Sphaerocarpus* the sex organs are closely crowded on the dorsal surface of the thallus. The male plants, often purplish, are minute and much smaller than the female plants (Fig. 141). The antheridial involucres are flask-shaped and each contains an ovoid short-stalked antheridium. In development, two transverse walls appear in the outer cell arising from a transverse division of the papillate initial (Fig. 142*A*, *B*). In the upper two segments vertical walls are formed at right angles to each other and then periclinal walls cut off a layer of outer sterile cells from a central group of spermatogenous cells (Fig. 142*C E*). Further development takes place as in the Marchantiales. The archegonial involucres, each enclosing an archegonium, are tubular or nearly spherical. The archegonium develops as in the Marchantiales (Fig. 143). It has two to four neck canal cells, its neck showing six cells in cross section. Following fertilization, the calyptra becomes two-layered. It is soon ruptured by the sporophyte.

In *Geothallus* the sex organs are borne and develop as in *Sphaerocarpus*, but are much less numerous and the male plants are only slightly smaller than the female. In *Riella* the antheridia occur in a series along the margin of the wing, each enclosed in a pocket. The archegonia are arranged serially on the axis, each surrounded by a flask-shaped involucre.

Sporophyte. The sporophyte of the Sphaerocarpales is more advanced than that of *Riccia* but simpler than that of nearly all the other Marchantiales. It has a foot, capsule, and very short seta (Fig. 144*A*). In

Sphaerocarpus the first division of the fertilized egg is transverse, the capsule arising from the outer segment and the foot and seta from the inner segment, as in the Marchantiales. Each segment again divides transversely at least once before vertical walls come in. The foot becomes bulbous and the capsule spherical. In all genera some of the sporogenous cells develop into spore mother cells and others into small

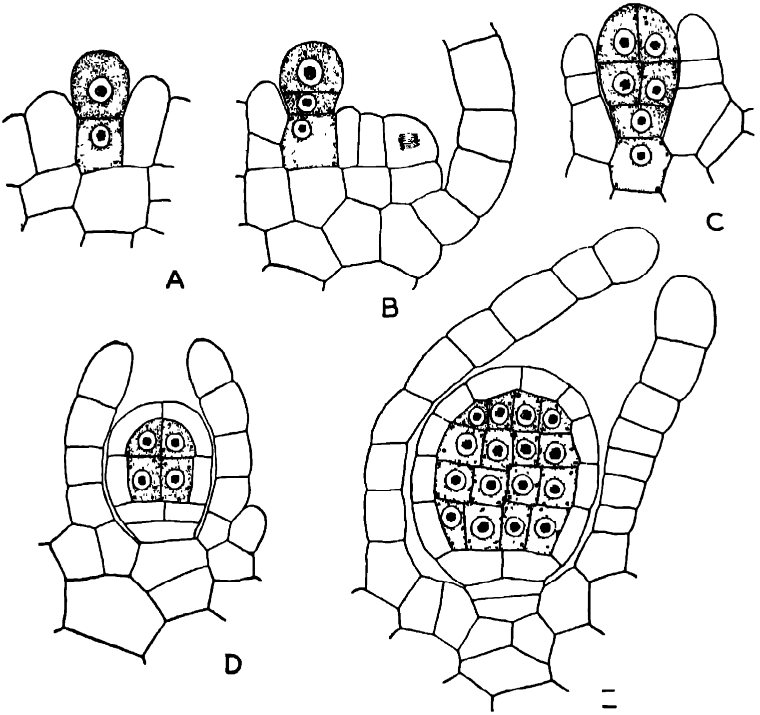

FIG 142. Early stages in the development of the antheridium of *Sphaerocarpus texanus*, ×500. *A*, division of initial into inner and outer cell; *B*, first division of outer cell; *C*, formation of vertical walls; *D*, formation of periclinal walls; *E*, later stage, showing sterile jacket surrounding spermatogenous cells, with stalk below.

sterile cells that do not become elaters (Fig. 144*B*). Instead, they function as nutritive cells, being finally absorbed by the spores. As in the Marchantiales, the spore mother cells are not lobed. The capsule has no regular dehiscence. Its wall consists of a single layer of cells without local thickenings.

Sex Determination. The mechanism of sex determination in *Sphaerocarpus* is of particular interest because here the occurrence of sex chromosomes in plants was first observed. In addition to seven ordinary chromosomes, the cells of the female gametophyte have a very large X chromosome, while those of the male gametophyte have a very small

Y chromosome. Consequently all the eggs carry an X chromosome, all the sperms a Y chromosome, and the zygote is always XY. This develops into a sporophyte with eight pairs of chromosomes, seven ordinary pairs and the XY pair. When meiosis occurs at sporogenesis, two of the spores in each tetrad have an X chromosome and two have a Y chromosome. The spores with an X chromosome always develop into female gametophytes and those with a Y chromosome into male plants.

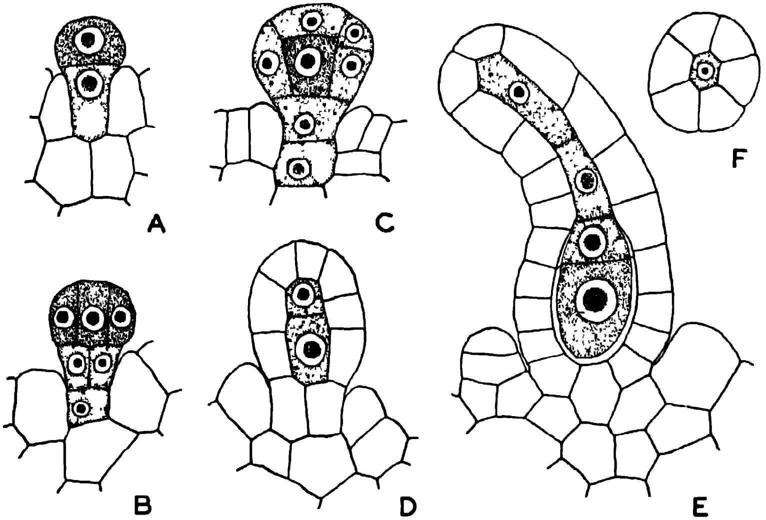

Fig. 143. Development of the archegonium of *Sphaerocarpus texanus*, ×500 *A*, division of initial into inner and outer cell; *B*, appearance of three vertical walls in the outer cell; *C*, formation of cover cell and central cell; *D*, formation of primary neck canal cell and primary ventral cell; *E*, nearly mature archegonium with egg, ventral canal cell, and two neck canal cells; *F*, cross section of neck.

Summary. The Sphaerocarpales are an aberrant group of liverworts showing a distinct relationship to the Marchantiales on the one hand and to the Jungermanniales on the other. They resemble the Jungermanniales in the form and structure of the gametophyte, but are like the Marchantiales in the structure and development of the sex organs and in the structure of the sporophyte. As in the Marchantiales, the apical cell is cuneate, the neck of the archegonium has six cells in cross section, and the spore mother cells are not four-lobed. The development of the antheridium shows a closer resemblance to the Marchantiales than to the Jungermanniales. The sporophyte consists essentially of a foot and capsule, the latter indehiscent and with a wall composed of a single layer of cells. In addition to the spores, the capsule contains sterile nutritive cells but no elaters. The most distinctive feature of the Sphaerocarpales is the presence of a special involucre around each antheridium and each archegonium. On the whole, they are a primitive group, with a simple gametophyte and a sporophyte only slightly more advanced than that of *Riccia*.

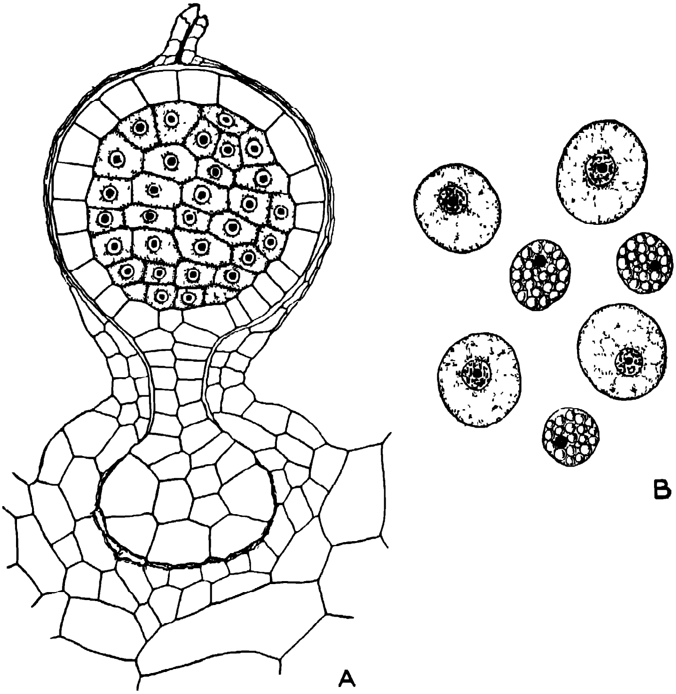

FIG. 144. Sporophyte of *Sphaerocarpus texanus*, ×250. *A*, early stage, showing foot, seta, and capsule with sporogenous tissue; *B*, spore mother cells and smaller, starch-filled nutritive cells.

3. Jungermanniales

The Jungermanniales are by far the largest order of Hepaticae, embracing 150 genera and approximately 5,500 species. They are most abundant in tropical regions, where they grow on the ground, on decaying logs, and as epiphytes on the stems and leaves of trees. They require abundant moisture and good drainage. Although much less numerous than in the tropics, the group is well represented in temperate regions also. The Jungermanniales comprise two great series, the Anacrogynae and the Acrogynae. These will be considered separately.

1. ANACROGYNAE

In the "anacrogynous" Jungermanniales all the archegonia originate behind the apical cell, none ever arising from the apical cell itself (Fig. 145*A*). Thus the archegonia and sporophytes are always dorsal. Most of the Anacrogynae are thallose, but some are leafy. They include 20 genera and about 500 species. The principal genera, all widely distributed, are *Riccardia, Metzgeria, Pallavicinia, Symphyogyna, Pellia,* and *Fossombronia.* The largest genus, *Riccardia,* has over 100 species.

Gametophyte. The Anacrogynae have a dorsiventral gametophyte that is thalloid in most forms but more or less leafy in others (Fig. 146). While tending toward a diversity of form, the gametophyte has remained structurally simple, displaying little or no internal differentiation. In fact, it is composed of compact, almost uniform tissue. The gametophyte is sometimes unbranched, but generally branches dichotomously or, in some forms, by means of ventral adventitious shoots. Growth takes place through the activity of an apical cell that is prevailingly *dolabrate* (hatchet-shaped), cutting off segments on two sides, alternately left and right (Fig. 145). Rhizoids, usually formed in abundance, are all of the smooth-walled type. Ventral scales are rarely present.

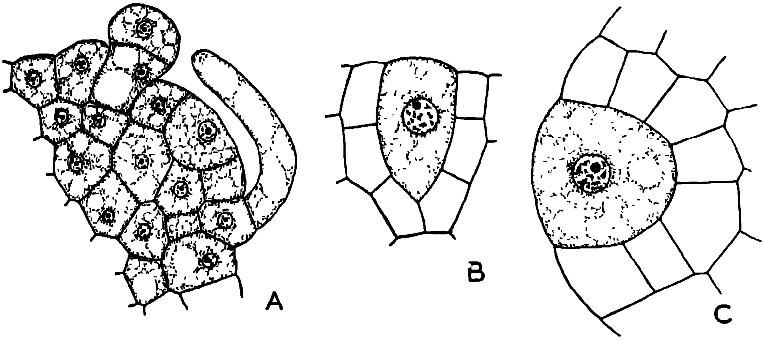

FIG. 145. *Fossombronia cristula.* *A*, longitudinal section through apical region of thallus, showing the apical cell, a young archegonium, and a mucilage hair, ×500, *B*, horizontal longitudinal section of apical cell, ×600; *C*, vertical longitudinal section of apical cell, ×600. (*After Haupt.*)

The gametophyte of *Pellia* is one of the simplest in the Bryophyta. It consists of a thin, flat thallus, wavy along the margin, and with a broad indistinct midrib gradually passing into lateral wings composed of a single layer of cells (Fig. 146*A*). Some of the species of *Riccardia* have a similar thallus, while others have one like that of *Metzgeria,* with a narrow distinct midrib sharply marked off from the wings. A distinct midrib is also present in *Pallavicinia* and *Symphyogyna,* but in both of these genera some species have an entire or wavy margin, others a margin that is deeply lobed (Fig. 146*B*, *C*). *Fossombronia* represents an advanced condition, the wings of the thallus being dissected into two lateral rows of leaf-like segments, the midrib forming a stem. This series leads directly into the Acrogynae, where differentiation of the plant body into a leafy axis reaches its highest expression.

Vegetative propagation in the Anacrogynae occurs by death of the older parts of the thallus, resulting in the isolation of branches. Also, gemmae are produced in certain genera, such as *Riccardia* and *Metzgeria*, while others produce tubers that live over from one growing season to the next.

Sex Organs. The antheridia and archegonia are borne either on the same gametophyte or on separate gametophytes, according to the species. They are always dorsal in position, generally occurring singly or in groups on the main thallus or, less frequently, on special short branches that in *Riccardia* are lateral and in *Metzgeria* are ventral in origin. The sex organs, unlike those of the Marchantiales, are never borne on stalked receptacles. The archegonia are usually protected by an involucre. The antheridia are protected in various ways: in *Metzgeria*, by incurving of the thallus; in *Riccardia* and *Pellia*, by upgrowth of adjacent tissues; in *Pallavicinia* and *Symphyogyna*, by a special involucre.

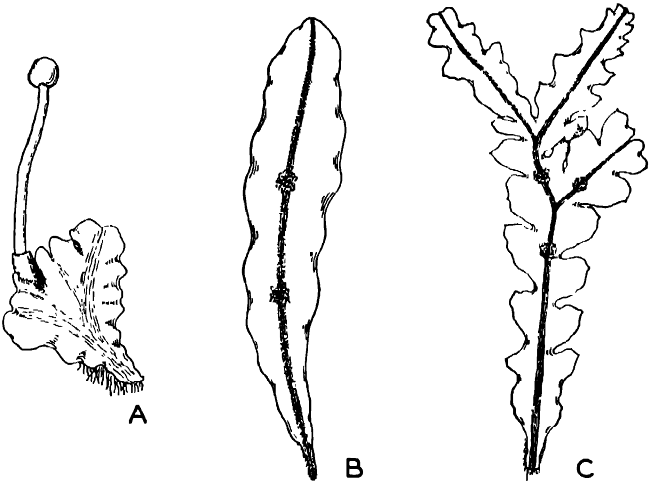

FIG. 146. Thallus of *Pellia epiphylla* (*A*) with a mature sporophyte, of *Pallavicinia lyellii* (*B*) with two groups of archegonia, and of *Symphyogyna brongniartii* (*C*) with three groups of archegonia, twice natural size.

In the Jungermanniales the development of the antheridium is characteristic, differing considerably from that seen in the Marchantiales and Sphaerocarpales. The antheridium arises as a papillate initial that undergoes a transverse division (Fig. 147*A*). Another transverse wall usually appears in the outer cell, but the third wall is a median vertical one (Fig. 147*B*, *C*). In each of the two terminal segments thus formed a periclinal division takes place. Two additional periclinal walls then come in at right angles to the first ones, intersecting both these and the median wall. As a result, four primary wall cells are cut off from two central spermatogenous cells (Fig. 147*D*, *E*). Further development of the antheridium corresponds to that of the Marchantiales. The mature antheridium is generally spherical and either long-stalked or short-stalked.

In all the Anacrogynae, as previously stated, the formation of archegonia never involves the apical cell, all of them arising from its segments (Fig. 145*A*). The development of the archegonium is essentially like that of the Marchantiales and Sphaerocarpales, but the venter is usually more slender and the neck shows but five cells in cross section (Fig. 148). The number of neck canal cells is variable, but is commonly 6 or 8. In such forms as *Pallavicinia* and *Pellia*, however, this number may reach 18. The calyptra, developed from the venter of the archegonium, may become massive, as in *Riccardia*, *Metzgeria*, and *Symphyogyna*. In addition to the involucre, a pseudoperianth is formed in *Pallavicinia*, becoming conspicuous after fertilization.

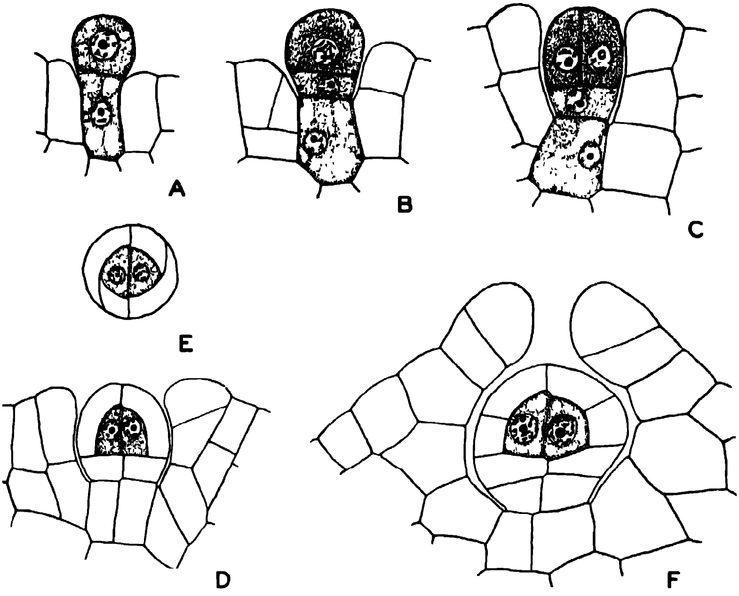

FIG. 147. Early stages in the development of the antheridium of *Pellia epiphylla*, ×400. *A*, division of initial into an inner and outer cell, *B*, division of outer cell into a stalk cell and primary antheridial cell, *C*, vertical division of antheridial cell; *D*, appearance of periclinal walls; *E*, cross section of same; *F*, later stage, showing two primary spermatogenous cells surrounded by sterile jacket, with stalk below.

Sporophyte. The sporophyte of the Jungermanniales is more advanced than that of the Marchantiales and Sphaerocarpales in that a greater amount of sterile tissue is formed. Following the first division of the fertilized egg, which is transverse, the lower cell often does not contribute to the embryo proper, but forms an appendage to it. This may become haustorial, as in *Riccardia*. The upper cell undergoes several transverse divisions before vertical walls appear, so that the embryo becomes elongated (Fig. 149*A–C*). A foot, seta, and capsule, always present, are differentiated early. The formation of periclinal walls in the upper part of the embryo delimits the amphithecium from the endothecium, the former giving rise to the capsule wall, the latter to the sporogenous tissue (Fig. 149*D*).

