to the leaf, two leaf traces girdle the cortex in opposite directions, each passing about halfway around the stem in going from their point of origin to the leaf.

The cones of the Bennettitales, each occurring in the axil of a leaf, are borne laterally along the stem. In *Macrozamia* and *Encephalartos* the cones are also lateral and axillary, although arising close to the stem tip.

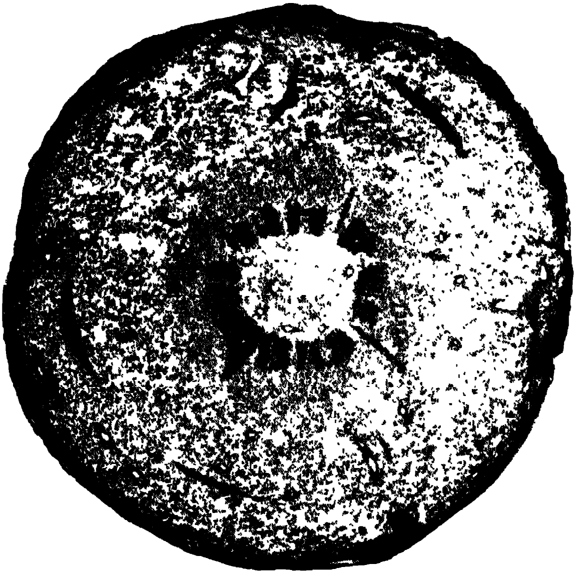

FIG. 269. Cross section of the stem of *Zamia floridana*, showing large pith, thin vascular cylinder, and thick cortex with portions of the girdling leaf traces, ×4.

In the other genera the original apical meristem is used up in the formation of a cone, and a new meristem appears at its base. This produces a branch that soon becomes erect and gives rise to a new crown of leaves. Thus the first cone produced by a plant is terminal, but all the rest are morphologically lateral, although borne at the summit of the stem. All cycads are monosporangiate and dioecious.

Staminate Strobilus. The staminate strobili are usually borne singly, but in *Zamia*, *Macrozamia*, and *Encephalartos* several or many may occur together (Fig. 270*B*). They are composed of an axis bearing many spirally arranged microsporophylls (stamens) that are always compactly organized. The microsporophylls are not at all leaf-like, but are narrow below and broadened above into a sterile tip (Fig. 271). The microsporangia are abaxial and borne in sori of two to five, but not in synangia. They range in number from over a thousand on each sporophyll in *Cycas* to a comparatively few in *Zamia*. Their development is eusporangiate, the initials being hypodermal in origin rather than epidermal as in the