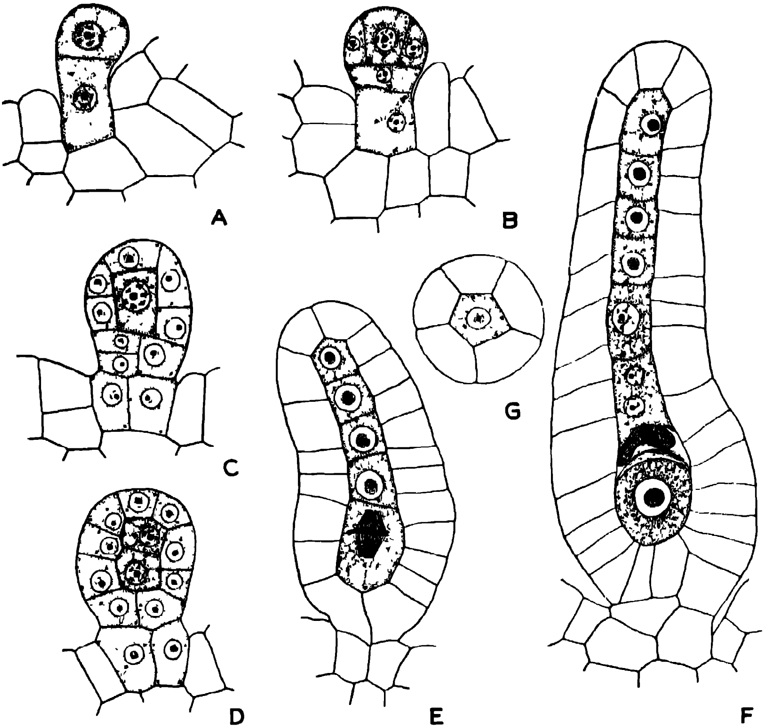

FIG. 148. Development of the archegonium of *Pellia epiphylla*, ×400. *A*, division of initial; *B*, appearance of vertical walls in outer cell; *C*, formation of cover cell and central cell; *D*, formation of primary neck canal cell and primary ventral cell; *E*, formation of four neck canal cells and division of primary ventral cell; *F*, nearly mature archegonium with egg, ventral canal cell, and six neck canal cells; *G*, cross section of neck

The seta undergoes considerable elongation, especially upon the ripening of the spores. The capsule is highly developed, producing both spores and elaters. It may be spherical, as in *Pellia*, or more or less elongated, as in *Pallavicinia*. In some genera an elaterophore is developed inside the capsule. It may be either apical, as in *Riccardia* and *Metzgeria*, or basal, as in *Pellia* (Fig. 150). The elaterophore consists of a group of sterile cells to which some of the elaters are attached. The fixed elaters generally are shorter than the free elaters and often have a greater number of spiral bands. The spore mother cells, unlike those of the Marchan-

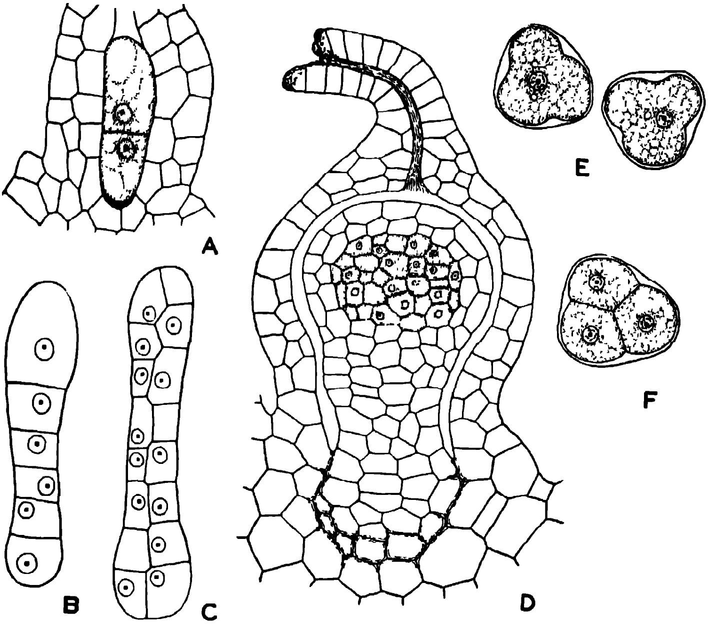

FIG. 149. Development of the embryo of *Fossombronia cristula*. *A*, two-celled embryo within calyptra, ×350; *B* and *C*, later stages, ×350; *D*, older embryo within calyptra, showing the foot, seta, and capsule with sporogenous tissue differentiated, ×250; *E*, two spore mother cells, ×500, *F*, a spore tetrad, ×500 (*After Haupt.*)

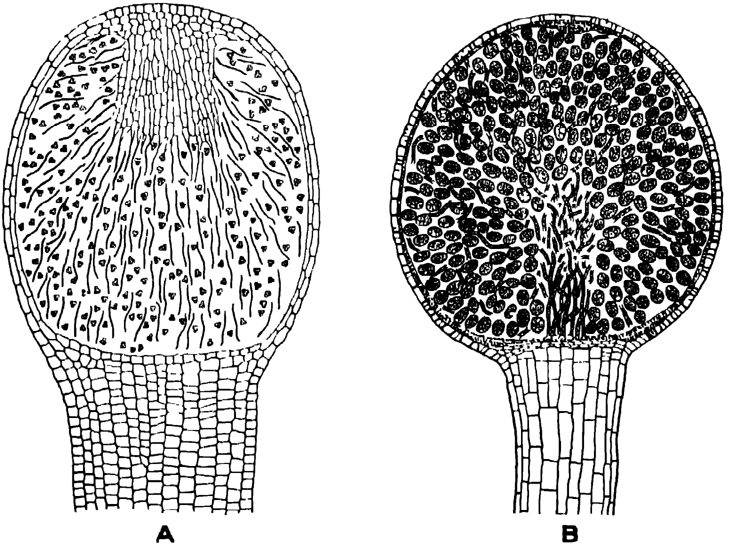

FIG. 150. Longitudinal section of the capsule of *Riccardia* (*A*), with apical elaterophore, and of *Pellia* (*B*), with basal elaterophore; *A*, ×40; *B*, ×28.

tiales and Sphaerocarpales, become four-lobed just previous to the formation of tetrads (Fig. 149*E*, *F*). The capsule wall is two or more layers of cells in thickness, or only one layer by resorption of the inner layer at maturity. Annular thickenings are generally present on one or both layers, but are constantly absent in a relatively few forms, such as *Pallavicinia* and *Symphyogyna*. Dehiscence of the capsule is nearly always effected by splitting into four valves.

2. ACROGYNAE

In the "acrogynous" Jungermanniales archegonia may arise from segments of the apical cell, but sooner or later the apical cell itself becomes an archegonium. The terminal position of the archegonia and sporophytes is in marked contrast to their dorsal position in the Anacrogynae. Practically all members of the group are leafy. The Acrogynae are a well-defined assemblage, comprising 130 genera and about 5,000 species. Notwithstanding its size, the group is fairly uniform in regard to general morphological features. Some of the largest genera are *Nardia*, *Plagiochila*, *Lophocolea*, *Radula*, *Porella*, *Frullania*, *Cephalozia*, *Scapania*, and *Lejeunia*.

Gametophyte. The gametophyte of the Acrogynae is a dorsiventral, branching, leafy axis. Only a few genera are thalloid and even these produce leafy fertile shoots. *Herberta* and a few other genera have an erect stem bearing three rows of similar, radially arranged leaves. The other Acrogynae have a prostrate stem bearing two rows of dorsal leaves and generally a row of ventral leaves (Fig. 151*A*, *B*). The ventral leaves, which are reduced, are known as *amphigastria*. In a number of genera amphigastria are not present. The dorsal leaves overlap and are generally bilobed, the lobes being unequal in size or, in a few cases (*e.g.*, *Lophocolea*), equal. The leaves nearly always consist of a single plate of cells and, with rare exceptions, are without a midrib. The stems are composed of essentially uniform tissue. Rhizoids are usually abundant on the lower side of the stem. They are chiefly anchoring in function, as much water absorption takes place directly through the leaves.

In practically all the Acrogynae the gametophyte grows by means of a *tetrahedral* apical cell (Fig. 151*C*). This has the form of a triangular pyramid, cutting off segments on three sides. The two rows of dorsal segments give rise, in part, to the dorsal leaves and the single row of ventral segments, in part, to the amphigastria. Branching in the Acrogynae is varied but most commonly is *monopodial*, with a main axis and lateral branches. Vegetative propagation is well developed. Often branches break off and give rise to new plants. One-celled or two-celled gemmae are frequently borne on the margins or at the apices of leaves, while multicellular discoid gemmae are produced in some forms.

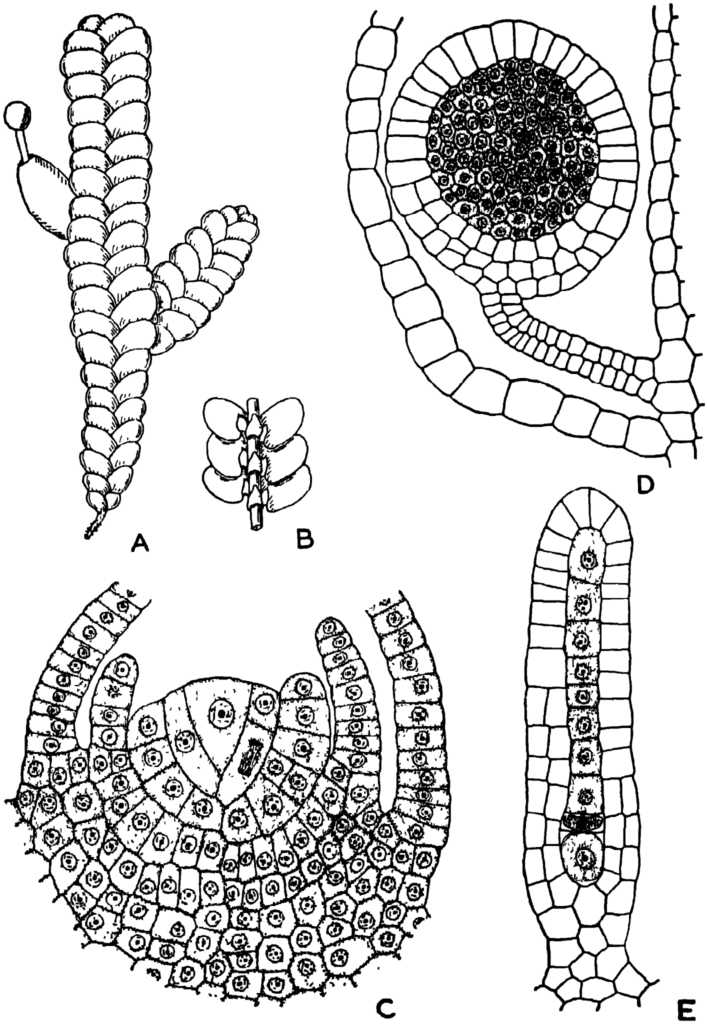

FIG. 151. *Porella bolanderi*. *A*, dorsal view of gametophyte with nearly mature sporophyte, ×30; *B*, ventral view of same, showing row of reduced ventral leaves and dorsal leaves with small ventral lobes; *C*, horizontal longitudinal section of tip of gametophyte, showing apical cell and developing leaves, ×400; *D*, longitudinal section of antheridium, ×250; *E*, longitudinal section of nearly mature archegonium, showing egg, ventral canal cell, and eight neck canal cells, ×400.

Sex Organs. The antheridia and archegonia may occur on the same plant or on separate plants, depending on the species. They are never sunken in the tissues of the gametophyte. The antheridia arise in the leaf axils, very commonly in groups of two to four; but sometimes they are solitary, as in *Porella*, or in groups of more than four. Often the antheridia are accompanied by paraphyses. In *Lophozia*, *Nardia*, and other simple forms the antheridia are borne on unmodified shoots, but in *Porella* and most members of the group they occur on special, short, lateral branches. The antheridia are globular and mostly long-stalked, developing as in the Anacrogynae except that the wall usually becomes several layers of cells in thickness (Fig. 151*D*).

The archegonia are generally borne on short lateral branches and are always terminal. They occur singly or in a small group. They are commonly intermixed with paraphyses, usually surrounded by a perianth and often also by an involucre lying outside the perianth. Both of these envelopes are formed of united leaves. The archegonia develop as in the Anacrogynae. In *Porella* six to eight neck canal cells are formed (Fig. 151*E*).

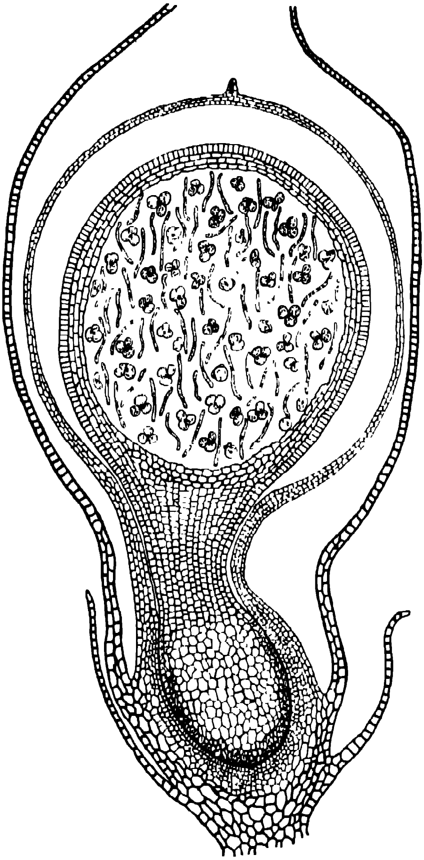

FIG. 152. Longitudinal section of sporophyte of *Porella*, showing capsule with spore mother cells and young elaters, ×40.

Sporophyte. The sporophyte of the acrogynous Jungermanniales is similar to that of the anacrogynous forms in that the seta is considerably elongated and relatively little of the embryonic tissue becomes sporogenous (Fig. 152). The embryogeny is known only in a few species. The lower cell arising from the first transverse division of the fertilized egg may become an appendage to the foot in some forms but not in others. Elaters are always present, but there is no claterophore, except in *Gottschea,* which has a basal one. The spore mother cells are conspicuously four-lobed. The capsule wall is usually two layers thick, sometimes more, the inner layer generally having spiral thickenings. Dehiscence occurs by means of four valves, as in the Anacrogynae.

Summary. In contrast to the Marchantiales, the Jungermanniales have a gametophyte that, while remaining simple in structure, is more or less differentiated in form. In the lower members the gametophyte is a simple thallus, becoming in the higher members a leafy stem. The apical cell is dolabrate in most of the Anacrogynae, tetrahedral in the Acrogynae. In the Anacrogynae the sex organs are nearly always borne singly or in groups on the dorsal surface of the gametophyte, sometimes on special branches, but never on stalked receptacles. In the Acrogynae the antheridia are axillary, the archegonia terminal. The early development of the antheridium is characteristic, the formation of two transverse walls in the initial cell being followed by a median vertical wall in the terminal segment. The neck of the archegonium shows five cells in cross section.

The sporophyte always consists of a foot, seta, and capsule. There is much sterilization of potentially sporogenous tissue, the development of the seta being especially marked. The capsule, varying in form from spherical to cylindrical, produces both spores and elaters. It nearly always dehisces by means of four valves. The capsule wall consists of two or more layers of cells The spore mother cells are deeply four-lobed. In the Jungermanniales a relatively simple gametophyte is combined with a complex sporophyte.

4. Anthocerotales

The Anthocerotales constitute an isolated order of 4 genera and over 100 species. They are so distinct that they are often set apart from the other liverworts as a distinct class of bryophytes. *Anthoceros,* with 60 species, and *Notothylas* are widely distributed in both temperate and tropical regions, while *Megaceros* and *Dendroceros* are chiefly confined to the tropics. *Dendroceros* is epiphytic on tree trunks, stems, and leaves, while the other members grow mainly on damp earth.

Gametophyte. The gametophyte of the Anthocerotales is a dorsiventral plate-like thallus often growing in an irregularly dichotomous manner (Fig. 153). It is frequently more or less lobed, but does not have any leaves. In *Dendroceros* the thallus is narrow, consisting of a thickened midrib and lateral wings composed of a single layer of cells. In the other genera the thallus is several layers of cells thick and without a midrib. There is no internal differentiation of tissues. The cells are peculiar in having, as a rule, a single large chloroplast with a conspicuous pyrenoid, a feature of most green algae but not of any other bryophyte. In some members of the group two or more chloroplasts are present.

The thallus grows by means of a cuneate (wedge-shaped) apical cell, as in the Marchantiales. There are no air chambers or air pores, but some species of *Anthoceros* and *Dendroceros* have intercellular mucilage cavities that open by clefts to the ventral surface, and in these cavities colonies of *Nostoc* may live. Smooth rhizoids are present, but there are no ventral scales. In some species of *Anthoceros* vegetative propagation is accomplished by the isolation of branches, in other species (*e.g.*, *Anthoceros hallii*) by the formation of small tubers that rest in the soil until the next growing season.

Sex Organs. In most of the Anthocerotales the antheridia and archegonia are borne on the same plant but in separate groups, the antheridia appearing first. Both kinds of sex organs are embedded in the dorsal surface of the thallus and develop endogenously.

The antheridium initial is a superficial cell arising close to the growing apex. It does not become papillate, as in the other Hepaticae, but divides transversely, the inner cell giving rise to the antheridium. Between the two cells a mucilage-filled cleft appears that later becomes the antheridial chamber, the roof of which is formed by the derivatives of the outer cell. In the inner cell two vertical walls at right angles to each other now appear, followed by two transverse walls (Fig. 154*A*). As a result, three tiers are formed with four cells in each tier. The stalk is derived from the lowest tier. Periclinal walls in the two upper tiers separate the outer sterile jacket from the inner spermatogenous cells (Fig. 154*B*, *C*). Further development follows the usual liverwort pattern.

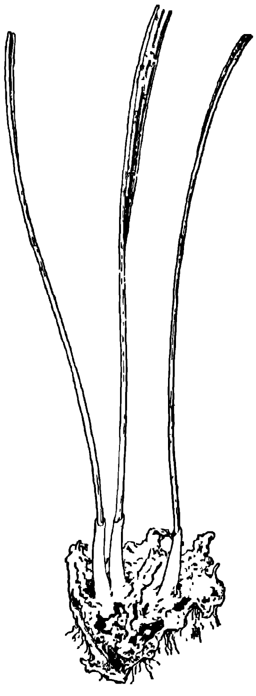

FIG. 153. *Anthoceros fusiformis*, with three sporophytes arising from the gametophyte, ×3.

The mature antheridia are spherical or nearly so, generally long-stalked, and often bright orange-yellow. When the sperms are ripe, the roof of the antheridial chamber bursts. In *Notothylas* and most species of *Anthoceros* two or four antheridia develop in the same chamber, all coming from the inner segment of the same initial cell. This divides by a vertical wall, or by two vertical walls at right angles to each other, each segment giving rise to an antheridium. Frequently additional antheridia are budded off from the base of the others.

The archegonium initial is a superficial cell that, like the antheridium initial, does not become papillate. The usual three vertical walls appear, cutting off the wall cells from the primary axial cell. The latter divides transversely (Fig. 154*D*), while a second transverse division occurs in the outer cell, resulting in a row of three cells (Fig. 154*E*). These are the

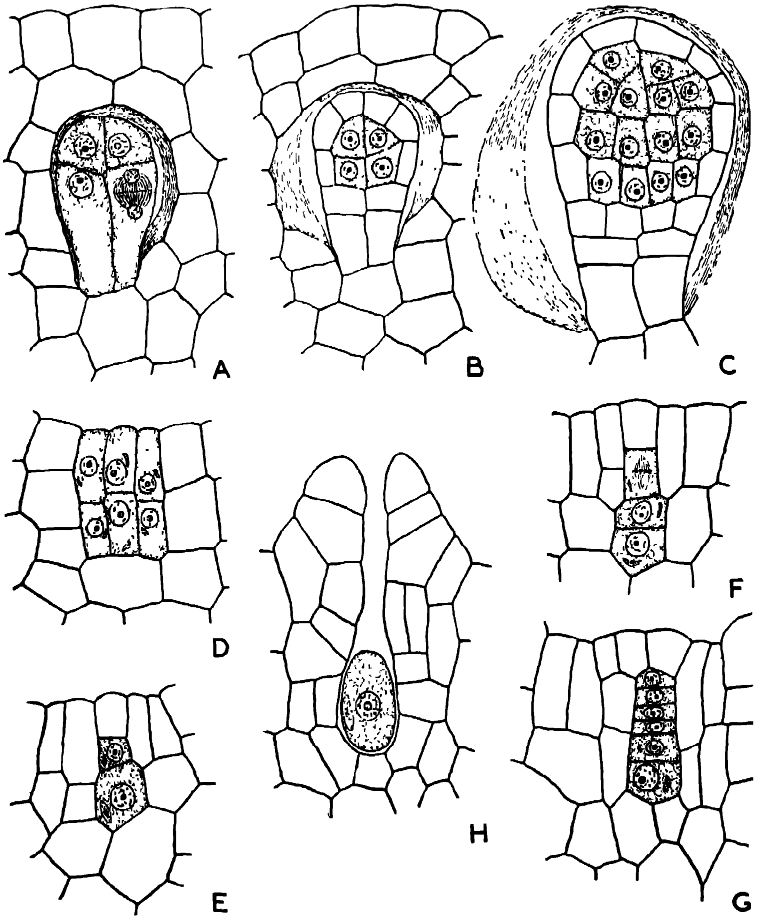

FIG. 154. Sex organs of *Anthoceros*, ×500. *A*, *B*, *C*, stages in development of the antheridium; *D*, young archegonium showing transverse division of axial cell; *E*, formation of cover cell, primary neck canal cell, and primary ventral cell; *F*, division of primary neck canal cell and formation of ventral canal cell and egg; *G*, later stage with four neck canal cells; *H*, mature archegonium with egg ready for fertilization. (*A* to *C*, *Anthoceros pulcherrimus*; *D* to *H*, *Anthoceros fusiformis*.)

cover cell, primary neck canal cell, and primary ventral cell. The cover cell later divides by one or two vertical walls; the primary neck canal cell gives rise to four or sometimes six neck canal cells; and the primary ventral cell produces the ventral canal cell and the egg (Fig. 154*F*, *G*). Just previous to fertilization the cover cells and canal cells break down, leaving the egg in a cavity below the surface of the thallus (Fig. 154*H*). ✓

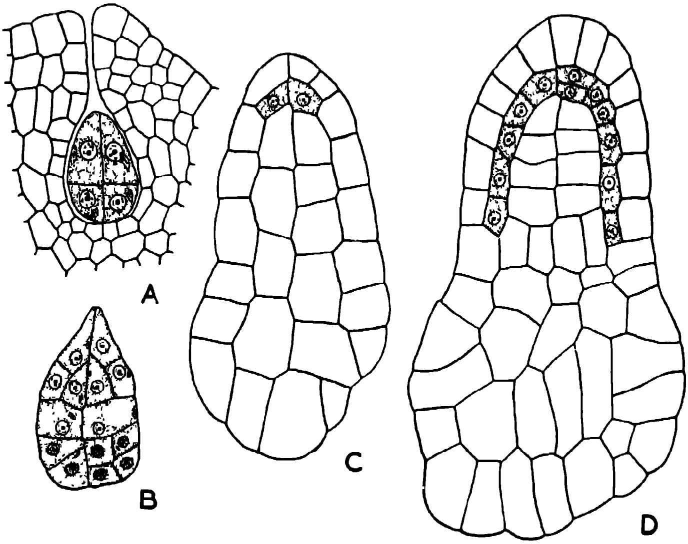

FIG. 155. Embryos of Anthocerotales, ×300. *A*, young embryo of *Anthoceros fusiformis; B*, slightly older embryo of *Anthoceros punctatus*, showing differentiation of amphithecium and endothecium; *C*, embryo of *Megaceros*, showing two sporogenous cells cut off from amphithecium, *D*, later stage, showing further development of sporogenous tissue.

Sporophyte. In *Anthoceros* the first division of the fertilized egg is vertical, the second transverse, and the third vertical at right angles to the plane of the first division (Fig. 155*A*). A fourth division occurs transversely in the upper part of the embryo, resulting in three tiers of four cells each. The upper tier produces the capsular region, the middle tier an intermediate zone, while the lower tier forms the foot. In the development of the capsular region, which occurs very early, the amphithecium is cut off from the endothecium by periclinal walls (Fig. 155*B*). The latter forms the *columella*, an axis of sterile tissue. The amphithecium soon becomes two-layered, the inner layer giving rise to the sporogenous tissue and the outer layer to the sterile wall (Fig. 155*C*, *D*). The derivation of the sporogenous tissue from the amphithecium rather than from the endothecium is very characteristic and stands in marked contrast to the condition in the other Hepaticae. In some species of *Notothylas*, however, the endothecium does not produce a sterile columella but, instead, gives rise to the sporogenous tissue.

The foot becomes bulbous and in many species penetrates the thallus by means of rhizoid-like papillae (Fig. 156). The intermediate zone is meristematic. It contributes somewhat to the development of the foot, but is chiefly concerned with the elongation of the capsular region. There is no seta. *Notothylas* has a short capsular region, the other genera a long one. The young sporophyte is protected by the surrounding tissue of the thallus, which grows upward with it to form a massive involucre. This is later ruptured by the elongation of the sporophyte, forming a basal sheath. ✓ 6·11·71

The columella consists of elongated cells. It may be regarded as representing the beginning of a conducting system. In *Anthoceros* the columella shows about 16 cells in cross section. In the young sporophyte the sporogenous tissue caps the columella in a dome-like manner. It soon becomes two-layered above and then gives rise to spore mother cells. Meanwhile new sporogenous tissue continues to be differentiated in the meristematic region lying just above the foot (Fig. 156*B*). Although, in *Anthoceros*, the sporogenous tissue generally becomes two-layered, it may remain one-layered, as in *Anthoceros hawaiiensis*, or may become three or four layers thick, as in *Anthoceros hallii* and *Megaceros*. In *Notothylas* the amount of sporogenous tissue is greatly increased; in some species a definite columella is not formed and the sporogenous tissue arises from both the amphithecium and endothecium, or from the endothecium alone.

The wall of the capsule becomes four to eight layers of cells thick. In *Anthoceros*, but not in the other genera, the outer layer, constituting the epidermis, develops stomata. These are not like the air pores seen in the gametophyte of the Marchantiales, but resemble the stomata of the higher plants. The wall layers beneath the epidermis develop chloroplasts and intercellular spaces, thus becoming a photosynthetic region.

The intermediate zone elongates constantly, adding to the capsular region from below. Thus spores continue to be produced over a long period. It is noteworthy that the Anthocerotales are the only bryophytes whose sporophyte displays indeterminate growth. Some of the sporogenous cells become sterile, small groups of these alternating with groups of spores and so tending to break up the spore mass into separate units. As a rule, these sterile cells give rise to peculiar short elaters that are often branched. In *Anthoceros* the elaters, where present, are smooth-walled; in *Notothylas* they have short, curved, thickened bands on their walls; in *Megaceros* and *Dendroceros* the elaters have spiral thickenings like those of other liverworts. The capsule dehisces by splitting into two valves.

Summary. The Anthocerotales are of phylogenetic interest in that they may represent a stage of progress through which the higher plants have passed in the course of their evolution. As in the Jungermanniales, the gametophyte is simple and the sporophyte complex, but the complex-

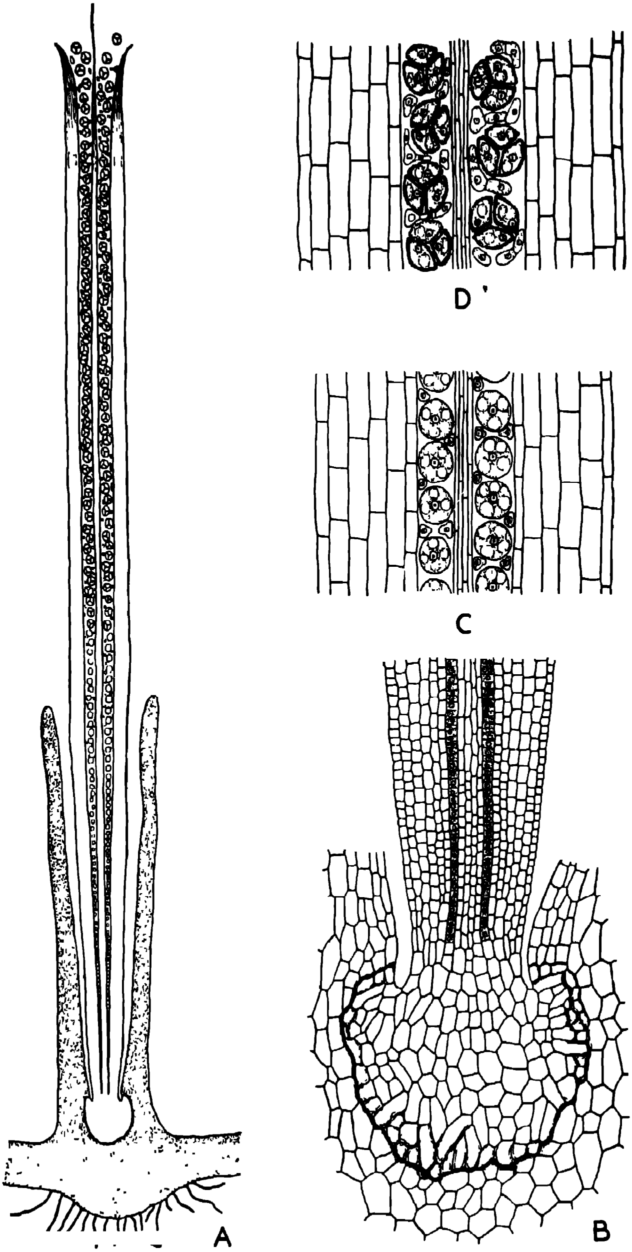

FIG. 156. Longitudinal sections of the sporophyte of *Anthoceros laevis*. *A*, entire sporophyte with foot embedded in the gametophyte, ×20, *B*, basal region, showing origin of sporogenous tissue, ×100; *C*, higher level, showing spore mother cells, ×100; *D*, level where spore tetrads are forming, ×100.

ity is of an entirely different kind. The gametophyte is a flat thallus without structural differentiation. It grows by means of a cuneate apical cell. The sex organs are endogenous. The antheridium is formed from the inner half of the initial cell and the sequence of early wall formation is distinctive. The archegonium represents a new departure in that the primary neck canal cell is cut off from the outer segment arising from a transverse division of the initial.

The sporophyte consists of a foot and a cylindrical capsule. It displays a great development of sterile tissue. The presence of green tissue, stomata, and rhizoid-like processes suggests that the sporophyte is becoming independent. The breaking up of the sporogenous tissue into smaller units may represent an initial stage in the formation of sporangia. The establishment of a sterile axis by the transfer of sporogenous tissue from the endothecium to the amphithecium may represent the beginning of a conducting system. A meristematic region in the sporophyte results in its continued growth. Dehiscence of the capsule is accomplished by means of two valves.

2. MUSCI

The mosses constitute the larger and more highly developed class of bryophytes, numbering about 14,000 species. They are widely distributed and, although abundant in arctic and alpine regions, are represented in nearly all habitats except the ocean. The fossil history of the group is very fragmentary, there being few reliable evidences of its existence earlier than the Tertiary. The gametophyte is leafy and, in contrast to that of the liverworts, is typically radial rather than dorsiventral. The leaves generally have a midrib. The rhizoids are septate and usually branched. The Musci comprise three orders, the Sphagnales, Andreaeales, and Bryales.

1. Sphagnales

The Sphagnales, or bog mosses, are a group of about 350 species, all belonging to the genus *Sphagnum*. They are relatively large, pale mosses generally living in bogs at high altitudes and high latitudes. Because their accumulated remains form peat, they are often called peat mosses.

Gametophyte. Upon germination, the spore produces a short filament that, in turn, gives rise to a flat green thallus (Fig. 157*A*). This consists of a single layer of cells bearing numerous septate rhizoids. The thallus gives rise to an erect leafy branch and then disappears (Fig. 157*B*). The erect shoot develops rhizoids below and becomes the mature gametophyte. The rhizoids soon die but the shoot continues to grow from year to year (Fig. 158*A*). Branching in *Sphagnum* is very profuse, there being branches of limited growth crowded near the apex of the main stem and others occurring in tufts farther down. The stem grows by means of a tetrahedral apical cell, and from each of its three rows of segments a row of leaves arises, these being spirally arranged.

The leaves are composed of a single layer of cells and lack a midrib. They are peculiar in structure, some cells being enlarged, rhomboidal, and hyaline, while others are small, narrow, and green (Fig. 158*E*). The green cells form the meshes of a network enclosing the hyaline cells. The latter are dead cells filled with water; their walls bear large circular pores and usually spiral thickenings as well. The leaves have an extraordinary power of absorbing and retaining water. At first the leaf cells are uniform, but later from each a narrow cell is cut off on two sides, as represented by Fig. 158*B–D*.

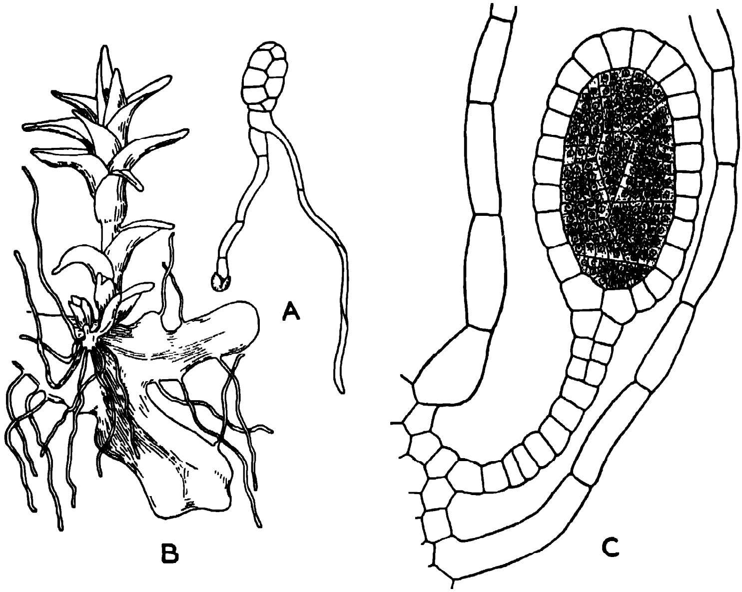

FIG. 157. *Sphagnum*. *A*, young gametophyte, showing filament arising from the spore, a rhizoid, and the thallus beginning to develop by an apical cell; *B*, mature thallus, with rhizoids, producing a leafy shoot; *C*, an antheridium arising between two leaves, ×250. (*A and B, after Schimper*.)

The stem of *Sphagnum* is differentiated into three regions: (1) a cortex of dead hyaline cells that absorb and store water; (2) a cylinder of small elongated cells with thick walls; and (3) a pith-like axis. Vegetative propagation occurs by branching and death of the older parts of the plant. This is the principal method of reproduction.

Sex Organs. Depending on the species, *Sphagnum* is either monoecious or dioecious. The antheridia appear on special, short, lateral branches that arise near the apex of the main shoot. They are solitary in the leaf axils, unaccompanied by paraphyses, and arise in acropetal succession. The initial is a superficial cell that undergoes several transverse divisions, resulting in a short filament. Then the terminal cell functions as a dolabrate apical cell (one with two cutting faces), the lower segments forming the stalk and the upper ones the rest of the antheridium. The spermatogenous tissue is differentiated from the jacket cells by the formation of periclinal walls. The mature antheridia are long-stalked and nearly spherical, opening irregularly to discharge their sperms (Fig. 157*C*).

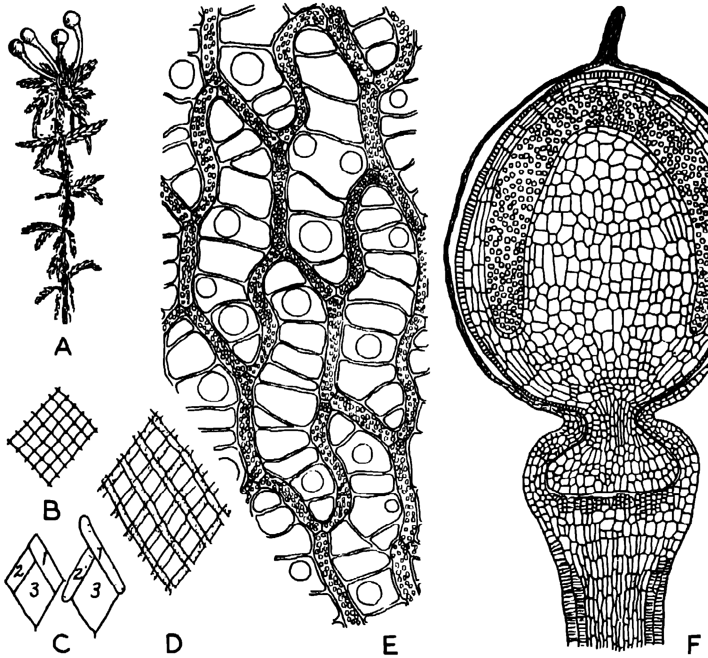

FIG 158. *Sphagnum*. *A*, leafy stem with terminal cluster of sporophytes, natural size, *B*, surface view of portion of very young leaf, ×260; *C*, diagram showing how the leaf cells divide, cutting off cells marked 1, and then cells marked 2; *D*, appearance of leaf after these cells have been cut off; *E*, surface view of portion of mature leaf, showing the narrow elongated cells with chloroplasts and the larger hyaline cells with pores and slender bands of thickening, ×300, *F*, longitudinal section of nearly mature sporophyte, showing the capsule, neck-like seta, and the foot, ×24 (*After Chamberlain.*)

The archegonia appear at the apex of short branches that, like the antheridial branches, arise at the upper end of the main shoot. They are borne in groups of one to five, without paraphyses, and are stalked and free. An archegonium arises directly from the apical cell, as in the acrogynous Jungermanniales, and then several others may arise from the last-formed segments of the apical cell. After a short filament has been produced by the formation of walls that may be either transverse or oblique, the usual three vertical walls appear in the terminal cell, cutting off three primary wall cells from the primary axial cell (Fig. 159*A*). The axial cell, by a transverse division, gives rise to the cover cell and central cell (Fig. 159*B*). The development of the axial row is similar to that of the Jungermanniales. The central cell divides to form the primary neck canal cell and primary ventral cell (Fig. 159*C*). The neck canal cells, numbering eight or nine, all arise directly from the primary neck canal cell, while the ventral canal cell and egg, approximately equal in size, are produced by a transverse division of the primary ventral cell (Fig. 159*D*–*F*). The mature archegonium has a long stalk, a massive venter, and a long twisted neck.

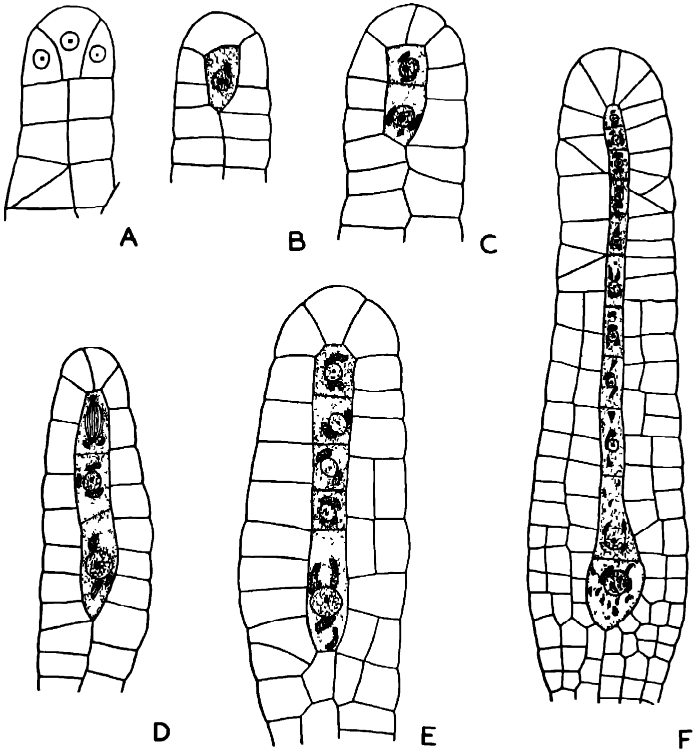

Fig. 159. Development of the archegonium of *Sphagnum subsecundum*. *A*, formation of primary axial cell, *B*, formation of cover cell and central cell; *C*, formation of primary neck canal cell and primary ventral cell, the cover cell divided vertically, *D*, archegonium with primary ventral cell and two neck canal cells; *E*, later stage with four neck canal cells; *F*, archegonium with egg, ventral canal cell, and nine neck canal cells; *A* to *E*, ×525; *F*, ×300. (*After Bryan.*)

Sporophyte. The fertilized egg of *Sphagnum* undergoes a series of transverse divisions that result in the formation of a short filament of six or seven cells (Fig. 160). Vertical walls then appear and the embryo becomes cylindrical. It next becomes differentiated into an upper fertile region (the capsule), a middle region (the neck), and a basal portion (the foot). As in *Anthoceros*, a columella is formed from the endothecium, the sporogenous tissue being cut off from the amphithecium and capping the columella like a dome. The sporogenous tissue becomes two to four layers of cells in thickness, while the outer portion of the amphithecium forms the capsule wall, eventually composed of five to seven layers of cells. This becomes a region of green tissue with intercellular spaces, the outer layer developing rudimentary stomata. The sporogenous tissue is surrounded by a definite nutritive layer, the *tapetum*. As in the other Musci, no elaters are formed, all the sporogenous cells becoming spore mother cells.

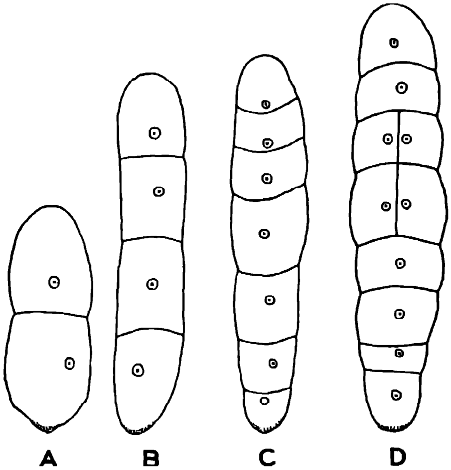

FIG. 160. Early stages in the development of the embryo of *Sphagnum subsecundum*, ×200. *A*, two-celled stage; *B*, four-celled stage, *C*, seven-celled stage; *D*, appearance of vertical walls. (*After Bryan.*)

The foot becomes large and bulbous, but the seta does not develop beyond the neck-like stage (Fig. 158*F*). The seta is replaced functionally by the *pseudopodium*, a leafless stalk developed from the stem of the gametophyte, in the tip of which the foot of the sporophyte is embedded. The pseudopodium elongates rapidly after the spores have ripened, carrying the capsule upward. When mature, the capsule is globular and dark brown or black. It dehisces by means of a lid or operculum, as in the Bryales. The spores are discharged with force. As in the Hepaticae, the sporophyte remains enclosed by the calyptra until the spores are ripe.

Summary. The Sphagnales are a synthetic group, combining characters found both in liverworts and mosses. A thallus like that of the anacrogynous Jungermanniales gives rise to an erect leafy shoot that becomes the mature gametophyte. This shows some internal differentiation, both in the leaves and stem. The antheridia are spherical and axillary, as in the acrogynous Jungermanniales, but in development resemble the Bryales. In position, origin, and development the archegonia show a resemblance to those of the acrogynous Jungermanniales, except that, when mature, the venter is massive, as in the Bryales. The general organization of the sporophyte is like that of the Anthocerotales, the sporogenous tissue being dome-shaped and derived from the amphithecium; but there is no meristematic region. The seta is replaced functionally by a pseudopodium. The capsule contains green tissue and rudimentary stomata. It dehisces by an operculum, as in the Bryales.

2. Andreaeales

This order comprises a single genus, *Andreaea*, of about 125 species. They are small, tufted, dark-colored mosses growing on rocks in dry situations, especially in cold regions. In warmer regions they are restricted to high mountains.

Gametophyte. In the germination of the spore, its protoplast produces inside the spore wall a mass of cells called the *primary tubercle*. After rupturing the wall, one or more of its superficial cells give rise to branching filaments. These correspond to the protonema of the Bryales. Some of the filaments turn brown and function as rhizoids, while others may give rise either to flat thalli or cylindrical masses. A leafy shoot is then organized (Fig. 161). It may arise from the flat thallus, from the cylinder, or directly from the protonema. The stem, which is prostrate, exhibits *sympodial* branching (like dichotomy, but with unequal branches). It produces many rhizoids. The stem is without a central strand, consisting of uniform, thick-walled cells. It grows by means of a tetrahedral apical cell. The leaves, formed in three rows, are generally without a midrib, being composed usually of thick-walled cells.

Sex Organs. *Andreaea* is generally monoecious, the antheridia and archegonia occurring in terminal groups on separate branches. The apical cell is involved in the formation of the sex organs. In development, the antheridium corresponds very closely to that of *Sphagnum* and similarly, when mature, is long-stalked and nearly globular. The archegonia develop as in the Bryales, the cover cell contributing to the row of neck canal cells.

Sporophyte. The first division of the fertilized egg is transverse, the inner segment forming the foot and the outer segment the rest of the sporophyte. A dolabrate apical cell is organized in the outer segment and about a dozen cells are formed before vertical walls come in. The sporogenous tissue is cut off from the endothecium as the outermost layer of cells and caps the columella as a dome. It eventually becomes two-layered. As in *Sphagnum*, a pseudopodium is formed, the seta remaining undeveloped. The calyptra encloses the sporophyte until it is nearly mature. The capsule is without an operculum, dehiscence taking place by means of four longitudinal slits, but these usually do not extend to the apex of the capsule (Fig. 161).