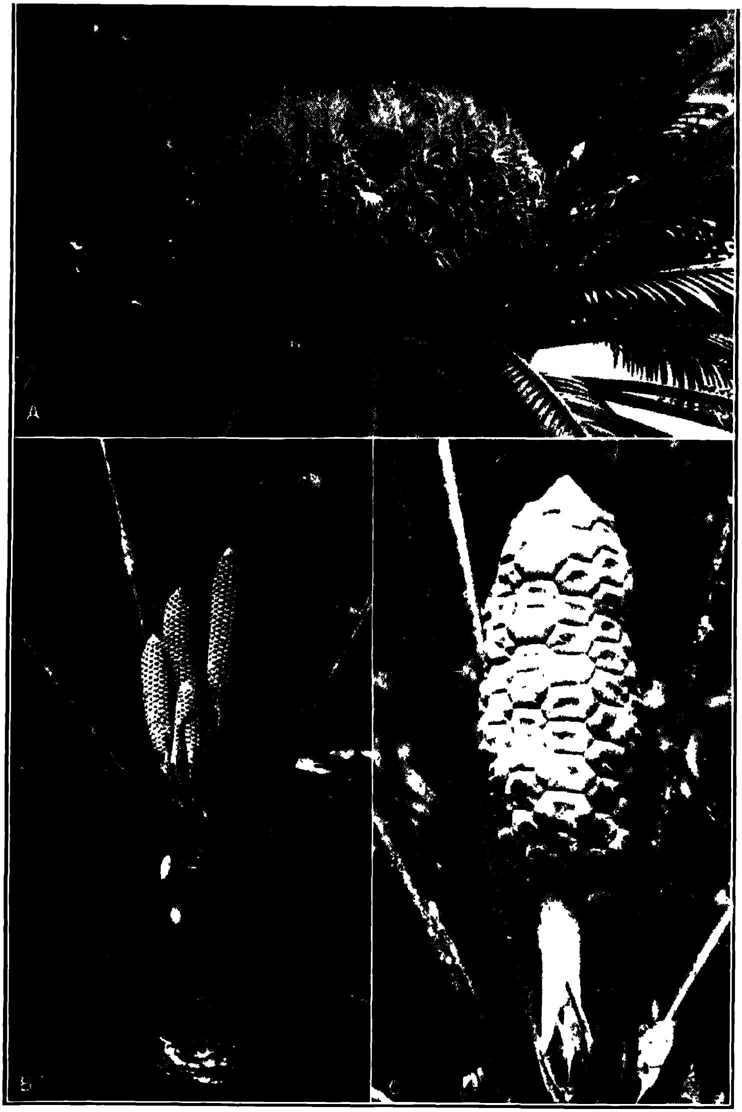

FIG. 270. Cones of cycads. *A*, female cone of *Cycas revoluta*, consisting of a loose rosette of megasporophylls; *B*, male cones of *Zamia skinneri*; *C*, female cone of *Zamia skinneri* with nearly ripe seeds.

pteridophytes. There may be only one initial or a row or plate of several initials. The initials divide transversely, the outer segments being the primary wall cells and the inner ones the primary sporogenous cells. A wall several layers in thickness is developed (Fig. 272). The tapetum is cut off rather late, and so it is uncertain whether it is derived from the wall or from the sporogenous tissue. The number of spores produced by each sporangium is high, ranging from 500 in *Zamia* to 30,000 in *Dioon*. Dehiscence occurs by means of a longitudinal slit. In general, the microsporangium of the cycads shows a striking resemblance to the sporangium of the Marattiales, particularly to that of *Angiopteris* (Fig. 229).

Ovulate Strobilus. In most genera the ovulate cones are borne singly, but in *Macrozamia* and *Encephalartos* they may occur in groups of two, three, or more. They are composed of many spirally arranged, fleshy megasporophylls (carpels). In *Cycas* the megasporophylls are very loosely arranged to form a rosette that surrounds the stem tip, which later continues its growth upward through the rosette (Fig. 270*A*). In *Dioon* the megasporophylls form a loose cone, but in all the other genera they are compactly organized (Figs. 267 and 270*C*). The megasporophylls of cycads exhibit a striking reduction series, ranging from pinnate types with six or eight ovules, in most species of *Cycas*, to peltate types with only two ovules, in the other genera (Fig. 273). Throughout this series the megasporophylls become less and less leaf-like and the strobilus increasingly more compact.

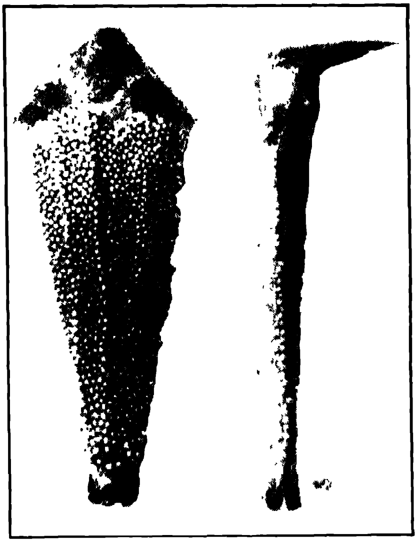

FIG 271 Microsporophylls of *Cycas circinalis*, showing back (abaxial) and side views, one and one-half times natural size

The main body of the ovule is the *nucellus* or megasporangium proper. It is surrounded by a single massive *integument* free from the nucellus only at its upper end and forming a narrow passageway, the *micropyle* (Fig. 274). A prominent nucellar beak is developed, in the center of which a pollen chamber later arises. The integument consists of an outer fleshy, a middle stony, and an inner fleshy layer. Vascular strands are found in both fleshy layers. They are composed of mesarch xylem. Deep within the nucellar tissue a megaspore mother cell becomes differentiated. It gives rise to a linear tetrad of megaspores. Of these, only the innermost megaspore functions, the other three degenerating.

Female Gametophyte. As in all seed plants, the megaspore germinates *in situ*, producing the female gametophyte. Its formation involves several stages. First, the megaspore enlarges and free-nuclear division occurs. Then, by further enlargement, a central vacuole is formed, resulting in a parietal placing of the nuclei. As nuclear division proceeds, walls come in, forming a tissue. This tissue develops centripetally until it reaches the center of the gametophyte. Two regions are now differentiated—a region of smaller cells that develops archegonia, situated near the micropylar end, and a deeper region of larger, nutritive cells.