Summary. Like the Sphagnales, the Andreaeales are a synthetic group. The gametophyte begins either as a thallus, as in the Sphagnales, as a filamentous protonema, as in the Bryales, or as a cylindrical body. The antheridia are terminal, as in the Bryales, but are long-stalked and globular, as in the Sphagnales. The archegonia develop like those of the Bryales. The sporogenous tissue is derived from the endothecium, a feature of the Bryales, but caps the columella in a dome-like manner, a feature of *Sphagnum*. Similarly, as in *Sphagnum*, a pseudopodium is developed. The capsule dehisces by means of four valves, as in the Jungermanniales.

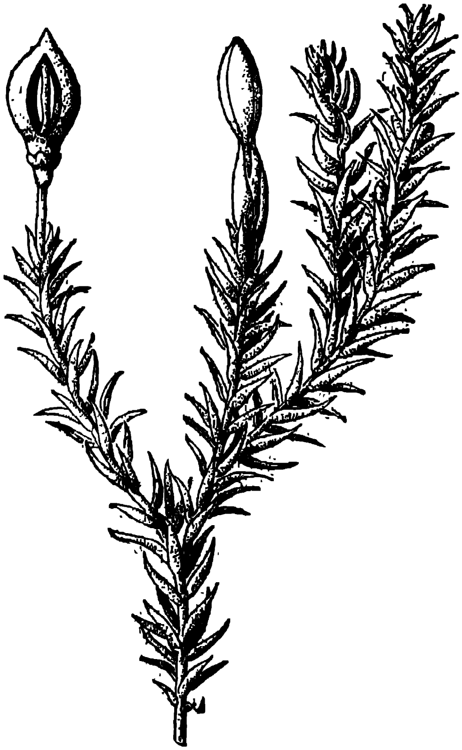

FIG. 161. Gametophyte of *Andreaea petrophila* with mature and immature sporophytes, ×3. (*From Gilbert M. Smith.*)

3. Bryales

The Bryales, or true mosses, are the culminating order of bryophytes. They constitute a highly specialized, as well as a very distinct group, displaying remarkable uniformity with respect to basic morphological features. The Bryales are by far the largest group of bryophytes, numbering about 13,500 species included in 80 families. Although world-wide in distribution, they are particularly abundant in moist northern regions. They grow on rocks, tree trunks, fallen logs, and on the ground, often forming extensive mats. Some grow in dry situations, while a few are aquatic. Some of the largest genera are *Fissidens*, *Leucobryum*, *Barbula*, *Tortula*, *Grimmia*, *Funaria*, *Bryum*, *Mnium*, *Bartramia*, *Hypnum*, *Polytrichum*, and *Pogonatum*.

Gametophyte. In nearly all the Bryales the spore produces a *protonema*—a green, branching, septate filament (Fig. 162). Some of the branches penetrate the soil, turn brown, and become rhizoids. The protonema, which is the morphological equivalent of the thallus of *Sphagnum*, gives rise to an erect leafy stem, the *gametophore*. This arises as a bud on the protonema and, in most genera, grows by means of a tetrahedral apical cell. After formation of the leafy shoot or, more commonly, of several or many leafy shoots, the protonema usually disappears; but it may persist, turn brown, and contribute to the mass of rhizoids that arise from the lower end of the stem. Branching of the stem, where it occurs, is nearly always monopodial (with a true main axis). Generally the leaves are spirally arranged and borne in three vertical rows (Fig. 163). Usually they consist of a single layer of cells, except for a slightly thickened midrib, which is nearly always present. The stems of such mosses as *Mnium* and *Polytrichum* contain a strand of elongated, often thick-walled cells, but the stem tissue of most mosses is uniformly thin-walled.

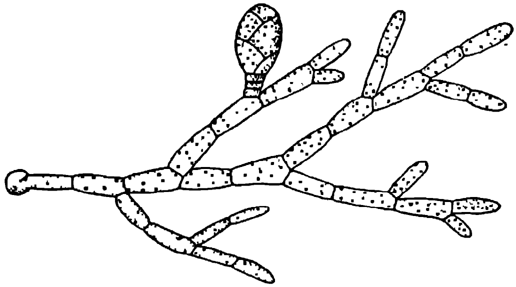

FIG. 162. Moss protonema arising from a spore and bearing a bud from which an erect leafy shoot will arise, ×100.

Vegetative propagation in the Bryales is highly developed and varied. It may occur by isolation of branches following death of the older parts of the plant, by small multicellular gemmae, by resting buds (bulbils) on the protonema, or by the formation of a protonema from almost any part of the plant.

Sex Organs. In many mosses sex organs are rarely produced, reproduction taking place chiefly by vegetative means. The sex organs occur in terminal groups (Fig. 163). In the "acrocarpous" forms they are borne at the apex of the main stem or its principal branches; in the "pleurocarpous" forms they occur at the apices of short lateral branches. The sex organs are usually surrounded by a sheath or rosette of modified leaves forming the *perichaetium*. According to the species, mosses may be

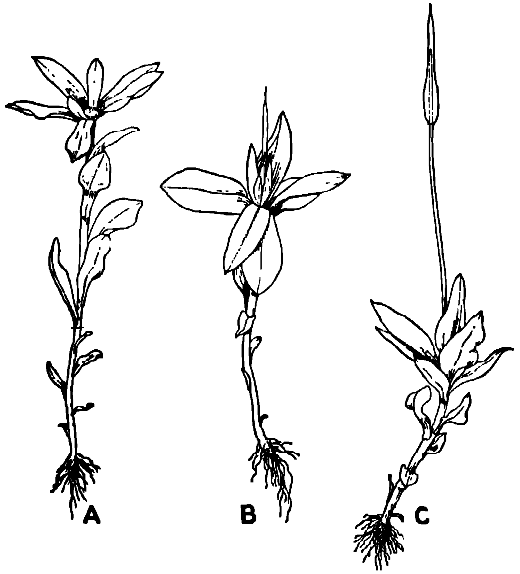

FIG. 163. Leafy shoots of *Funaria hygrometrica*, ×3. *A*, male plant with terminal cluster of antheridia; *B*, female plant with an archegonium in which an embryo sporophyte has started to develop; *C*, older stage, the sporophyte elongating and carrying the calyptra upward.

either monoecious or dioecious. If monoecious, the antheridia and archegonia usually occur in the same cluster. Multicellular paraphyses are commonly present. Both kinds of sex organs arise from segments of the apical cell, in many cases from the apical cell itself. The formation of sex organs limits growth of the vegetative axis.

The antheridium arises from a superficial cell that becomes papillate. Several transverse divisions may take place and then the terminal cell becomes a dolabrate apical cell (one with two cutting faces), cutting off a series of segments (Fig. 164*A*). Periclinal walls in the younger segments delimit the jacket cells from the primary spermatogenous cells (Fig. 164*B*, *C*). As additional divisions occur, the antheridium becomes club-shaped, with a stalk of variable length (Fig. 164*D*). A large number of sperm mother cells are formed, each giving rise to two sperms.

When mature, the antheridium ruptures at the apex, the sperms being discharged in a mass.

The archegonium also develops by means of a dolabrate apical cell, but only a comparatively few segments are cut off (Fig. 165*A*). In the terminal cell then appear the three characteristic walls that differentiate the primary wall cells from the primary axial cell (Fig. 165*B*). A transverse division of the axial cell results in the formation of the cover cell and central cell, the latter soon giving rise to the primary neck canal cell and primary ventral cell (Fig. 165*C*, *D*). Later development is characteristic in that the cover cell cuts off lateral segments that add to the neck cells and inner segments that contribute to the neck canal cells. Thus the upper neck canal cells are derived from the cover cell, the lower ones from the primary neck canal cell, while the ventral canal cell and egg, as usual, arise from the primary ventral cell (Fig. 165*E*–*H*). The mature archegonium has a long stalk, a massive venter, and many neck canal cells—sometimes up to 50 or 60.

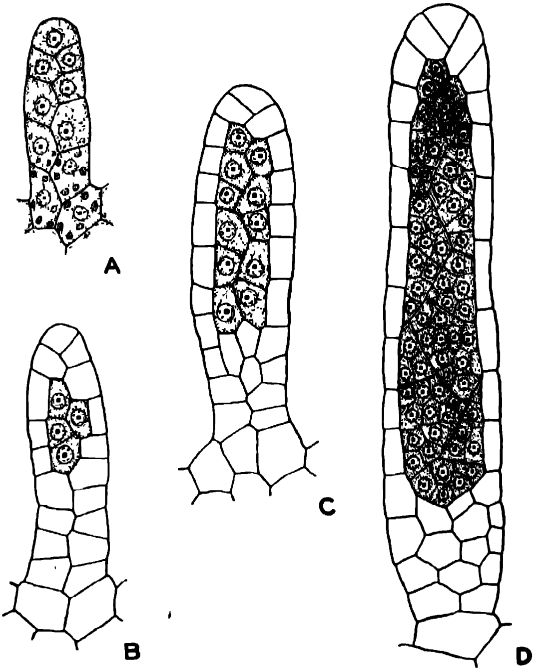

FIG. 164. Development of the antheridium of *Mnium affine*, ×400. *A*, young stage; *B*, beginning of differentiation of primary spermatogenous cells; *C*, slightly older stage; *D*, antheridium showing subdivision of spermatogenous tissue.

Sporophyte. In the Bryales the sporophyte reaches a high degree of specialization. During its early development a large calyptra is formed from the stalk and venter of the archegonium. This is soon ruptured and carried upward on the top of the sporophyte as a conspicuous hood, which may remain until the sporophyte is mature (Fig. 163*C*).

The first division of the fertilized egg is transverse or oblique. Each segment becomes an apical cell through the activity of which a slender elongated embryo is developed (Fig. 166). Apical growth continues for a long time. Finally, at the upper end of the embryo, after the appearance of two sets of four vertical walls, periclinal divisions cut off the amphithecium from the endothecium. The amphithecium gives rise to several

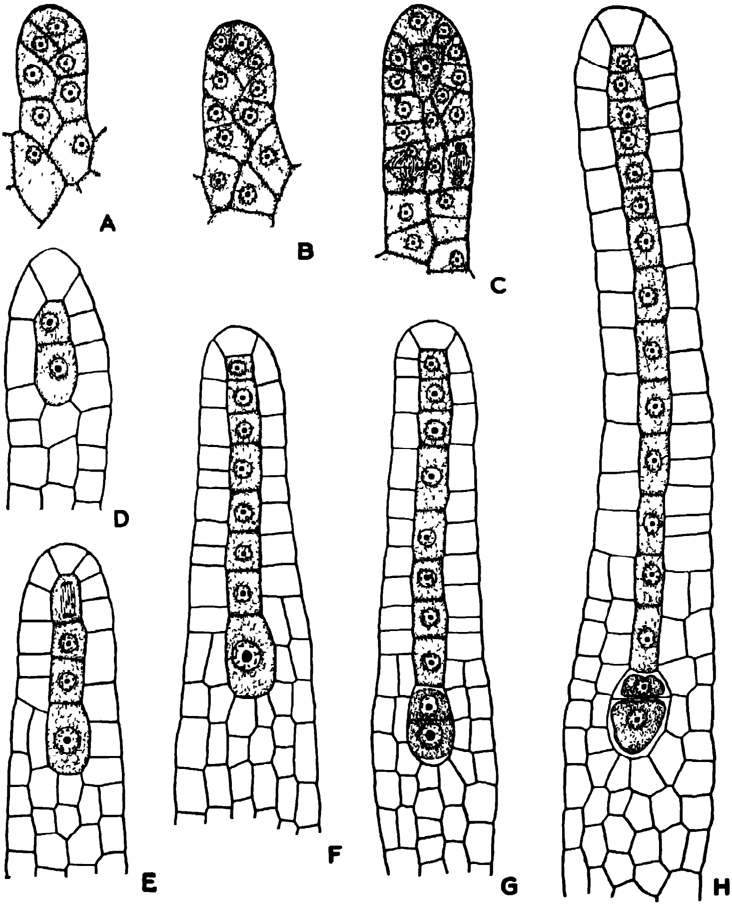

FIG. 165. Development of the archegonium of *Mnium affine*, ×400. *A*, young stage; *B*, formation of primary axial cell; *C*, formation of cover cell and central cell, the former divided by a radial wall; *D*, formation of primary neck canal cell and primary ventral cell; *E*, archegonium with primary ventral cell and three neck canal cells; *F*, later stage with seven neck canal cells; *G*, archegonium with egg, ventral canal cell, and eight neck canal cells; *H*, later stage.

layers of cells. The sporogenous tissue is cut off from the endothecium as the outermost layer of cells, the remainder forming a sterile columella. The sporogenous tissue is not continuous over the columella as a dome, but has the form of a hollow cylinder. It may extend to the base of the capsule, as in *Polytrichum*, or may not. The sporogenous tissue usually becomes two-layered, all its cells giving rise to spore mother cells.

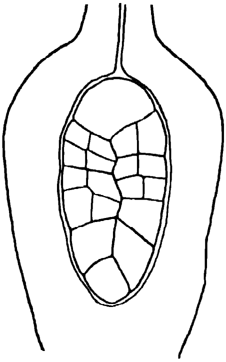

Fig. 166. Embryo of *Funaria hygrometrica* enclosed by the calyptra, ×500. (*After Sachs.*)

As seen in longitudinal section, the mature capsule is very complex, being made up of an epidermis with stomata, several wall layers of colorless cells, an air-chamber region consisting of green tissue, an outer tapetum, the sporogenous tissue, an inner tapetum, an inner air-chamber region (present only in highly specialized forms, such as *Polytrichum*), and a central columella (Fig. 167).

The *operculum*, which forms the upper part of the capsule, is complex in its development (Fig. 168). It is often dif-

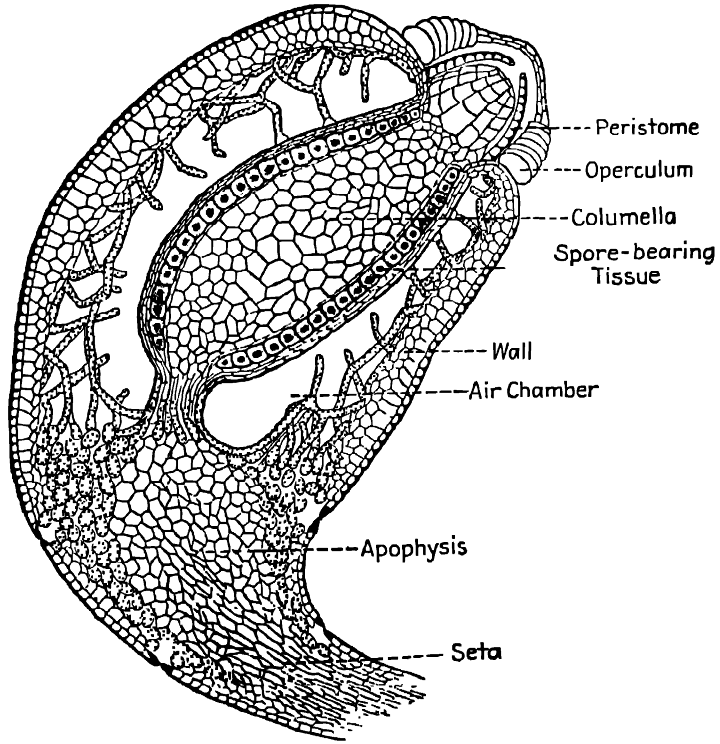

Fig. 167. Longitudinal section of the capsule of *Funaria hygrometrica*. (*From Sinnott.*)

ferentiated into an upper *annulus*, consisting of several series of large thin-walled cells, and a lower *rim*. When the capsule is mature, the annulus collapses and the operculum comes off, exposing the *peristome*. This consists of one or two rings of tooth-like projections that are anchored to the rim. The usual number of teeth is 16, but they may occur in some other multiple of 4. The teeth, which are hygroscopic, assist in spore dispersal, bending inward and outward. In a few genera, said to be "cleistocarpous," an operculum and a peristome are lacking, the capsule wall rupturing irregularly in dehiscence. In the other genera, which are "stegocarpous," an operculum and a peristome are present.

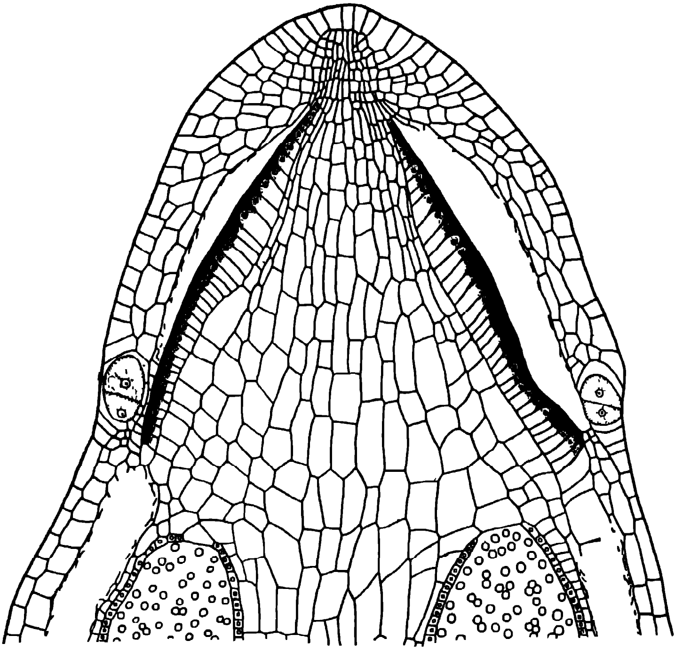

FIG. 168. Longitudinal section of the upper part of the capsule of *Mnium*, showing the operculum and two teeth of the peristome, × 90. (*After Chamberlain.*)

Often the lower portion of the capsule does not produce spores, but forms a chlorophyll-bearing region, called the *apophysis*, in which stomata are present (Fig. 167). In many mosses the apophysis is ring-like. The seta of mosses is nearly always very long. It has a central strand of elongated cells, but these are not conductive in function. The foot is simple.

Summary. The Bryales are the most highly developed group of bryophytes. The gametophyte consists of a protonema giving rise to a leafy shoot, the latter being differentiated in form and somewhat in structure. The antheridia are terminal and club-shaped, developing by means of a dolabrate apical cell, as in all the Musci. The archegonia have a long stalk, a massive venter, and a long twisted neck. The number of neck canal cells is greater than in any other group of plants. The sporophyte displays the greatest amount of sterilization of potentially sporogenous tissue seen in the Bryophyta. The sporogenous tissue arises from the outer part of the endothecium and has the form of a hollow cylinder. The seta is elongated, no pseudopodium being formed. The capsule shows an extraordinary degree of specialization, both in the organization of an operculum, peristome, and apophysis, and in its internal differentiation of tissues. It contains both green tissue and stomata.

COMPARISON OF LIVERWORTS AND MOSSES

The most important distinguishing characters of the Hepaticae (liverworts) and Musci (mosses) are as follows:

Hepaticae	Musci
Gametophyte almost invariably dorsiventral; thalloid or leafy	Gametophyte typically radial; leafy
Leaves, where present, without a midrib	Leaves generally with a midrib (except in *Sphagnum* and *Andreaea*)
Rhizoids unicellular and mostly unbranched	Rhizoids septate, mostly branched
Protonema, where present, small and transitory	Protonema usually conspicuous, relatively persistent
Sporophyte remaining enclosed by the calyptra, or breaking through only when spores are ripe	Sporophyte breaking through the calyptra at an early stage of development (except in *Sphagnum*)
Elaters usually present	Elaters absent

GENERAL CONCLUSIONS

The bryophytes, undoubtedly derived from aquatic ancestors, are the simplest group of green plants growing on land. Their position in the plant kingdom is an expression of the degree of evolutionary progress they have made, but is not necessarily an indication of their phylogenetic relationship to the higher plants. One theory holds that the bryophytes are an ancient stock from which the pteridophytes have been derived. Another theory contends that the pteridophytes have originated directly and independently from the algae and that, therefore, the bryophytes represent a blindly ending line of descent. But even if the latter view should prove to be the correct one, the first land plants may have passed through a general stage of development similar to that reached by the bryophytes of the present.

The bryophytes differ from the algae in the possession of archegonia, multicellular antheridia, and an established heteromorphic alternation of generations. Because the liverworts are simpler than the mosses, it seems very probable that they are more primitive and thus more ancient than the mosses. Both groups may have had a common origin, but it is more likely that the mosses were derived directly from the liverworts. Each has subsequently pursued its own course of evolution, the mosses having advanced considerably beyond the liverworts.

The Land Habit. The establishment of the land habit was one of the most important events in the history of plant life, for it made possible all subsequent progress. Its advantage lies in the greater opportunity for photosynthesis in the presence of more light. Its disadvantage lies in the danger of excessive transpiration. The first land plants may have arisen from some green alga consisting of a simple plate of cells, perhaps from a form somewhat like *Coleochaete*. Adjustment to the land environment must have involved structural changes facilitating the absorption of water from the soil and the retention of water by parts exposed to the air. This adjustment on the part of bryophytes is manifested chiefly by the development of compact bodies, absorptive filaments (rhizoids), jacketed sex organs, heavy-walled aerial spores, and, in some cases, by an epidermis with air pores, in others, by primitive conducting cells.

Because the simplest liverworts are thalloid, it is reasonable to suppose that they have given rise to the leafy forms. An alternative view is that the leafy body is primitive, the thalloid type having been derived from it by reduction. Since an erect leafy body permits the exposure of a greater photosynthetic surface to the light than is afforded by a flat thallus, it would seem to represent a more advanced state of adaptation to the land habit.

The Gametophyte. The bryophytes are a group in which the gametophyte is the dominant generation. It is always a green, independent plant body. In its simplest form it is a flat thallus, one to several layers of cells thick, and without any internal differentiation of tissues. Such a gametophyte is seen in *Sphaerocarpus*, *Pellia*, *Notothylas*, and a number of other Hepaticae. It may be regarded as having given rise to two divergent lines of descent: (1) a line in which the gametophyte, remaining thalloid, has undergone differentiation in structure; (2) a line in which the gametophyte has remained simple structurally but has become differentiated in form, finally becoming a leafy shoot. The first line of evolution has been followed by the Marchantiales, the second by the Jungermanniales. In the Musci the gametophyte reaches its highest development, the erect leafy shoot of the higher mosses, with its radial symmetry, showing differentiation in both form and structure.

The Sporophyte. The simplest sporophyte among the bryophytes is that of *Riccia*, where, except for the single layer of wall cells, all the cells are sporogenous. If this sporophyte be regarded as primitive rather than reduced, all subsequent progress has resulted from sterilization of potentially sporogenous tissue and its diversion to other functions. This is seen in the development of a foot and seta, as well as in the formation of elaters. The foot absorbs food from the gametophyte. The seta places the capsule in a favorable position with reference to spore dispersal. Except in *Riccia*, the Sphaerocarpales, and a few other forms, a seta is found in all bryophytes. Its absence in the Anthocerotales is correlated with the indeterminate growth of the elongated capsule and in the Sphagnales and Andreaeales with the presence of a pseudopodium, the functional equivalent of a seta. The development of a definite means of dehiscence, seen in nearly all bryophytes except *Riccia* and the Sphaerocarpales, represents an advanced feature. Elaters are present in almost all liverworts but not in any of the mosses, where spore dispersal is aided by other means, as by a peristome.

Further progress of the sporophyte has come about through additional sterilization and earlier diversion of potentially spoi ogenous tissue. Thus an elaterophore is developed in some of the Jungermanniales. The formation of a columella in the center of the capsule and of additional sterile tissue in its outer portion is an advanced feature of the Anthocerotales and Musci. The failure of a columella to develop in certain members of each group indicates that the entire central region of the capsule was originally sporogenous The sporophyte reaches its highest development in the Bryales, where the most extensive amount of sterilization seen in all bryophytes has resulted in a greatly elongated seta and a capsule of extreme complexity.

The bryophytes show two well-marked lines of evolution with respect to the sporophyte. The one, emphasizing spore dispersal, ends blindly with the mosses. The other, in which the sporophyte attains partial independence and exhibits indeterminate growth, culminates in *Anthoceros*.

Plan of the Mosses. In the mosses photosynthesis and fertilization are functions of the gametophyte, the sporophyte being concerned mainly with the production and dispersal of spores. An erect leafy gametophyte, best developed in this group, favors photosynthesis but at the same time hinders fertilization, since the sex organs are carried upward where it is difficult for swimming sperms to function. The moss sporophyte is highly specialized for spore dispersal, but without fertilization there can be no sporophyte. It is evident, therefore, that combining photosynthesis with fertilization as functions of the gametophyte is an unprogressive tendency, because these two functions have different requirements. It follows that the mosses must be regarded as a blindly ending evolutionary line.

Plan of Anthoceros. In the Anthocerotales the sex organs are borne on a flat thallus, and so fertilization is easily accomplished. Although still largely dependent upon the gametophyte, the sporophyte develops much green tissue and so exhibits a marked tendency toward independence. The combining of photosynthesis with spore dispersal as functions of the sporophyte permits of further progress, since both, favored by a tall body, have the same requirements. The plan of *Anthoceros* is the one carried forward by the higher plants, where the sporophyte is dependent upon the gametophyte only during early life. Thus *Anthoceros* displays a strong tendency that, if present in the ancestors of the pteridophytes, may have led to their origin.

CHAPTER VI

PTERIDOPHYTA

The pteridophytes are a comparatively small group of plants today, but in past geologic times they were much more numerous. They are represented by over 9,000 living species, very unequally divided among the four classes Psilophytinae, Lycopodiinae, Equisetinae, and Filicinae. Most pteridophytes are terrestrial plants, but some are epiphytic and a few are secondarily aquatic. They grow in a wide variety of habitats.

Pteridophytes may be characterized as vascular plants without seeds. Like the bryophytes, they display a distinct alternation of generations. Their great advance lies in the development of an independent sporophyte with complex roots, stems, and leaves, and one in which a prominent vascular system is present. The sporophyte has now become the dominant generation, the gametophyte always being small and inconspicuous.

The sporophyte presents a great range in size and habit, although one not so extreme as in the spermatophytes. Nearly all existing pteridophytes are herbaceous or somewhat woody, the tree ferns being a notable exception. Branching of the stem, where present, is dichotomous in some members, monopodial in others. Elongation of the root and stem generally occurs through the activity of an apical cell; in some forms this is replaced by a meristem. The spores are produced in sporangia, which are usually borne in connection with the leaves. Most living pteridophytes are *homosporous*, all the spores being alike. Some are *heterosporous*, with spores of two different kinds, these always being produced in separate sporangia. As in all bryophytes and spermatophytes, the reduction in chromosome number occurs in connection with the formation of spores. Consequently the sporophyte is the diploid generation, while the gametophyte, produced by a spore, is the haploid generation.

In the homosporous pteridophytes the gametophyte is either a simple green thallus or a tuberous body that is subterranean, colorless, and saprophytic. In the heterosporous forms the gametophytes are sexually differentiated and greatly reduced in structure, developing entirely or largely within the spore wall. The sex organs of pteridophytes are essentially similar to those of bryophytes, but are simpler. Generally both the antheridia and archegonia are embedded structures. Swimming sperms are universally present. Following fertilization, the embryo develops within the venter of the archegonium, which forms the calyptra. The young sporophyte lives on the gametophyte until able to maintain itself as an independent plant.

THE VASCULAR SYSTEM

The vascular system of pteridophytes and spermatophytes is made up mainly of two kinds of complex tissues: *xylem* and *phloem*. Each of these consists of several different kinds of elements. Xylem conducts water and dissolved substances absorbed from the soil, while phloem carries food away from the leaves and other organs where it is synthesized. The unit of the xylem is the *tracheid*—a slender, elongated, thick-walled cell generally pointed at each end and without living contents when mature. The most important element of the phloem is the *sieve tube*—an elongated, thin-walled, living cell whose end walls, and often side walls as well, have many fine pores (Fig. 314*A*, *B*).

The cell walls of tracheids are thickened with lignin, which is deposited on the inner surface to form a spiral, rings, parallel bars, or an irregular network, in accordance with which spiral, annular, scalariform, and reticulate types are recognized. Most commonly the lignin is so abundant that the walls are pitted, the pits being unthickened areas. *Vessels* resemble tracheids except that each represents a longitudinal row of cells whose end walls break down. Vessels are of rare occurrence in pteridophytes but are the chief xylem elements of angiosperms (Fig. 314*C*–*E*).

In addition to tracheids and/or vessels, xylem may contain parenchyma. Phloem may contain parenchyma in addition to sieve tubes. *Fibers*, which are elongated, thick-walled, nonconducting cells, may also form part of the xylem or phloem (Fig. 314*F*).

Development of Xylem. A short distance behind the apex of the root and shoot, which is composed of embryonic tissue, the first xylem is differentiated. This is known as *protoxylem*. The next xylem to lignify is called *metaxylem*. The position of the metaxylem with reference to the protoxylem is of considerable importance. There are three conditions, as follows:

(1) If the lignification begins at the outside (periphery) of the root or stem and proceeds toward the center, in a centripetal direction, the development is *exarch*. This type is characteristic of all roots and of the stems of lycopods (Figs. 176, 188, 220, 227, and 311). (2) If the lignification spreads out in all directions, so that the metaxylem surrounds the protoxylem, the development is *mesarch*. This type is characteristic of the stems of ferns (Fig. 239). (3) If the lignification begins near the center of the stem and proceeds outward, in a centrifugal direction, the development is *endarch*. Only a few pteridophytes have reached this condition, but it is almost universal in the stems of spermatophytes.

Protoxylem consists mainly of spiral and annular tracheids, while metaxylem is generally made up of scalariform or of pitted tracheids. Scalariform tracheids, in which the bands of thickening resemble the rungs of a ladder, are most common in pteridophytes and pitted tracheids in spermatophytes. *Primary xylem*, consisting of all wood differentiated directly from embryonic cells of a terminal meristem, includes both protoxylem and metaxylem. *Secondary xylem* is wood that arises through the activity of a cambium. It occurs in only a few living pteridophytes, but is characteristic of nearly all spermatophytes except the monocotyledonous angiosperms.

Types of Steles. The vascular tissues lie within the *stele*,[1] which in roots and stems generally forms a central core. This is surrounded by a cylindrical region, the *cortex*, outside of which lies a layer of cells constituting the *epidermis*. The innermost layer of the cortex is the *endodermis*. Four main types of steles occur in vascular plants and all of them are found in pteridophytes. These are as follows:

(1) The *protostele* is the simplest and most primitive type. Here the xylem forms a solid central strand surrounded by phloem, no pith being present (Figs. 176, 188, 200, 235, and 311). (2) The *amphiphloic siphonostele* has the xylem in the form of a hollow cylinder enclosing pith, with phloem both inside and outside the xylem (Figs. 236 and 249). (3) The *ectophloic siphonostele* also has the xylem surrounding pith, but there is no internal phloem (Figs. 221, 237, 269, 285, 294, and 315). (4) The *dictyostele* is the most advanced type. Here the vascular cylinder is broken up into a network of separate strands that, as seen in cross section, may be either arranged in a circle or scattered (Figs. 238 and 316).

The arrangement of xylem and phloem with reference to each other follows four general types, three of which occur in pteridophytes. (1) In the *radial* arrangement, which is most primitive, the xylem and phloem are in separate strands and occupy alternating radii (Figs. 171, 176, 220, 227, and 311). The xylem may or may not meet in the center. (2) In the *amphicribral* arrangement the phloem completely surrounds the xylem (Figs. 188 and 239). (3) In the *collateral* arrangement the xylem and phloem lie side by side on the same radius, with the phloem external to the xylem (Figs. 221, 294, and 315). Where the phloem occurs both outside and inside the xylem, the arrangement is *bicollateral*. (4) In the *amphivasal* arrangement the xylem surrounds the phloem. This is an advanced type occurring only among the monocotyledonous angiosperms (Fig. 317).

In practically all vascular plants the root is an exarch radial protostele. Stems display a great variety of vascular structure. Those of lycopods are much like roots and so are very primitive. The stems of ferns display all four stelar types, the amphiphloic siphonostele and the dictyostele

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[1] Practically all stems have a single stele, and thus are sometimes designated as *monostelic*. *Polystelic* stems, containing more than one stele, are very rare (see p. 231).

being most common. Most fern stems have mesarch amphicribral bundles. The characteristic stem of seed plants is an ectophloic siphonostele with endarch collateral bundles, a type that is uncommon in pteridophytes.

Traces and Gaps. In all vascular plants the conducting system is essentially continuous throughout the plant body. A strand of conducting tissue extending from the stele of the stem through the cortex to a leaf is called a *leaf trace.* A strand connecting the vascular tissue of the stem with that of a branch is a *branch trace*, while a *root trace* occurs where a root arises from a stem or from another root. A *gap* is a break or interruption in a siphonostele caused by the departure of a leaf trace or a branch trace (Fig. 221). It consists of parenchyma. Gaps are not formed by root traces. Branch gaps are present in all siphonostelic stems, but leaf gaps occur only in ferns and seed plants.

1. PSILOPHYTINAE[1]

The Psilophytinae comprise a group of primitive pteridophytes that were abundant and widespread during the Devonian, but are represented today by only two genera of somewhat restricted distribution (Fig. 258). They are all rootless plants and either leafless or provided with small, simple, spirally arranged leaves. The sporangia are solitary and terminal on branches that are elongated or, in modern forms, greatly reduced. The Psilophytinae comprise two orders, the extinct Psilophytales and the existing Psilotales.

1. Psilophytales

The Psilophytales are the oldest and most primitive of all known vascular plants. They appeared in the late Silurian and flourished during the early and middle Devonian. Their remains have been found in many parts of the world, but the best-preserved material has come from Scotland. The chief genera are *Rhynia*, *Hornea*, *Psilophyton*, and *Asteroxylon.*

The Psilophytales were small herbaceous plants that lived on land. Few exceeded 60 cm. in height. The sporophyte consisted of a rhizome bearing slender, erect, dichotomously branched shoots (Fig. 169). The stems of *Asteroxylon* were covered with small simple leaves, but the three other genera were leafless. In some species of *Psilophyton* the stems were spiny. Apparently true roots were not present, but in some genera the rhizome bore numerous rhizoids. In *Psilophyton* the tips of the branches were circinately coiled, as in the young leaves of ferns. In all members of the group the stem was a protostele, a narrow zone of phloem enclosing a central mass of xylem. Around the stele was a wide cortex surrounded by a cutinized epidermis with typical stomata. The presence of stomata

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[1] Also called Psilopsida.

on the erect stems demonstrates that they were aerial and green. In *Asteroxylon* the xylem was deeply lobed. The conducting tissues were very simple. There was no secondary thickening. The leaves, where present, were without veins, although the base of each leaf was con-

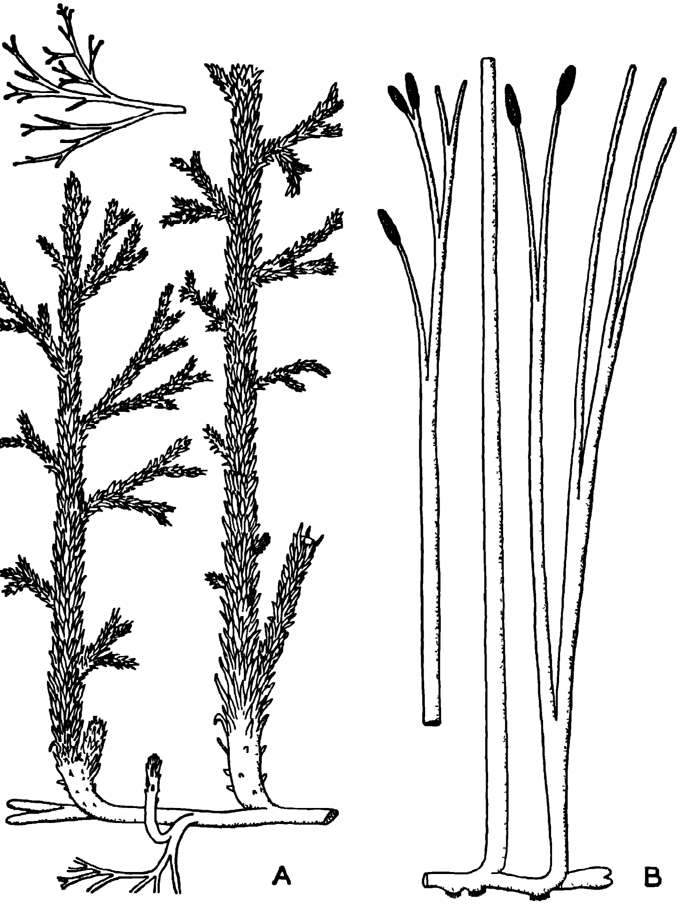

FIG. 169. Psilophytales from the Devonian of Scotland. *A, Asteroxylon mackiei; B. Rhynia major.* (*After Kidston and Lang.*)

nected with the stele by a strand of vascular tissue constituting a leaf trace.

The sporangia were borne singly at the ends of the branches and not in association with the leaves. They were relatively large (in some species up to 12 mm. long, but usually smaller), cylindrical, and homosporous. The sporangium wall was several layers of cells in thickness. As in other pteridophytes, the spores were formed in tetrads. In *Hornea* the sporogenous tissue was dome-shaped, capping a sterile columella, as in *Anthoceros* and *Sphagnum*. Nothing is known of the gametophyte generation.

Some botanists see in the simpler Psilophytales a resemblance to the liverwort *Anthoceros* and regard this group as a connecting link between the bryophytes and pteridophytes. Others feel that a closer relationship exists between the Psilophytales and the algae and that the Psilophytales were derived directly from alga-like ancestors. But, regardless of their origin, there is general belief that the group may have been ancestral to the other great pteridophyte lines—the lycopods, horsetails, and ferns—all of which are represented in the later Devonian deposits (Fig. 258).

2. Psilotales

The Psilotales are a modern order including only two genera. *Psilotum*, with two species, occurs in tropical and subtropical regions in both

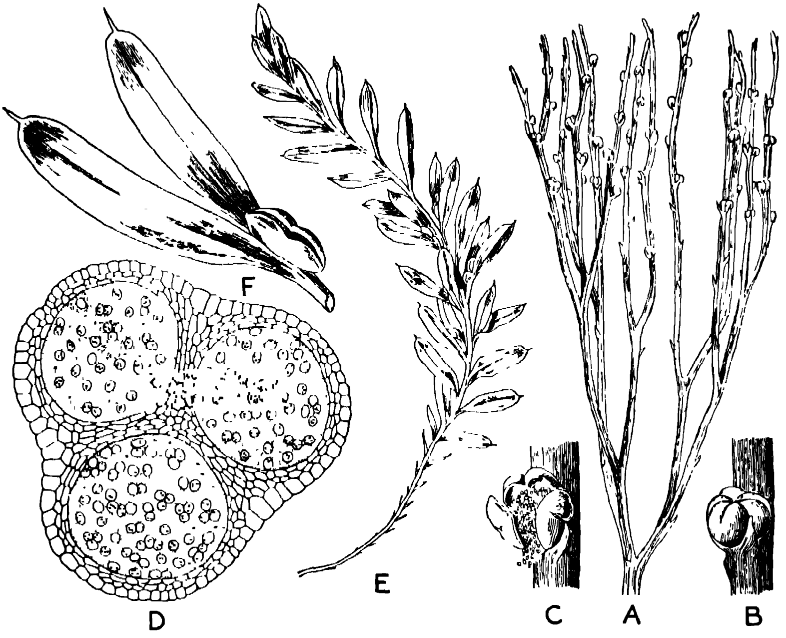

Fig. 170. Psilotales. *A*, upper portion of shoot of *Psilotum nudum* with sporangia, slightly reduced; *B*, closed sporangium of same, enlarged; *C*, open sporangium; *D*, cross section through an unripe sporangium, showing three locules containing spore mother cells; *E*, shoot of *Tmesipteris tannensis*, slightly reduced; *F*, a sporophyll of same, enlarged. (*After Wettstein.*)

the Eastern and Western Hemispheres. *Tmesipteris*, with a single species, is confined to Australia, New Zealand, the Philippine Islands, and parts of Polynesia. The Psilotales were formerly classified with the Lycopodiinae, but they are now generally regarded as being more closely related to the extinct Psilophytales.

Sporophyte. The sporophyte consists of a rhizome bearing rhizoids and giving rise to slender, green, aerial stems (Fig. 170*A*, *E*). A peculiar feature is the absence of roots. The aerial stems of *Psilotum* branch dichotomously and generally grow erect upon the ground, but are sometimes epiphytic and drooping. They reach a length of 20 to 100 cm. The leaves are few, scale-like, and without veins. *Tmesipteris* may grow as an erect terrestrial plant but is generally epiphytic and pendulous, especially on tree ferns. The stem is unbranched, rarely showing a single dichotomy. It reaches a length of 5 to 25 cm. The leaves are narrow, 12 to 18 mm. long, and have a single vein. In both genera the leaves are more or less spirally arranged. The rhizome and aerial stem grow by means of a tetrahedral apical cell (having the form of a triangular pyramid).

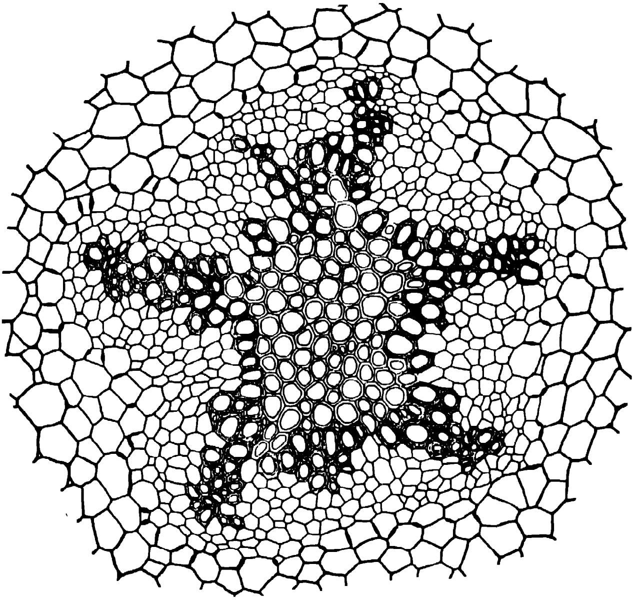

Fig 171. Cross section of the central portion of the aerial stem of *Psilotum nudum*, ×100. The protoxylem lies at the tips of the xylem rays, the phloem between them. The center of the stele is occupied by a group of fibers.

Vascular Anatomy. In both genera the rhizome is a protostele. In the aerial stem the xylem forms a star-shaped mass enclosing a pith that, in *Psilotum*, is occupied by a group of fibers (Fig. 171). The rhizome is exarch in both genera, the first-formed xylem (*protoxylem*) lying outside the later-formed xylem (*metaxylem*). The aerial stem is exarch in *Psilotum* but mesarch in *Tmesipteris*, in the latter the metaxylem surrounding the protoxylem. The phloem, which lies outside the xylem, is poorly developed. There is no cambium. An endophytic fungus is present in the outer cortical region of the rhizome.

Sporangium. The sporangia are borne singly in the axils of the upper leaves, which are bifurcated in both genera, a sporangium arising at the point of forking (Fig. 170). Each sporangium is situated at the end of a short stalk. In *Tmesipteris* the large sporangium is divided transversely by a sterile plate into two separate chambers, so that two sporangia seem to be present. In *Psilotum* the sporangium is three-chambered. The wall consists of several layers of cells. No tapetum is present, but among the spore mother cells are numerous sterile cells that are resorbed by the developing spores. Both genera of the Psilotales are homosporous. Dehiscence of the sporangium occurs by means of a longitudinal slit.