As a rule, 3 to 5 archegonia are formed, but there may be as many as 10. In *Microcycas*, which is unique in this respect, as many as 200 archegonia may appear. The archegonium initial is superficial and, by a periclinal division, an outer *primary neck cell* is differentiated from a *central cell* (Fig. 275*A*, *B*). The former undergoes a vertical division, thus forming two *neck cells*, a constant feature throughout the Cycadales (Fig. 275*C*, *D*). There are no neck canal cells. The central cell undergoes a marked enlargement. Its nucleus divides to form a *ventral canal nucleus* and an *egg nucleus*, but no wall is laid down between them. The ventral canal nucleus soon disorganizes and the egg is now ready for fertilization. An *archegonial chamber* is not present when the archegonia are young, but arises later. It is a depression formed by upgrowth of the adjacent tissue of the female gametophyte.

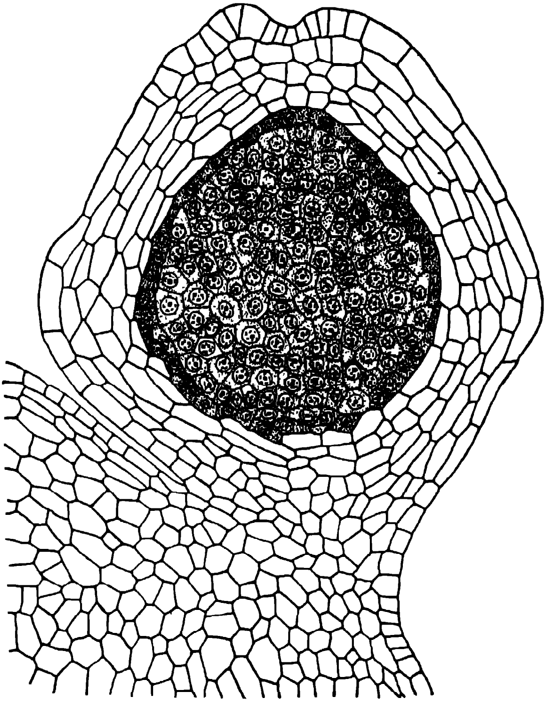

FIG. 272. Longitudinal section of microsporangium of *Zamia floridana*, showing sporogenous tissue surrounded by the tapetum (both shaded) and a wall five or six layers thick, ×150.

Male Gametophyte. The first division of the microspore nucleus results in the formation of a small persistent prothallial cell that is cut off close to the microspore wall. The larger cell divides again to form the *generative* and *tube cells*, and in this condition the pollen grain is shed (Fig. 276*A*, *B*). The pollen is transported by wind to the ovulate cone, whose sporophylls separate slightly at the time of pollination. A group of cells at the apex of the nucellus break down and form a droplet of liquid that exudes through the micropyle and to which some of the pollen grains adhere. As the droplet dries, the grains are drawn down into the pollen chamber formed by the disintegration of the cells that produced the droplet. Then a pollen tube develops from each pollen grain, growing laterally into the nucellus. Its basal end advances downward, carrying the prothallial and generative cells with it. In the cycads the pollen tube is an absorbing organ, obtaining nourishment from the nucellar tissue, which is thereby destroyed. Soon after the pollen tube has begun to develop, the generative cell forms the *stalk* and *body cells*, the latter finally giving