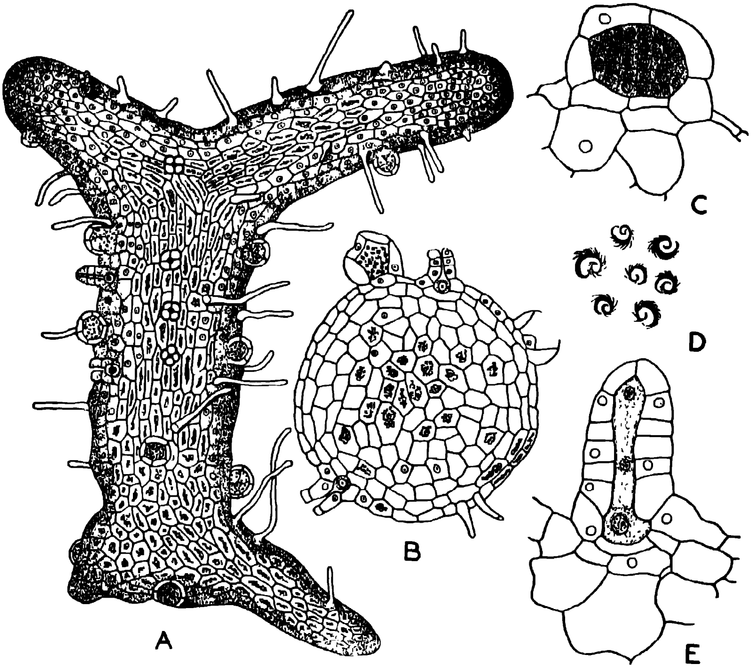

FIG. 172 Prothallium and sex organs of *Psilotum nudum*. *A*, surface view of an entire prothallium of rather small size, bearing rhizoids, antheridia, and archegonia, ×28; *B*, cross section of prothallium, showing two antheridia (one discharged), two archegonia, and endophytic fungus, ×38; *C*, a nearly mature antheridium, ×145, *D*, several sperms, ×450; *E*, a nearly mature archegonium, ×145. (*After Lawson.*)

The nature of the sporangium-bearing structures of the Psilotales is not clearly understood. One interpretation is that the upper, forked leaves are bifid sporophylls bearing solitary adaxial sporangia that are bilocular in *Tmesipteris* and trilocular in *Psilotum*. Another view is that the whole structure is a sporangiophore bearing two leaves and a terminal sporangium; that the sporangiophore is not a lateral branch but a reduced member of a dichotomous branch of the main stem. The existing evidence favors this second interpretation. It is also not clear whether the sporangium should be regarded as a single sporangium or a *synangium*, which is a group of united sporangia. In early developmental stages each mass of sporogenous tissue has an independent origin, but it is uncertain whether or not the partitions represent sterile sporogenous tissue.

Gametophyte. The prothallia of both *Psilotum* and *Tmesipteris* are tuberous, subterranean, saprophytic bodies without any chlorophyll (Fig. 172*A*, *B*). They are light brown, cylindrical, simple at first but later branched, and up to 20 mm. in length. Long rhizoids uniformly cover the surface. An endophytic fungus is present. In *Psilotum*, but not in *Tmesipteris*, the largest prothallia sometimes possess a strand of conducting tissue consisting of a few tracheids. Both kinds of sex organs occur in abundance on the same prothallium. The antheridia are globular and projecting, each producing many multiciliate sperms (Fig. 172*C*, *D*). The antheridium initial, which is superficial, undergoes a periclinal division, the outer cell giving rise to the sterile jacket and the inner cell to the spermatogenous tissue. The archegonia are sunken in the prothallium, but the neck protrudes (Fig. 172*E*). Apparently two neck canal cells are present.

Embryo. The embryos of *Psilotum* and *Tmesipteris* are very similar. They are peculiar in that no suspensor, root, or leaf is present. The fertilized egg divides transversely, the outer cell giving rise to the stem and the inner cell to the foot. In *Tmesipteris* a second stem tip often appears near the base of the first one; later both may grow erect and produce leaves.

Summary. The stem of *Psilotum* is elongated and branched, the leaves scale-like and relatively few. The stem of *Tmesipteris* is also elongated but generally unbranched; the leaves are small and numerous. Roots are absent in both genera. The stem is differentiated into an underground and an aerial portion. The rhizome is an exarch protostele. The aerial stem, which is medullated, is exarch in *Psilotum* and mesarch in *Tmesipteris*. The arrangement of xylem and phloem is amphicribral. There is no cambial activity. The sporangia are borne singly in the axils of the upper leaves, each at the end of a short sporangiophore. There is no definitely organized strobilus. The sporangium is either bilocular (*Tmesipteris*) or trilocular (*Psilotum*), homosporous, and longitudinally dehiscent. A tapetum is not organized. The prothallia are subterranean and tuberous. The antheridia produce many multiciliate sperms. The archegonia have two neck canal cells. The embryo is without a suspensor. The Psilotales form an isolated order not closely related to other living pteridophytes.

2. LYCOPODIINAE[1]

The lycopods, numbering nearly 950 species, are an ancient group represented in our modern flora by only four surviving genera. They were abundant in the Devonian but reached their greatest display during the Carboniferous (Fig. 258), when some were trees 30 m. tall. Today all lycopods are herbaceous, generally growing close to the ground. They are characterized by leaves that are mostly small, simple, and spirally arranged and by sporangia that are always solitary, adaxial, and unilocular. There are four orders, the Lycopodiales, Selaginellales, Lepidodendrales, and Isoetales. Of these, the third is extinct.

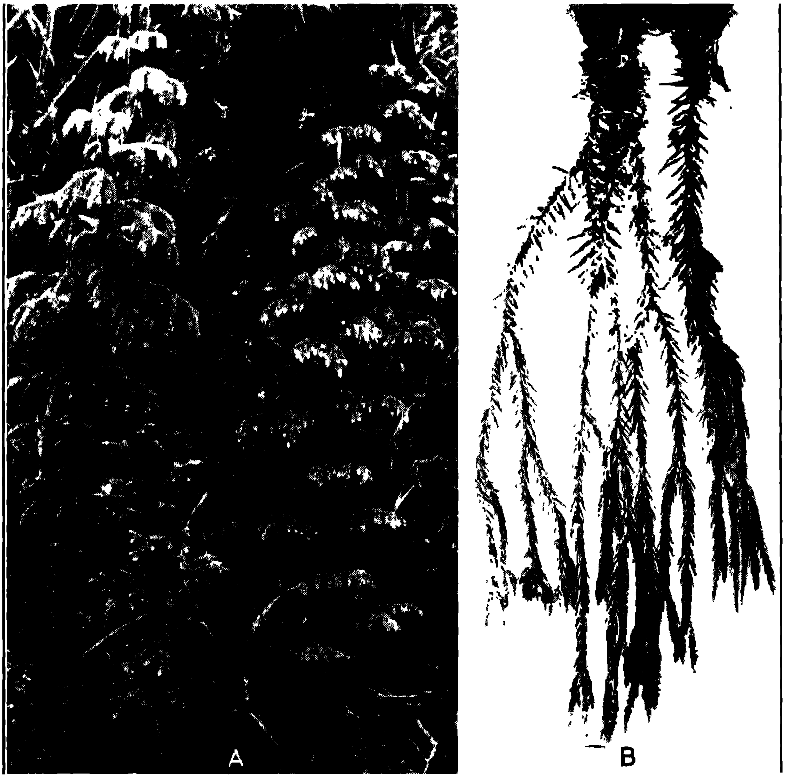

FIG. 173. Two tropical species of *Lycopodium* from Costa Rica, about one-third natural size. *A*, *Lycopodium cernuum*, a terrestrial species with upright stems and nodding cones; *B*, *Lycopodium tubulosum*, a pendent epiphytic species with loosely organized cones at the ends of the branches.

1. Lycopodiales

Only two living genera belong to this order. *Lycopodium*, with 180 species, is widely distributed throughout the world but is most abundant

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[1] Also called Lycopsida.

in the tropics. *Phylloglossum* has a single species confined to Australia, Tasmania, and New Zealand. Fossil forms known as *Lycopodites* have been found in Carboniferous and later formations.

Sporophyte. The sporophyte of *Lycopodium* consists of a slender stem, generally branched, and bearing roots and numerous small leaves. Most of the species are terrestrial plants either with erect stems or, more commonly, with elongated, trailing or subterranean stems giving rise to upright branches (Figs. 173*A*, 179, and 180). Many of the tropical species are epiphytes with erect or pendent stems (Fig. 173*B*). The terrestrial species grow close to the ground, few exceeding 30 cm. in height. Numerous roots penetrate the soil. Generally both the roots and stems branch dichotomously, but in some species the branching of the stem is apparently monopodial, the branches arising laterally from a true main axis. The leaves are small and often scale-like, simple, entire, and densely cover the branches. They are generally borne in spiral arrangement. Growth of the root and stem takes place by means of an apical meristem, no apical cell being present (Fig. 174).

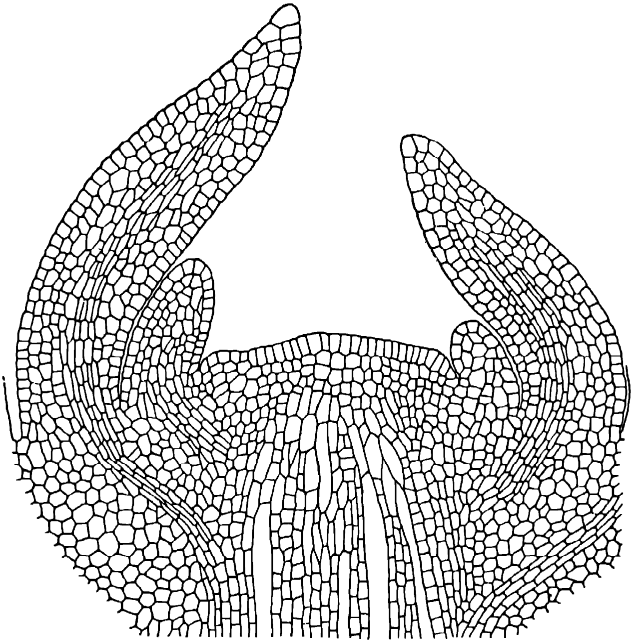

FIG. 174 Median longitudinal section through the stem tip of *Lycopodium reflexum*, showing the apical meristem and developing leaves, × 100.

Although *Phylloglossum* is much simpler than *Lycopodium*, it is generally regarded, not as a primitive form, but as one reduced from more highly developed ancestors. The sporophyte is only 3 to 5 cm. high and consists of a short tuberous stem bearing a few small fleshy leaves that form a cluster around the stem apex (Fig. 175). As a rule, only a single root is present, but sometimes there are two or three roots. In some species of *Lycopodium* the sporophyte begins its development as a small tuberous body like that of *Phylloglossum.* This disappears after giving rise to the ordinary type of leafy stem with roots. In other species no embryonic body of this kind occurs in the life history.

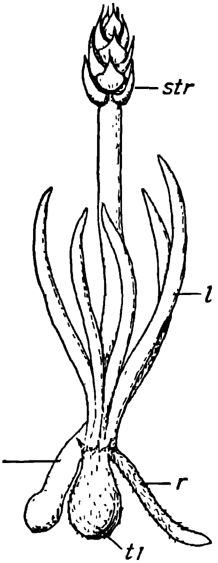

FIG. 175. Fertile plant of *Phylloglossum drummondii,* twice natural size; *str,* strobilus; *l,* leaves; *r,* root; *t1,* primary tuber; *t2,* secondary tuber.

Vascular Anatomy. Anatomically the roots and leaves of *Lycopodium* are essentially like those of other vascular plants. The leaves are only a few layers of cells in thickness and consist of uniform mesophyll enclosed above and below by an epidermis with stomata. Each leaf has a single median vein.

The stem structure of *Lycopodium* is very primitive. A cross section shows an outer cortex and a central cylindrical stele. Because of the absence of a pith, this type of vascular system is a protostele. In some species the xylem forms a star-shaped mass between the rays of which lies the phloem (Fig. 176). In other species, although fundamentally radial, a modification is seen in that the xylem and phloem are somewhat intermixed (Fig. 177), while in still others the two kinds of conducting tissues occur in alternating, transverse, parallel bands (Fig. 178). A protostele that is star-shaped in outline is often designated as an *actinostele;* one that is circular in outline is called a *haplostele;* while the type with separate, parallel plates of xylem is termed a *plectostele.* The radial type is most primitive and the banded type most advanced. This is shown by the development of the vascular system in a young plant, where, if the banded condition appears, it is always preceded by the radial condition. Also, in many species, the growing stem is radial at the tip and gradually becomes banded farther back.

All the vascular tissues are primary, there being no cambial activity. The smaller cells at the tips of the radiating arms of xylem are the first elements to lignify, subsequent lignification proceeding toward the center of the stem. Thus the development of the xylem is exarch, the protoxylem lying external to the metaxylem (Figs. 176, 177, 178). The protoxylem is composed of narrow, spiral, and annular tracheids, the metaxylem of larger, scalariform tracheids.

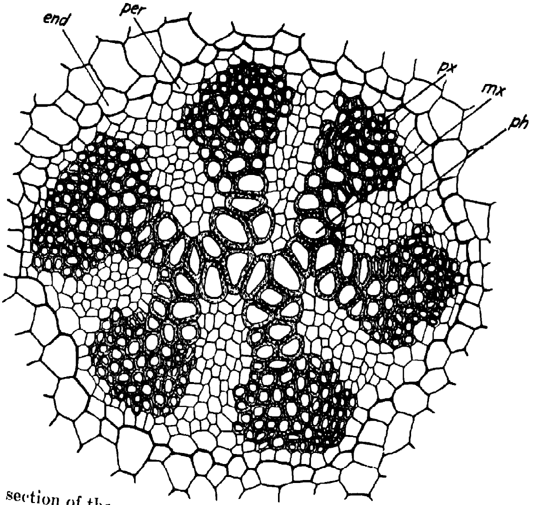

FIG. 176. Cross section of the central portion of the stem of *Lycopodium lucidulum*, showing the "radial" type of stele, ×250; *end*, endodermis; *per*, pericycle; *px*, protoxylem; *mx*, metaxylem; *ph*, phloem.

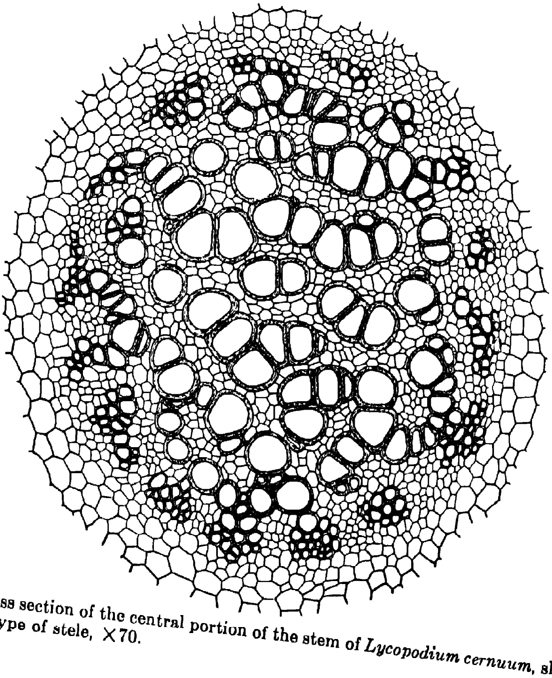

FIG. 177. Cross section of the central portion of the stem of *Lycopodium cernuum*, showing the "mixed" type of stele, ×70.

The stele is enclosed by a parenchymatous pericycle, one or more layers of cells in thickness, outside of which is an ill-defined endodermis, consisting of a layer of cells with cutinized walls (Fig. 176). As in all vascular plants, the conducting system is essentially continuous throughout the plant body. From the stele of the stem a strand of conducting tissue, called a *leaf trace*, extends through the cortex to enter each leaf and become its vein. Similarly each branch is connected with the stele of the main stem by a *branch trace* and each root by a *root trace*. These traces are present in all vascular plants.

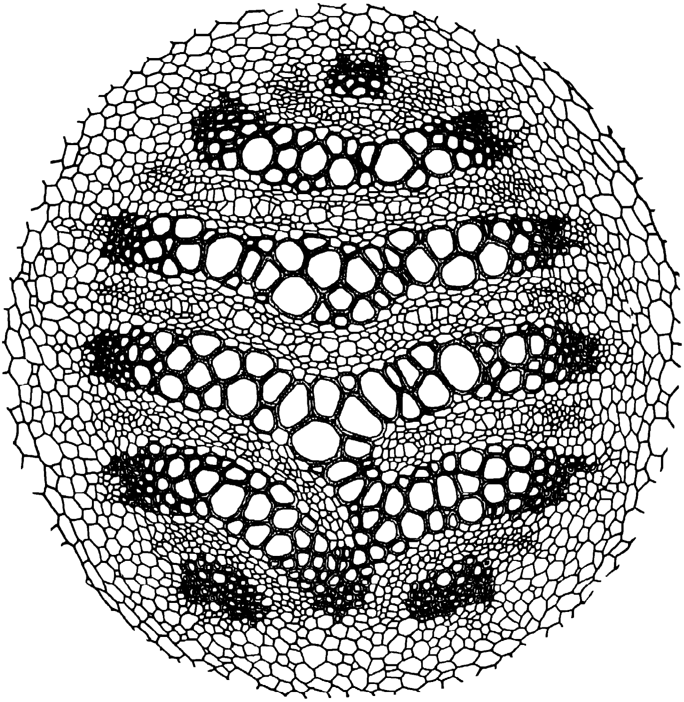

FIG. 178. Cross section of the central portion of the stem of *Lycopodium complanatum*, showing the "parallel-banded" type of stele, X 130.

Like the stem, the root of *Lycopodium* is an exarch protostele, but nearly always shows the radial arrangement of xylem and phloem, even where the stem is of the mixed or parallel-banded type. The striking similarity between the root and stem of *Lycopodium* bespeaks a very ancient origin for the genus, for in the higher groups of vascular plants the organization of the stem becomes increasingly more advanced, while that of the root remains unchanged.

The vascular system of *Phylloglossum* is poorly developed and shows evidences of reduction. The tuber consists mainly of compact storage parenchyma with a small amount of xylem in its upper portion. Apparently no phloem is present. In sterile plants the vascular system is a protostele, but in fertile plants the xylem surrounds a central mass of parenchyma and is thus a siphonostele. The development of the xylem is mesarch, the metaxylem arising both inside and outside the protoxylem. This is a more advanced condition than that seen in *Lycopodium*.

Fig. 179. *Lycopodium reflexum*, an upright tropical species in which most of the leaves are sporophylls; about natural size.

Sporangium. The sporangia of *Lycopodium* are borne singly in the leaf axils. Each sporangium is large and more or less kidney-shaped, with a very short stalk, a wall several layers of cells in thickness, and a central mass of small, yellow, thick-walled spores. When mature, it dehisces by means of a transverse slit. A leaf that bears a sporangium is termed a *sporophyll*.

In the simplest species of *Lycopodium* every leaf on the plant is a sporophyll, or at least potentially so, but in most species just the upper leaves bear sporangia, the lower leaves being sterile and functioning merely as foliage leaves (Figs. 179 and 180). An aggregation of sporophylls is called a *cone* or *strobilus*. The sporophylls may be loosely arranged but, more commonly, are compactly organized. They may be similar to the foliage leaves but generally are smaller, of a different form, and without chlorophyll.

FIG. 180. *Lycopodium obscurum*, a common species occurring throughout the northeastern United States, about one-half natural size. Upright branches bearing terminal cones arise from long trailing stems.

Because of this variation among the species of *Lycopodium*, it is not difficult to arrange a series representing progressive stages in the differentiation of the sporophylls and organization of a strobilus. It seems reasonable to suppose that such a series represents the course of evolution that the more complex species have followed. This is confirmed by other characters. Thus most of the species without a definite strobilus have

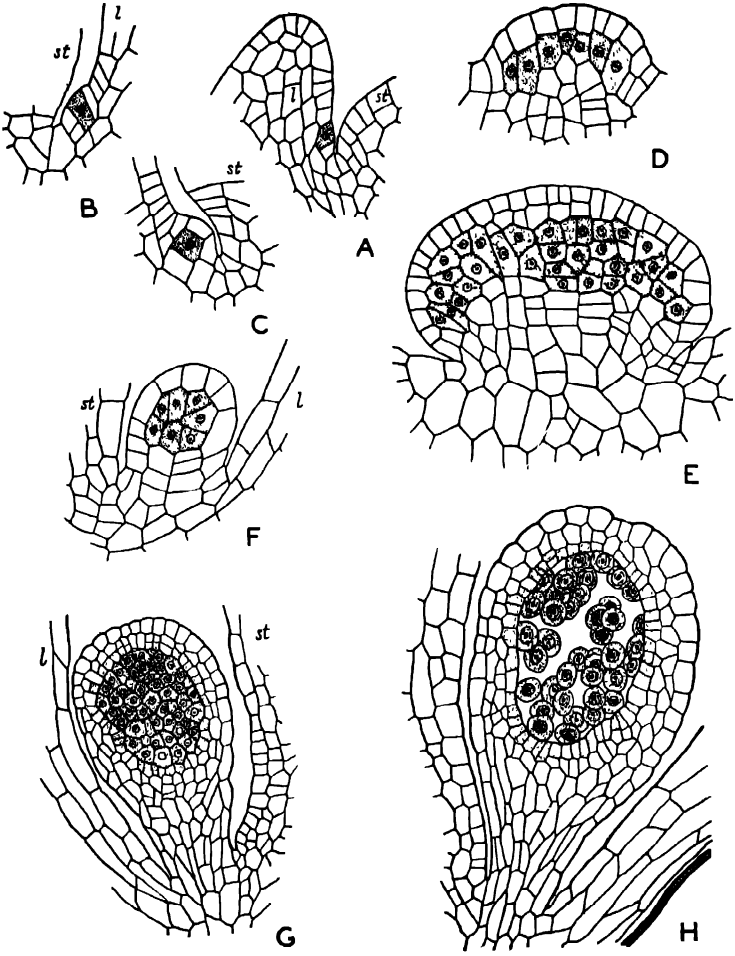

Fig. 181. Early development of the sporangium of *Lycopodium selago*. *A*, radial section of base of young sporophyll (*l*) arising from stem (*st*), showing initial cell (one of a transverse row); *B*, slightly later stage; *C*, division of initial into primary wall cell and primary sporogenous cell (latter shaded); *D*, tangential section of same; *E*, further development of sporogenous tissue; *F*, radial section of same; *G*, later stage, showing development of tapetum; *H*, sporangium showing stalk, wall, tapetum, and spore mother cells. (*After Bower*.)

dichotomously branched stems showing the radial type of stele, while many of the cone-bearing species have stems with monopodial branching and most of them show the parallel-banded type of stele.