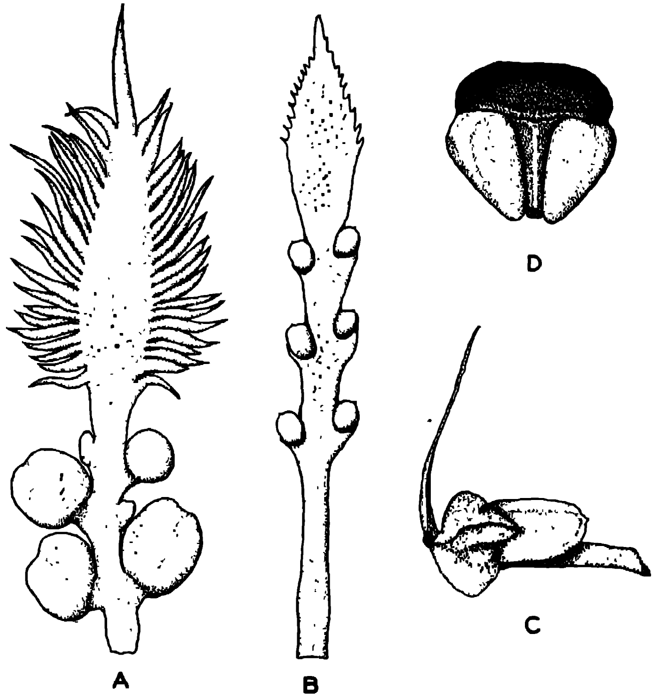

FIG. 273. Megasporophylls of cycads. *A*, *Cycas revoluta*, showing pinnate blade with conspicuous leaflets; *B*, *Cycas circinalis*, the leaflets reduced to teeth; *C*, *Macrozamia denisonii*, side view of sporophyll, the blade reduced to a spine; *D*, *Zamia floridana*, with peltate sporophyll; *A*, *B*, *C*, two-fifths natural size; *D*, four-fifths natural size.

rise to two *sperm mother cells* (Figs. 276*C–E*). From each of these a motile sperm is organized. The sperms of cycads are large and multiciliate, the cilia arising from a blepharoplast (Figs. 277 and 278). In *Microcycas* 16 to 22 sperms are formed in each pollen tube.

After the pollen tube has penetrated the nucellar tissue and entered the archegonial chamber, it ruptures and frees the sperms, which then make their way toward the archegonia (Fig. 278). An entire sperm enters an egg, but its nucleus soon separates from the cytoplasm and band of cilia, moving toward the egg nucleus and fusing with it.

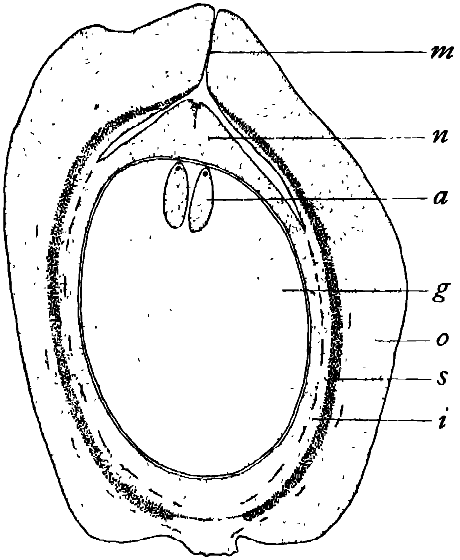

FIG 274 *Zamia floridana*. Longitudinal section of the ovule shortly after pollination, ×4. *m*, micropyle; *n*, nucellus; *a*, archegonium, *g*, female gametophyte; *o*, outer fleshy layer of integument; *s*, middle stony layer; *i*, inner fleshy layer.

Embryo. The nucleus of the fertilized egg undergoes 8 to 10 simultaneous divisions (only 6 in *Bowenia*) without the formation of cell walls (Fig. 279*A*). As a result, as many as over a thousand free nuclei may be produced. This free-nuclear stage is common to all cycads, but differences now appear. In the *Cycas* type of embryogeny persistent cell walls are formed throughout the fertilized egg. In the *Dioon* type cell walls appear throughout the egg but soon disappear except at its base. In *Zamia* wall formation is confined to the basal portion, not even evanescent walls appearing in the main body of the egg (Fig. 279*B*).

The cells at the base of the egg constitute the *proembryo*. Even where persistent cell walls appear above, the upper portion functions as a large food reservoir, contributing no cells to the formation of the new plant.

The proembryo soon becomes differentiated into three regions: an upper haustorial portion in contact with the nutritive material above, a middle zone of elongating cells forming the suspensor, and a terminal group of cells constituting the embryo itself (Fig. 279C). The suspensor becomes enormously elongated and highly coiled, pushing the embryo deep within