The large solitary sporangium is always adaxial in its relation to the sporophyll and is also unilocular. The sporangium arises from a superficial group of initials consisting of a transverse row of 6 to 12 cells (Fig. 181*A*, *B*). In some species there may be two or three such rows. Each initial divides by a periclinal wall to form an outer and an inner row, the former constituting the *primary wall cells* and the latter the *primary sporogenous cells* (Fig. 181*C*, *D*). The sporangium wall becomes at least three layers of cells thick, the inner layer forming the *tapetum* (Fig. 181*E–G*). This is a nutritive layer that, instead of disorganizing, as in the horsetails and ferns, remains intact for a long time. After the sporogenous cells have increased in number, spore mother cells are organized and from each a tetrad of spores arises (Fig. 181*H*). The development of the sporangium of *Lycopodium* takes place according to the *eusporangiate* method. This means that the sporogenous tissue is derived from the inner segment following the first periclinal division of the initial. All vascular plants, except the higher ferns, are eusporangiate.

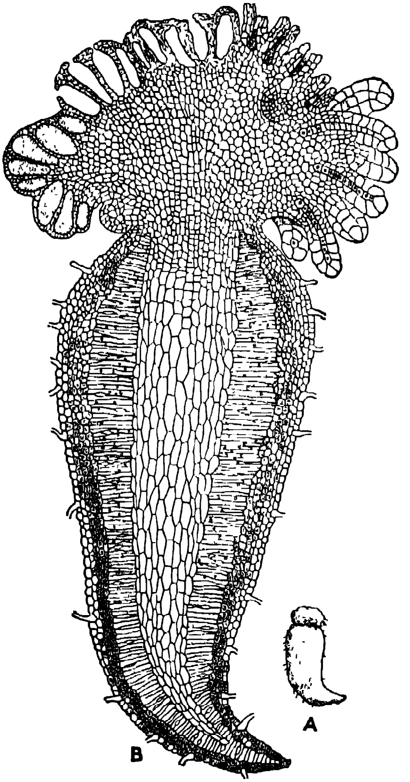

FIG. 182. Gametophyte of *Lycopodium complanatum*. *A*, the entire gametophyte, twice natural size; *B*, longitudinal section with antheridia to the left, some of which have shed their sperms, and with archegonia to the right, in one of which an embryo has developed, ×25. The shaded cells in the lower portion contain a fungus. (*After Bruchmann.*)

In *Phylloglossum* the apex of the tuber gives rise to an erect naked stalk bearing a small terminal strobilus (Fig. 175). If no strobilus is formed, the stem tip produces a new tuber at the close of the growing season, but otherwise a secondary tuber appears adventitiously at the end of a short stalk. The strobilus consists of a few spirally arranged sporophylls, each bearing a solitary, unilocular, adaxial sporangium. The sporangium is short-stalked and kidney-shaped. It consists of a central mass of sporogenous tissue surrounded by a wall three layers of cells in thickness, the inner layer forming the tapetum. As in *Lycopodium*, dehiscence occurs by means of a transverse slit.

Gametophyte. The spores of *Lycopodium* are remarkably long-lived and often do not germinate for a number of years. Eventually they give rise to gametophytes, or *prothallia* as they are usually called. These are small tuberous bodies that vary widely in form, depending on the species, being turnip-shaped, cylindrical, flat, or irregularly bulbous. In *Lycopodium cernuum*, a widespread tropical species, the prothallium is an erect cylindrical body only 2 or 3 mm. long. It grows at the surface of the ground and consists of a colorless basal portion buried in the soil and a conspicuously lobed aerial crown that is green and bears the sex organs. The lower portion produces rhizoids and contains an endophytic fungus. The spores germinate promptly and the prothallium reaches maturity in a single season. Several other species of *Lycopodium*, as well as *Phylloglossum*, have a similar type of prothallium but some lack the fungus.

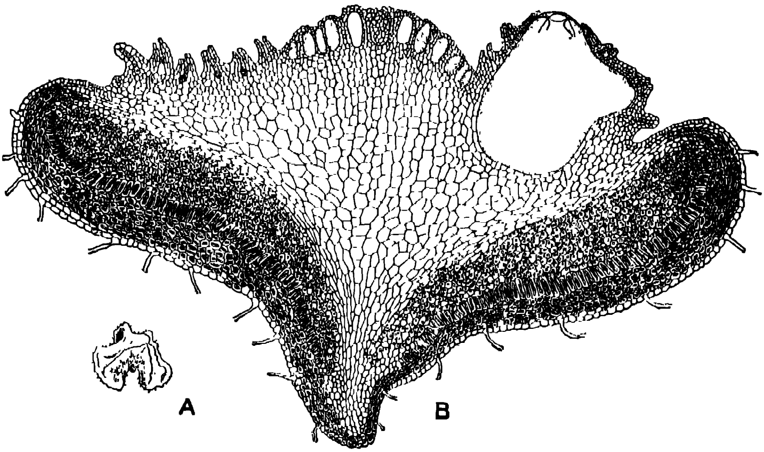

FIG. 183. Gametophyte of *Lycopodium clavatum*. *A*, the entire gametophyte, twice natural size; *B*, longitudinal section with antheridia in center and archegonia to the left and right, ×20. In the embryo, shown in outline, a young shoot has developed above, a young root to the right, and a large foot below and to the left The shaded cells in the lower portion of the prothallium contain a fungus. (*After Bruchmann.*)

In most other species, including nearly all those of the North Temperate Zone, the prothallium is larger, commonly 12 to 18 mm. long, and entirely subterranean, colorless, and saprophytic (Figs. 182 and 183). An endophytic fungus, restricted to the lower portion of the prothallium, is always present and seems to play an essential part in its nutrition. The spores do not germinate for 3 to 8 years and the prothallium may not reach maturity for an equally long period, growth being extremely slow. The production of sex organs may continue for a number of years. The gametophyte may be erect and somewhat turnip-shaped, as in *Lycopodium complanatum*, with the sex organs borne on an irregularly lobed crown that is not as well developed as in *Lycopodium cernuum* (Fig. 182). In certain other species, such as *Lycopodium clavatum*, the crown is reduced even more, the prothallium being flat and irregularly cup-shaped, with a depressed center surrounded by a broad rim (Fig. 183). The sex organs are borne in the center. This type of prothallium grows farthest below the surface of the ground and requires the greatest number of years to reach maturity.

It is an interesting fact that only species with a green aerial prothallium have a sporophyte that passes through a *Phylloglossum*-like stage in its early development. The prothallium of such species doubtless represents a primitive type from which the colorless subterranean prothallia have been derived. Their development may have been caused by delayed germination of the spores, resulting in their burial in the soil.

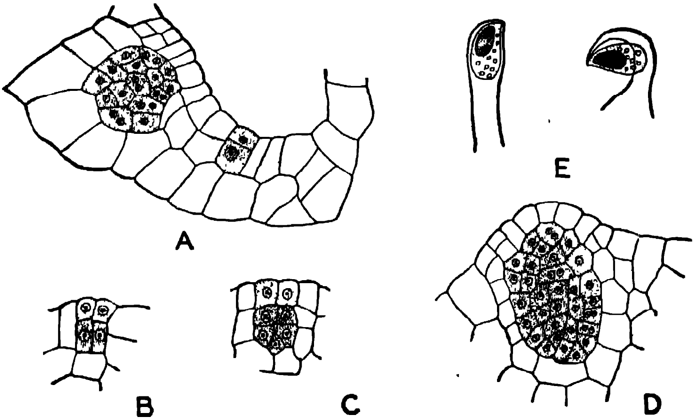

FIG. 184. Antheridial development in *Lycopodium clavatum*, ×150. *A*, to the right, a young antheridium after first division of initial cell, to the left, a much older stage; *B*, vertical division of primary wall cell and primary spermatogenous cell; *C*, further division of spermatogenous cells; *D*, nearly mature antheridium, showing wall and spermatogenous tissue; *E*, two sperms, ×625. (*After Bruchmann.*)

In fact, in some species, a spore will produce a green prothallium if it germinates on the surface of the ground and a colorless one if it germinates below the surface.

Both kinds of sex organs are borne in rather large numbers on the same gametophyte. The antheridia are either completely embedded or slightly projecting. They are globular, have a sterile jacket consisting of a single layer of cells, and produce many small, slightly curved, biciliate sperms (Fig. 184). In development, a superficial initial divides by a periclinal wall to form an outer *primary wall cell* and an inner *primary spermatogenous cell*. The former gives rise to the sterile jacket, the latter to the mass of spermatogenous tissue.

The archegonia are also embedded in the prothallium, only the neck protruding (Fig. 185). The initial is superficial and gives rise, by a periclinal division, to an outer *primary neck cell* and an inner cell that again divides to form the *central cell* and *basal cell* (Fig. 185*A*, *B*). The central cell gives rise to two cells, the outer one being the *primary neck canal cell* and the inner one the *primary ventral cell* (Fig. 185*C*). The primary neck canal cell, by additional transverse divisions, gives rise to a variable number of *neck canal cells,* while the primary ventral cell, by a single transverse division, produces the *ventral canal cell* and *egg* (Fig. 185*D–F*). In some species there are 4 to 6 neck canal cells. In *Lycopodium cernuum* the number has been reduced to 1, while in *Lycopodium complanatum* as many as 16 have been counted. The presence of numerous neck canal cells is a primitive feature not seen in other living pteridophytes.

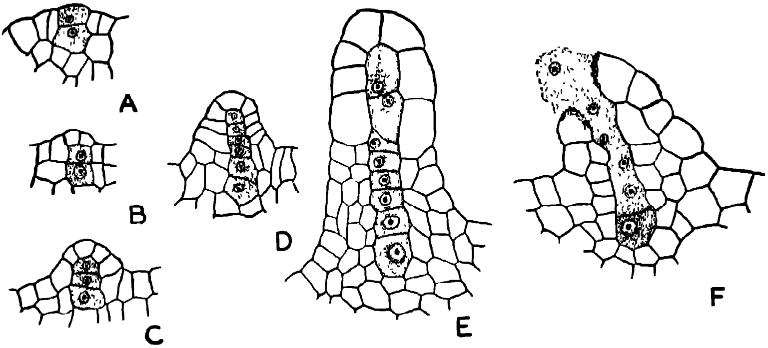

FIG. 185. Archegonial development in *Lycopodium clavatum,* ×150. *A*, young archegonium after first division of initial cell; *B*, vertical division of primary neck cell and transverse division of inner cell to form basal cell and central cell (both shaded); *C*, division of central cell to form primary neck canal cell and primary ventral cell; *D*, later stage, showing basal cell, primary ventral cell, and four neck canal cells, *E*, nearly mature archegonium with egg, ventral canal cell, and six neck canal cells; *F*, older stage, the canal cells breaking down. (*After Bruchmann.*)

Embryo. The fertilized egg divides transversely to form an outer suspensor cell and an inner embryonal cell (Fig. 186*A*). The suspensor cell may or may not divide again but usually elongates and pushes the embryo a short distance into the prothallium. The embryonal cell, by two vertical divisions at right angles to each other, gives rise to quadrants, each of which then divides transversely to form eight cells in two tiers (Fig. 186*B–E*). Of these, the tier lying next to the suspensor develops the foot, while the lower tier gives rise on one side to the stem and on the other side to the leaf (Fig. 186*F–I*). The foot is a temporary organ that absorbs food from the gametophyte. It persists until the sporophyte has become independent. The primary root is formed relatively late and arises from the same tissue that produces the leaf.

Summary. In *Lycopodium* an elongated, generally branched stem bears numerous small leaves. In *Phylloglossum* a short tuberous stem produces a few small leaves in a cluster. The vascular system of the stem of *Lycopodium* is a protostele, fundamentally radial in organization, with exarch development of xylem. Secondary thickening is absent. In the simplest species of *Lycopodium* all the leaves are sporophylls, but in the more advanced species a differentiation exists between sporophylls and foliage leaves, the former forming a more or less distinct strobilus. All the Lycopodiales are homosporous. Dehiscence of the sporangium occurs by means of a transverse slit. The gametophyte is a subterranean tuberous body, sometimes with an aerial portion. The antheridia develop endogenously and produce many small biciliate sperms similar to those of bryophytes. The archegonia are primitive, being characterized by a large number of neck canal cells. The embryo has a suspensor. On the whole, the Lycopodiales are a very primitive group of pteridophytes.

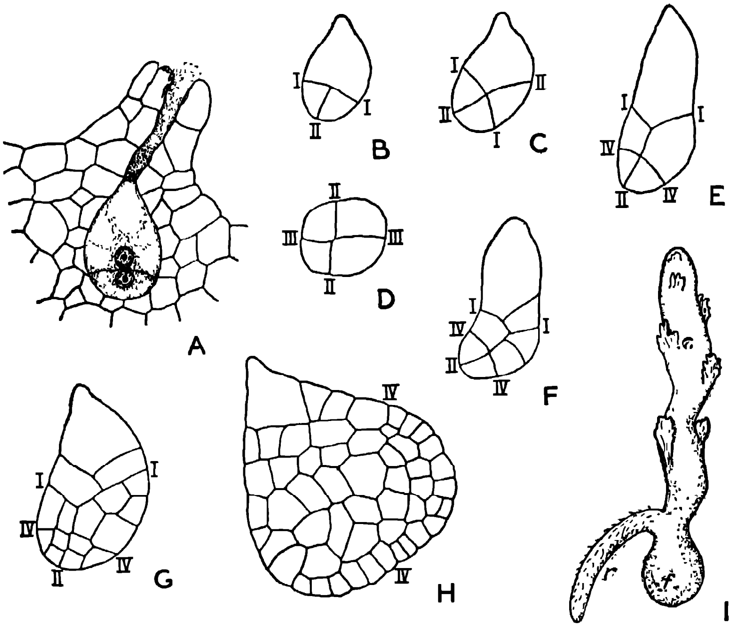

Fig. 186. Development of the embryo of *Lycopodium clavatum*. *A*, first division of the fertilized egg into suspensor and embryonal cells; *B*, second division of embryonal cell; *C*, second division of suspensor cell, *D*, cross section, showing third division of embryonal cell; *E*, transverse division (IV) of four cells derived from the embryonal cell; *F*, *G*, *H*, later stages; *I*, young sporophyte, showing foot (*f*), primary root (*r*), and stem bearing scale leaves. (*After Bruchmann.*)

2. Selaginellales

The Selaginellales include a single genus, *Selaginella*, with nearly 700 species. The great majority of these are tropical or subtropical in distribution, but a few occur in temperate regions. Most species require abundant moisture and shade, while some grow in open, dry situations. *Selaginellites*, a fossil genus, has been recognized in deposits as old as the Lower Carboniferous.

Sporophyte. In general, the sporophyte of *Selaginella* has the same habit as that of *Lycopodium*, but is nearly always smaller and more delicate. The stems are dichotomously branched and usually trailing, but are often erect or climbing. *Rhizophores*, which are special leafless branches of the main stem, are found in many species. They produce adventitious roots at their tips. The leaves are scale-like and numerous, generally occurring in four longitudinal rows. Each leaf bears a *ligule*, a minute flap-like outgrowth arising from the basal portion of the adaxial surface. The ligule is prominent only during the early development of the leaf.

In some species of *Selaginella* the leaves are all alike and symmetrically arranged around the stem, but in most species the leaves are spread out horizontally and usually of two kinds. These are regularly arranged with reference to each other, there being two rows of small dorsal leaves and two rows of large ventral ones (Fig. 189*A*). In contrast to *Lycopodium*, a definite apical cell is usually present at the tip of the root and stem, but some species appear to have an apical meristem (Fig. 187).

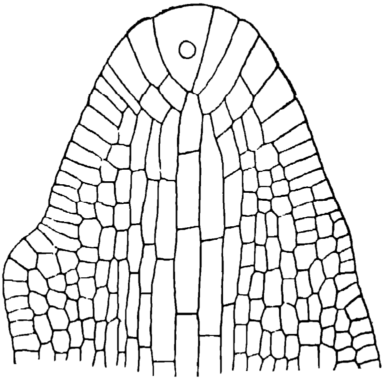

FIG. 187. Median longitudinal section through the stem tip of *Selaginella bigelovi*, showing the apical cell and its derivatives, × 500.

Vascular Anatomy. The leaves have an epidermis and a loose mesophyll, the stomata usually being confined to the lower surface. The chloroplasts are large and few in number, sometimes only one occurring in each cell. Each leaf has a single median vein. The adult stem generally consists of a single, dorsiventrally flattened protostele with two lateral protoxylem groups (Fig. 188). The metaxylem develops toward the center, and so the stem is exarch. In some species the stele is cylindrical and in some two, three, or more separate steles are present. One species has reached the siphonostelic condition. The conducting tissues show an amphicribral arrangement, the xylem being completely surrounded by the phloem. Outside the pericycle, which is generally one-layered, a broad air space occurs. This is traversed by elongated cells (trabeculae) consisting of endodermal cells united with one or more cells that have a common origin with the endodermis. As in *Lycopodium*, no cambium is present and so there is no secondary thickening. In some species the cortical cells are thick-walled.

Sporangia. In all species of *Selaginella* definite terminal strobili are present. Where the foliage leaves are all alike, the sporophylls and leaves are either similar or only slightly differentiated. Where the foliage leaves are of two kinds, the sporophylls are smaller than the large leaves (Fig. 189*A*). As in *Lycopodium*, the sporangia are solitary, adaxial, unilocular, and eusporangiate in development (Fig. 189*B*, *C*). Each is probably derived from a transverse row of initials. These generally appear on the stem just above the place where the young sporophyll arises from it (Fig. 190*A*–*C*). Although cauline in origin, the young sporangium is soon carried out on the sporophyll and then looks as if it had originated there. The wall of the young sporangium consists of a single layer of cells but it soon becomes two-layered. In contrast to the other lycopods, the tapetum is not derived from the wall tissue but from the outermost layer of sporogenous tissue. As in *Lycopodium*, it does not break down until the spores are formed. The innermost wall layer also disorganizes at this time, and so the mature sporangium has only a single layer of wall cells. Each sporangium is borne on a short stalk. Dehiscence takes place by means of a vertical slit.

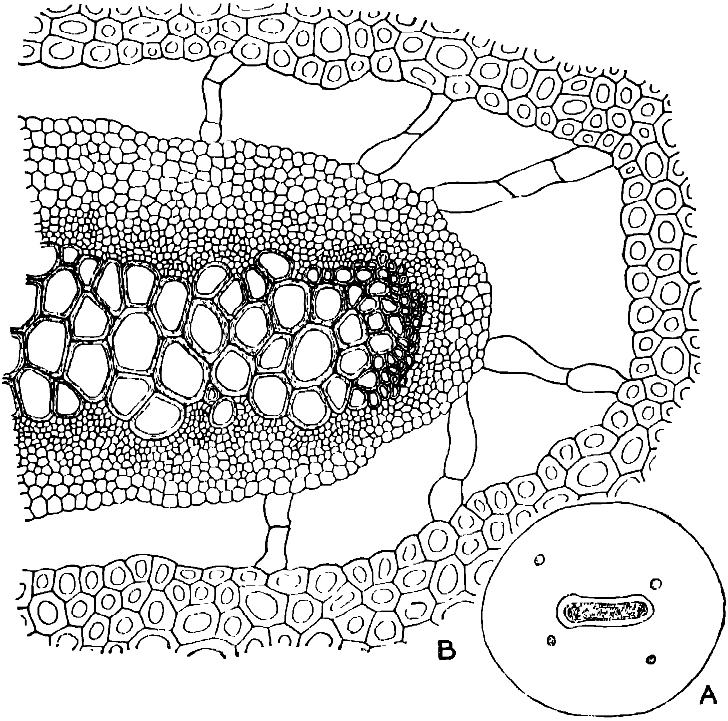

FIG. 188. Stem structure of *Selaginella flabellata*. *A*, diagram of cross section, showing central flattened protostele surrounded by cortex, × 10 *B*, enlarged view of portion of stele, showing exarch xylem surrounded by a wide zone of phloem and an air space traversed by trabeculae, × 200.

Selaginella is heterosporous, each strobilus usually bearing two kinds of sporangia—*microsporangia* and *megasporangia* (Fig. 189*B*, *C*). The microsporangia, which are often reddish, generally occur in the upper part of the strobilus, while the megasporangia, which are commonly yellowish, are borne below. The megasporangia are usually slightly larger than the microsporangia and are generally four-lobed.