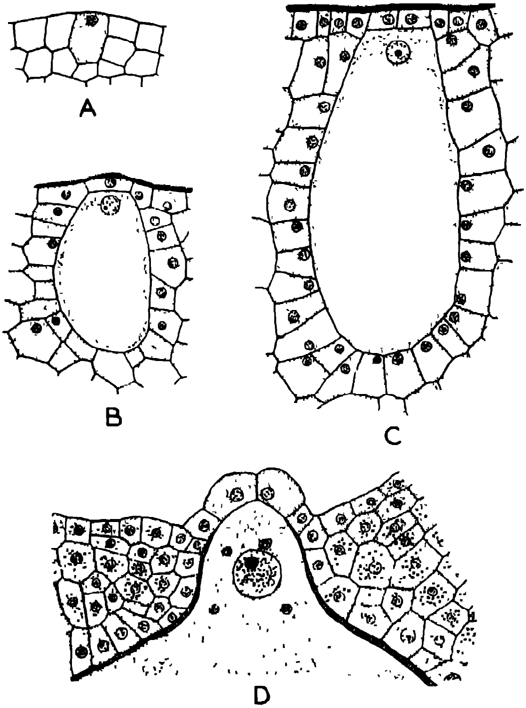

FIG. 275. Development of the archegonium of *Dioon edule*, ×85. *A*, archegonium initial; *B*, formation of primary neck cell and central cell; *C*, later stage with two neck cells; *D*, upper portion of archegonium with two neck cells and central cell nucleus. (*After Chamberlain.*)

the tissue of the female gametophyte. When mature, the embryo has a short axis, the *hypocotyl*, terminating at the end next to the suspensor in a root tip, or *radicle*. This is enclosed in a hard covering, the *coleorhiza*. At the opposite end of the hypocotyl is a minute stem tip, the *plumule*, lying between a pair of seed leaves, or *cotyledons*. The presence of two cotyledons is a constant feature of the Cycadales. As the embryo develops, food is stored in the vegetative tissue of the female gametophyte, forming "endosperm." This is a feature of all gymnosperms. The stored food is later absorbed by the embryo when the seed germinates. The ripe seed is usually white, cream-colored, orange, or red.

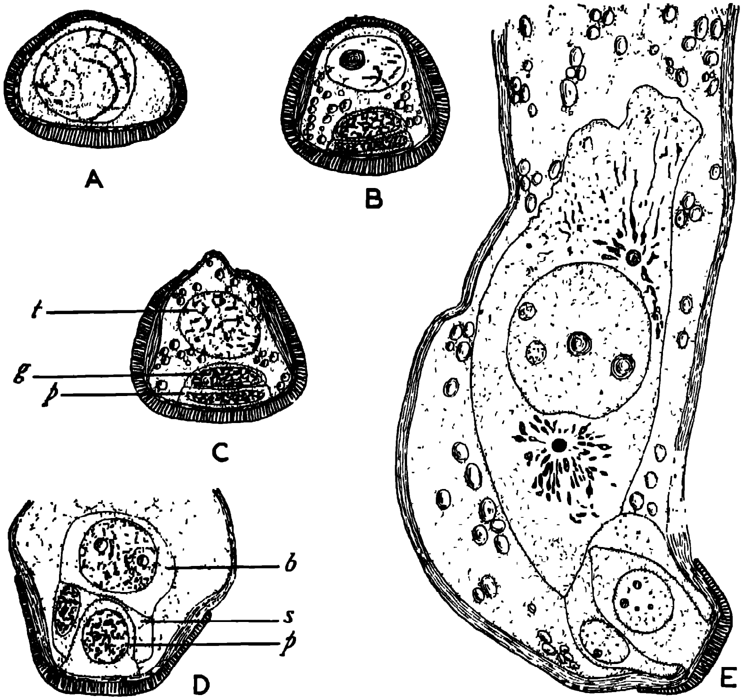

FIG. 276. Development of the male gametophyte of *Dioon edule*. *A*, microspore with nucleus in early prophase of first mitosis; *B*, shedding condition of pollen grain; *C*, beginning of pollen tube formation, showing prothallial cell (*p*), generative cell (*g*), and tube nucleus (*t*); *D*, formation of stalk cell (*s*) and body cell (*b*) from generative cell, *E*, later stage, the body cell much elongated and with two blepharoplasts showing conspicuous radiations; *A*, *B*, *C*, ×1,235; *D*, ×980; *E*, ×618. (*After Chamberlain.*)

The cycads are unique in that the seed germinates promptly, without going into a resting stage. The stony coat is broken by the coleorhiza enclosing the elongating root tip. The coleorhiza is soon destroyed by the root tip, which then rapidly grows downward into the soil. The stem remains inconspicuous, but a leaf soon develops. The cotyledons remain inside the seed coat, absorbing food from the "endosperm" and transferring it to the developing seedling.