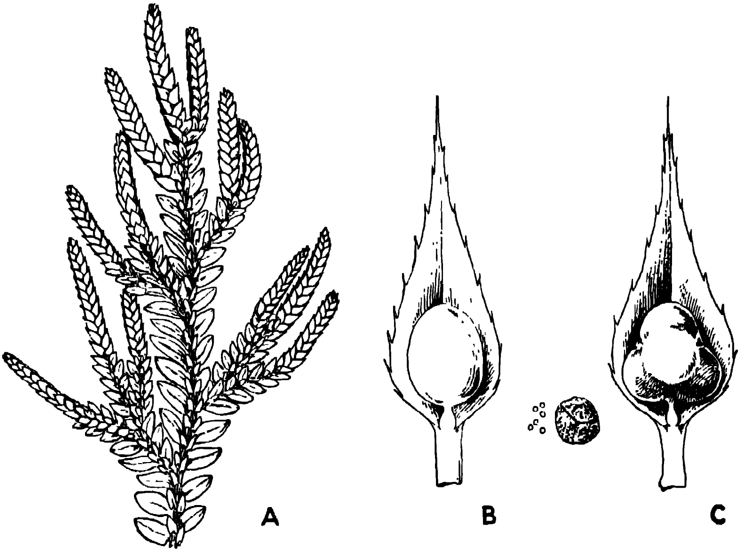

FIG. 189. *Selaginella willdenovii* *A*, branch with leaves and strobili, twice natural size; *B*, a microsporophyll with a microsporangium containing numerous microspores, ×25; *C*, a megasporophyll with a megasporangium containing four megaspores, ×25, several microspores and a megaspore drawn to the same scale are also shown.

Both kinds of sporangia develop alike as far as the stage in which the sporogenous tissue is differentiated. In the microsporangium practically all the mother cells divide to produce tetrads, and consequently many small spores are formed (Fig. 192*A*). These are the *microspores*. In the megasporangium, on the other hand, all the mother cells degenerate but one, which greatly enlarges and forms a tetrad of thick-walled spores that eventually fill the sporangium (Figs. 191 and 192*B*). These are the *megaspores*. The sporophylls that produce the microsporangia are *microsporophylls*, while those bearing megasporangia are *megasporophylls*. Usually the sporophylls themselves, however, are of approximately the same size and form. Like the foliage leaves, each sporophyll bears a ligule. It is situated just beyond the sporangium (Figs. 190 and 192).

Upon germination, the microspores give rise to male gametophytes and the megaspores to female gametophytes. Thus heterospory involves not only a differentiation of spores but also a differentiation of gametophytes,

Gametophytes. The male gametophyte of *Selaginella* is developed entirely within the microspore. It is without chlorophyll and greatly reduced. Its development is initiated before the spore is shed from the sporangium and is completed later. A small *prothallial* or *vegetative* cell is cut off, the large remaining cell forming a single antheridium (Fig. 193). At first this consists of four primary spermatogenous cells surrounded by a sterile jacket of eight cells, and usually the male gametophyte is shed from the microsporangium in this condition. Later the spermatogenous cells increase in number to 128 or 256, each finally giving rise to a sperm. Meanwhile the jacket cells disintegrate, leaving the mass of sperms free within the microspore wall. The sperms are small, curved, and biciliate.

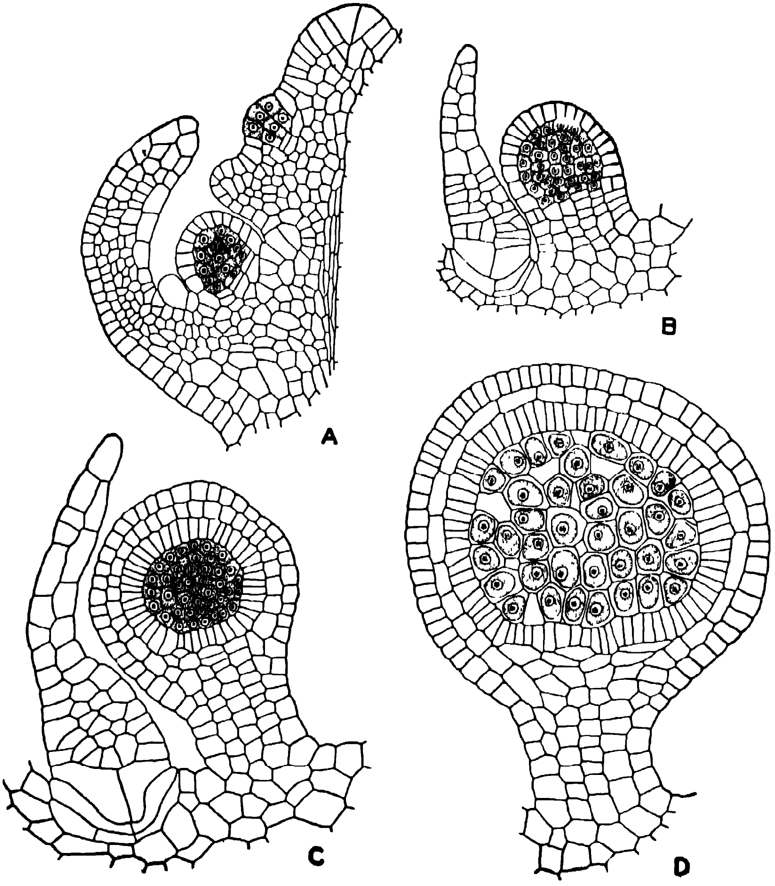

FIG. 190. Development of the microsporangium of *Selaginella galeottii*, ×320. *A*, median longitudinal section of portion of apex of strobilus, showing early stages; *B*, slightly later stage with ligule to the left; *C*, young sporangium with sporogenous tissue surrounded by tapetum and two wall layers; *D*, older sporangium, the sporogenous cells beginning to round up.

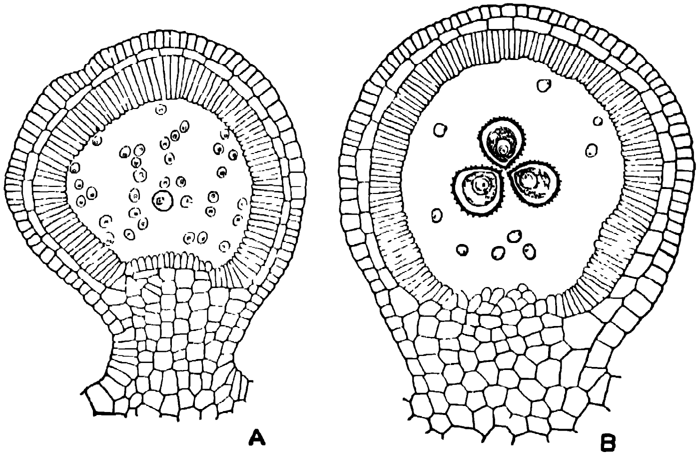

FIG. 191. Longitudinal sections of young megasporangia of *Selaginella*, ×200. *A*, megasporangium of *Selaginella emmeliana* with spore mother cells, the functional one enlarging; *B*, megasporangium of *Selaginella apoda*, showing three of the four megaspores.

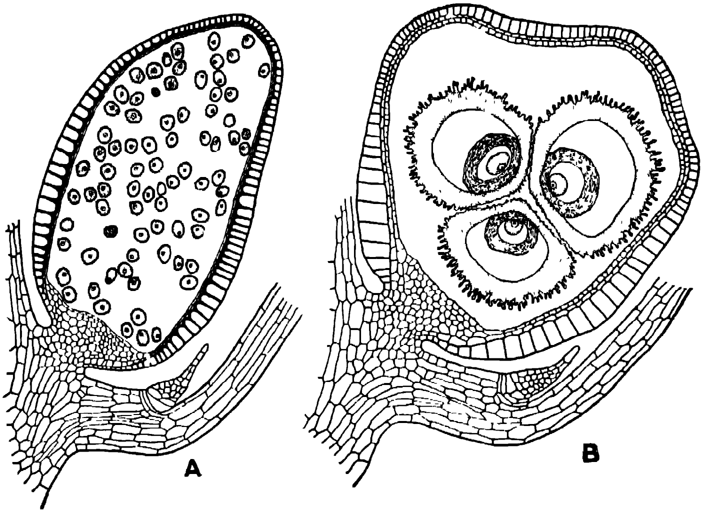

FIG. 192. Longitudinal sections of sporangia of *Selaginella emmeliana*, ×80. *A*, a microsporangium with numerous microspores; *B*, a megasporangium with three of the four developing megaspores.

The female gametophyte develops within the megaspore but is not so greatly reduced as the male gametophyte. The megaspore germinates while still within the megasporangium and long before it has reached its full size. The protoplast of the young megaspore is apically situated and consists of a vesicle with a small nucleus. It has a thick membrane that seems to grow more rapidly than itself, leaving a fluid-filled space between the protoplast and the membrane. The membrane soon differentiates into an outer and inner layer that also separate as a result of a more rapid growth of the outer layer, thus forming a second fluid-filled space (Figs. 191*B* and 192*B*). The female gametophyte begins to develop by free-nuclear division. Its protoplast enlarges until it comes in contact with the inner spore coat, which later comes in contact with the outer coat, thereby obliterating both cavities. The nuclei in the young gametophyte lie in a peripheral layer of cytoplasm surrounding a large central vacuole (Fig. 194*A*).

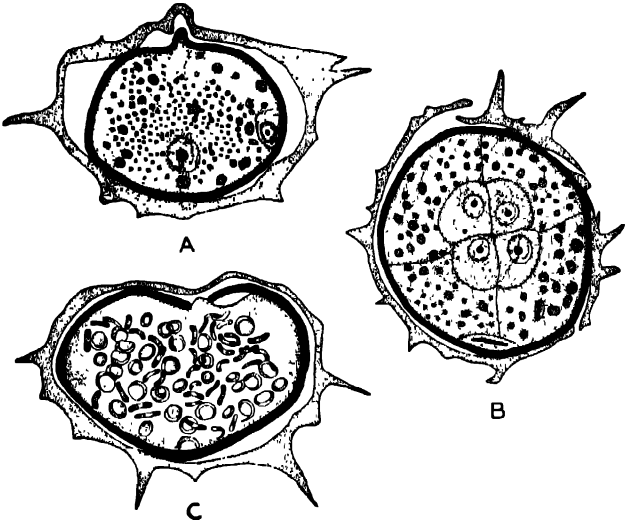

FIG. 193. Sections through the male gametophyte of *Selaginella kraussiana* in different stages of development. *A*, early stage, consisting of a small prothallial cell and an antheridial cell; *B*, later stage with prothallial cell and antheridium consisting of four primary spermatogenous cells surrounded by eight jacket cells, *C*, mature gametophyte with nearly ripe sperms lying free inside microspore wall. (*After Slagg.*)

After the female gametophyte has undergone a series of free-nuclear divisions, wall formation begins at the apical (pointed) end. At this place the spore wall ruptures and the gametophytic tissue protrudes slightly, developing archegonia and in some species rhizoids also, or rhizoids and chlorophyll. The main portion of the gametophyte, lying within the megaspore wall, acts as a large food reservoir. In many species there is a marked differentiation between the deeper nutritive region and the exposed portion, and often the former is not divided into cells (Fig. 194*B*). The development of the archegonium is similar to that of *Lycopodium* except that the neck is very short and no basal cell is formed. There is usually only one neck canal cell.

Although, in most species, the early development of the female gametophyte occurs while the megaspore is still within the megasporangium, archegonia generally do not appear until the megaspore is shed. In some species the megaspore is retained until fertilization has occurred, or even until the embryo has appeared. Here the male gametophytes are carried to the megasporophylls by wind or gravity and there they liberate their sperms. In such cases it is apparent that a condition closely approaching seed formation is reached.

Embryo. The embryo of *Selaginella* resembles that of *Lycopodium* in a general way, but shows certain important differences and some variation among the different species (Fig. 195). Commonly the first division of the fertilized egg, which is transverse, separates an outer suspensor cell from an inner embryonal cell, but the suspensor usually becomes more highly developed than in *Lycopodium*. No quadrant stage is formed. Instead the embryonal cell produces three cells - a terminal one, which forms the stem, and two lateral ones, each of which gives rise to a leaf. One of the leaf segments produces the foot and later the primary root. In some species the foot and root, as well as the suspensor, are derived from the upper cell that arises from the first division of the fertilized egg.

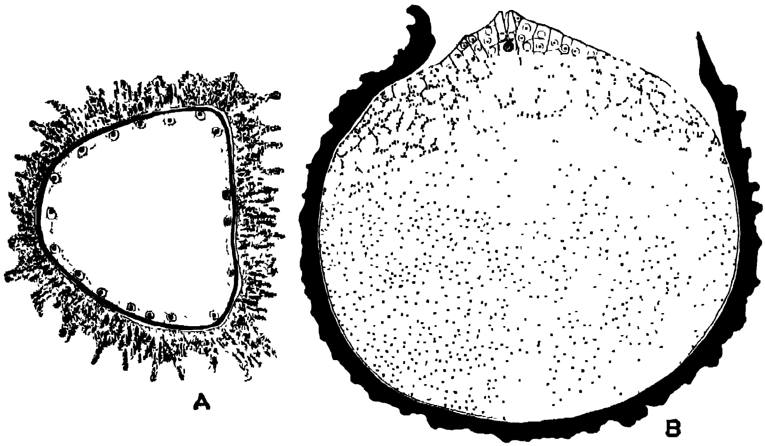

FIG. 194. Female gametophyte of *Selaginella apoda*. *A*, section of megaspore containing young gametophyte in free-nuclear stage; *B*, section of megaspore with mature gametophyte, consisting of a large nutritive cell and small-celled tissue in which an archegonium has developed (*After Lyon.*)

Summary. The stem of *Selaginella* is elongated and branched, the leaves numerous and small. Each leaf bears a ligule. The vascular system of the stem is typically an exarch protostele with amphicribral organization; sometimes more than one stele is present. There is no secondary thickening. All species have a definite strobilus and are heterosporous. The microsporangia produce many microspores, the megasporangia four megaspores. Dehiscence takes place by means of a vertical slit. The male gametophyte, developed entirely inside the microspore, consists of only one prothallial cell and one antheridium, the latter producing many small biciliate sperms. The female gametophyte, with relatively extensive vegetative tissue, develops largely within the megaspore, the protruding portion forming several archegonia. These are of an advanced type

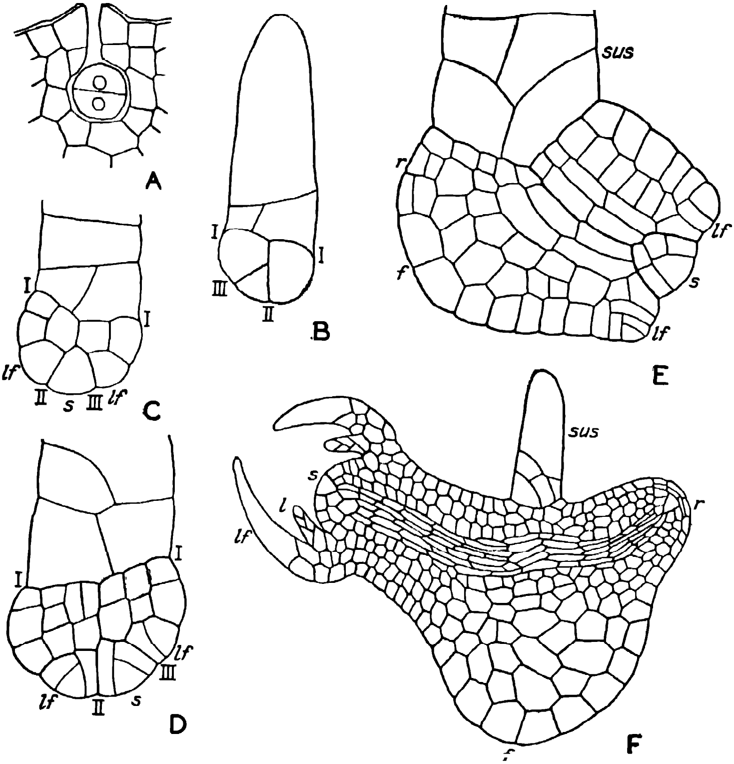

Fig. 195. Development of the embryo of *Selaginella martensii*. *A*, first division of fertilized egg into suspensor and embryonal cells, *B*, embryonal cell divided into three cells; *C*, differentiation of stem and leaf primordia; *D*, later stage, the stem and leaf primordia developing by an apical cell; *E*, later stage, showing differentiation of foot and root; *F*, older embryo; *sus*, suspensor; *s*, stem tip, *lf*, leaf; *l*, ligule; *r*, root tip; *f*, foot. (*After Pfeffer.*)

with only one neck canal cell. The embryo has a suspensor. *Selaginella* is related to *Lycopodium*, differing from it chiefly in being heterosporous.

3. Lepidodendrales

The Lepidodendrales are a Paleozoic group of lycopods. They ranged from the Devonian through the Permian but made their greatest display during the Upper Carboniferous, when they were one of the dominant plant groups. They were chiefly tree-like and often reached a height of 30 m. or more. The two most prominent genera were *Lepidodendron* and

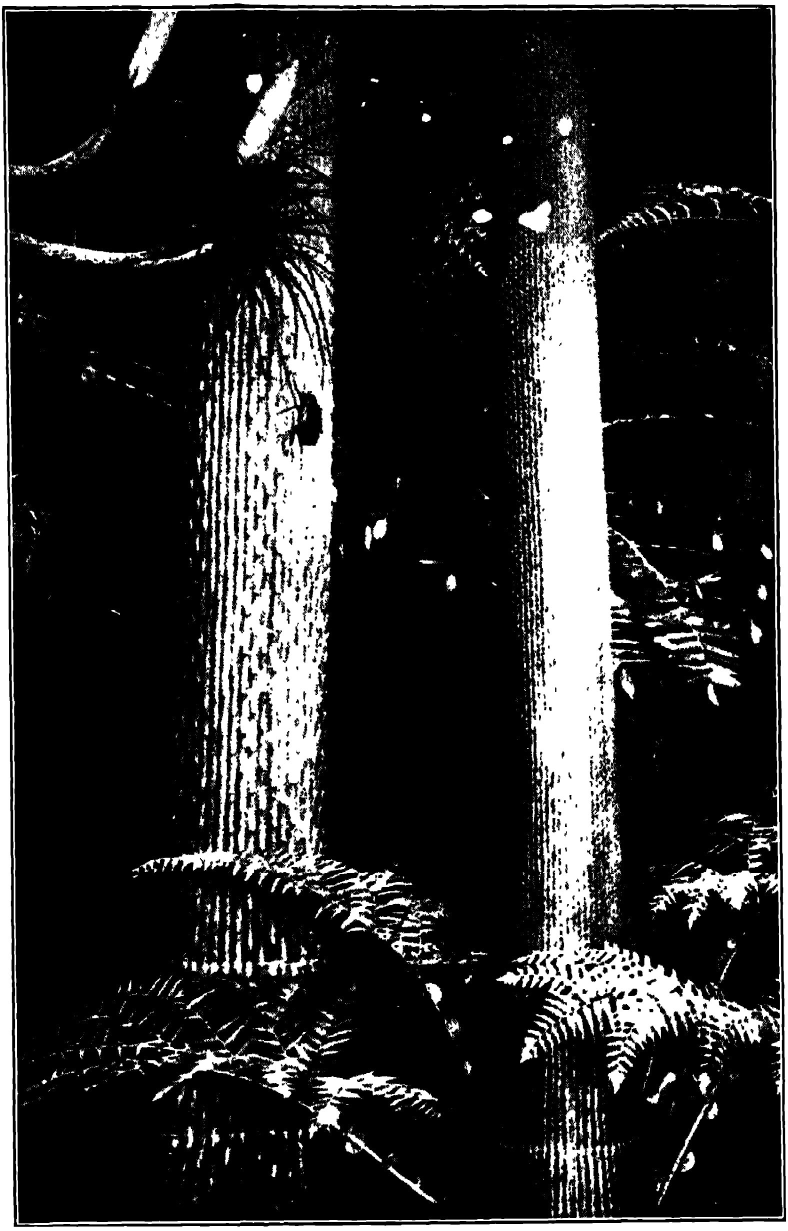

FIG. 196. Portion of restoration of Carboniferous swamp forest in the Chicago Natural History Museum, showing trunks of *Sigillaria rugosa* (to left) and *Sigillaria saulli* (to right), and cones of *Lepidostrobus ovatifolius* (upper left); also two seed ferns: *Neuropteris decipiens* (right center) and *Neuropteris heterophylla* (below).

Sigillaria[1] (Fig. 196). Both bore numerous narrow simple leaves that, upon falling, left characteristic scars on the stem. The stems of *Lepidodendron* were dichotomously and freely branched and the leaves were frequently up to 15 or 20 cm. long. The stems of *Sigillaria* were slightly or not at all branched and the leaves, in some species, reached a length of 1 m. The leaves of all the Lepidodendrales had a single vascular bundle and in all of them a ligule, deeply sunken in a pit, was present. In both *Lepidodendron* and *Sigillaria* the base of the main stem was attached to four descending branches (rhizophores) that spread out horizontally and underwent repeated forking. They were covered with roots.

FIG. 197. Transverse section of stem of *Lepidodendron wunschianum*, an ectophloic siphonostele. The central pith is surrounded, in turn, by a narrow cylinder of primary wood, an extensive zone of secondary wood, and an outer layer of bark.

The stem was either a protostele or, more commonly, an ectophloic siphonostele (with the phloem outside the xylem). A primitive feature was the presence of exarch primary wood. The stem was characterized by marked secondary thickening (Fig. 197). The stem of *Sigillaria* sometimes reached a diameter of 2 m.

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[1] Plant fossils usually occur as detached organs or fragments. Only rarely is one part of the plant found attached to another part. Until such connections are found, detached organs of the same kind are placed in a "form genus." For example, *Lepidodendron* was originally a stem genus. Its leaves were placed in the form genus *Lepidophyllum* and its cones in *Lepidostrobus*. Its root-bearing parts, indistinguishable from those of *Sigillaria*, are included in the form genus *Stigmaria*.