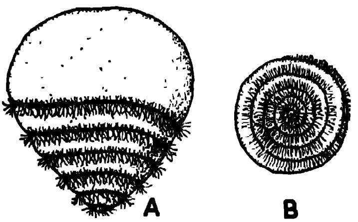

FIG. 277. Side (*A*) and top (*B*) views of a sperm of *Zamia floridana*, showing numerous cilia on a spiral band, ×100. (*After Webber.*)

Summary. The cycads resemble the ferns in their general habit, vascular anatomy, form and venation of the leaves, occurrence on the microsporophylls of abaxial sporangia in sori, structure of the microsporangia, and multiciliate sperms. All these characters, as well as the ovule structure,

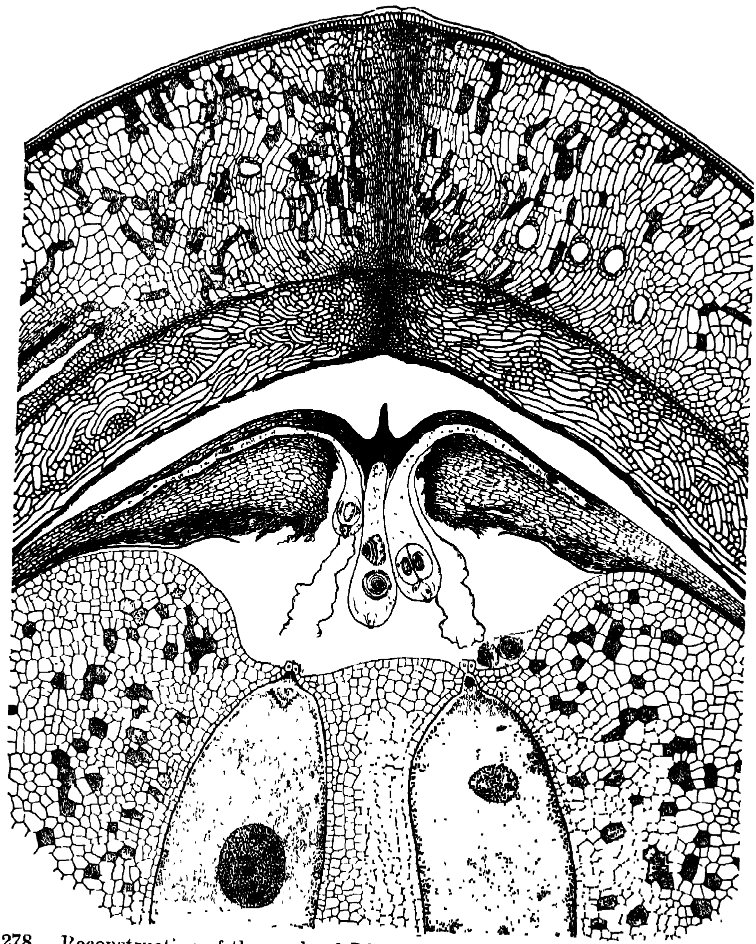

FIG. 278. Reconstruction of the ovule of *Dioon edule* at the time of fertilization. Pollen tube on the left shows undivided body cell, the one in the middle shows two sperms and remains of prothallial and stalk cells; the one on the right shows two sperm mother cells. Two pollen tubes have discharged their sperms. A sperm has entered the egg on the left; the one on the right still shows the ventral canal nucleus. Two sperms, in the thick liquid discharged from the pollen tube just above them, are ready to enter the egg. The dark line below the nucellus is the megaspore membrane. (*From Chamberlain.*)

are common to the Cycadofilicales, Bennettitales, and Cycadales. These three orders, considered together, are called cycadophytes. They represent a distinct line of evolution reaching far back into the Paleozoic. The stem of the Cycadales, like that of the Bennettitales, is an endarch siphonostele with a narrow zone of wood, the xylem in other aerial parts of the plant being mesarch. The dicotyledonous embryo is also suggestive of that of the Bennettitales. As compared with the other cycadophytes, the

Cycadales display the following distinctive features: infrequent branching of the stem, indirect and double leaf traces, monosporangiate and apparently terminal strobili, reduced microsporophylls, and, except in *Cycas*, reduced peltate megasporophylls with only two ovules.

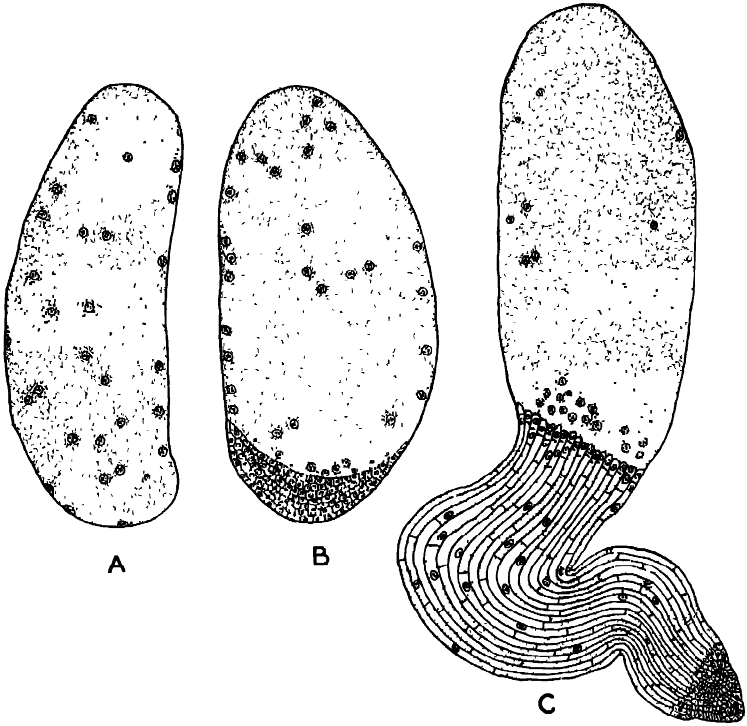

FIG. 279. Early stages in embryogeny of *Zamia floridana*, ×25. *A*, proembryo with free nuclei; *B*, wall formation at base of proembryo; *C*, differentiation into suspensor and embryo.

4. Cordaitales

The Cordaitales comprise an extinct group of Paleozoic gymnosperms, contemporaneous with the Cycadofilicales, but plants of a very different aspect. They appeared late in the Devonian, made their greatest display during the Upper Carboniferous, and almost disappeared before the end of the Permian (Fig. 258). Although the Cordaitales differ in many ways from the Cycadofilicales, their resemblances are such as to indicate that both groups may have had a common origin.

Sporophyte. The Cordaitales were tall trees with slender, branched stems often reaching a height of 30 m. (Fig. 280). The branches were covered with simple leaves that were generally long and narrow and borne in spiral arrangement. A cross section of the stem, which was an ectophloic siphonostele, shows a large pith, a thick or thin vascular cylinder, and a small cortex. In contrast to the mesarch collateral bundles of the Cycadofilicales, those of the Cordaitales were endarch and collateral. Secondary wood was well developed, its tracheids having bordered pits in

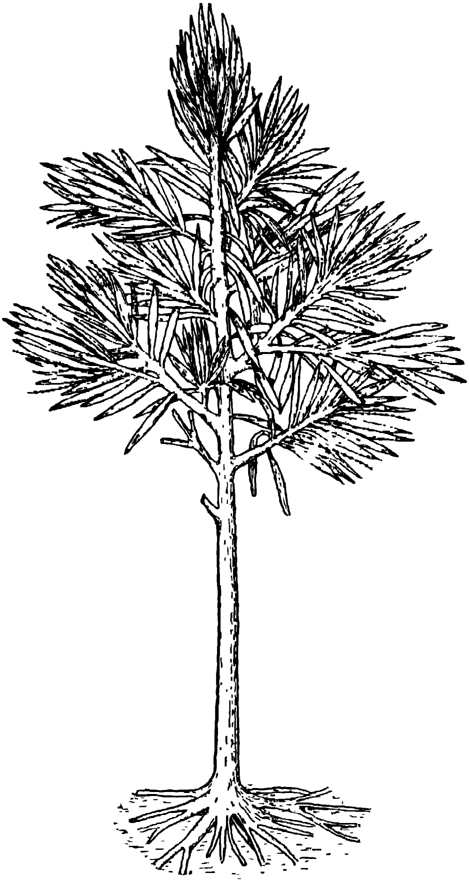

FIG. 280. Restoration of *Dorycordaites*, showing the roots, branching stem, simple leaves, and clusters of strobili borne on lateral branches. The stem was actually much longer than shown here. (*After Grand'Eury.*)

several rows, as in the modern coniferous genus, *Araucaria*. The leaf traces were double, collateral, and endarch, becoming mesarch in the leaves. In most cases the venation of the leaves was dichotomous.

Strobili. A feature of the Cordaitales was the presence of small strobili of two kinds, both occurring on the same plant and borne in clusters on lateral branches (Fig. 281). The strobili, about a centimeter in length, were completely ensheathed by sterile bracts. The staminate strobili were composed of spirally arranged microsporophylls and bracts, the latter representing sterile microsporophylls (Fig. 282*A*). The microsporophylls (stamens) were long-stalked and bore two to five erect microsporangia at the tip.

The ovulate strobili were composed of bracts and ovules, the latter borne on secondary axes in the axils of the bracts (Fig. 282*B*). Thus the strobilus was compound. The integument of the ovule had an outer fleshy and a middle stony layer, but no inner fleshy layer. The nucellus was entirely free from the integument, its peripheral region being traversed by one set of vascular strands, another set occurring in the outer fleshy layer of the integument. A prominent nucellar beak and pollen chamber were developed, indicating that the sperms were swimming.

FIG. 281 *Cordaites laevis.* Restoration of foliage-bearing branch with numerous strobili, a large bud is shown at the right. (*From Arnold, after Grand'Eury.*)

Gametophytes. As in the Cycadofilicales, a group of cells has been found within the pollen grain, but it is uncertain whether they represent vegetative or spermatogenous tissue. The female gametophyte was similar to that of modern gymnosperms. There were two archegonia, separated by a beak-like upgrowth of gametophyte tissue. This is also a feature of the modern genus *Ginkgo*. The seeds were very similar to those of the Cycadofilicales. In neither group have seeds with embryos been found.

Summary. The Cordaitales, a dominant Paleozoic group, seem not to have been derived from the Cycadofilicales, although both groups may have had a common origin. The stem is an endarch siphonostele. The primitive features of the group, which they share with the Cycadofilicales and the other cycadophytes, include a large pith, mesarch leaf bundles, the ovule structure, and swimming sperms. The advanced features are the branching habit, thick vascular cylinder, form of the leaves, and compound ovulate strobili. The Cordaitales seem to have given rise to both the Ginkgoales and Coniferales.

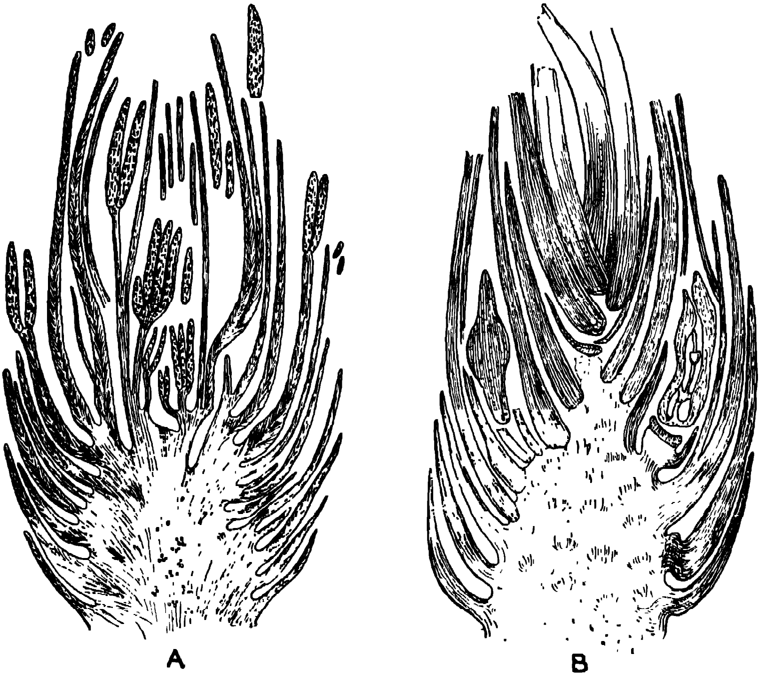

FIG. 282. Strobili of *Cordaianthus*, ×8. *A*, longitudinal section of staminate strobilus, showing sterile bracts and microsporophylls bearing terminal sporangia; *B*, longitudinal section of ovulate strobilus, showing sterile bracts and two stalked axillary ovules. (*After Renault.*)

5. Ginkgoales

The Ginkgoales are represented by only one living species, *Ginkgo biloba*, a native of western China. It is widely cultivated but virtually unknown in the wild state. The order, probably derived from the Cordaitales during the Carboniferous, has been recognized as far back as the Permian. Its members were most abundant during the Mesozoic, particularly in the Jurassic, when the order had almost a world-wide dis-

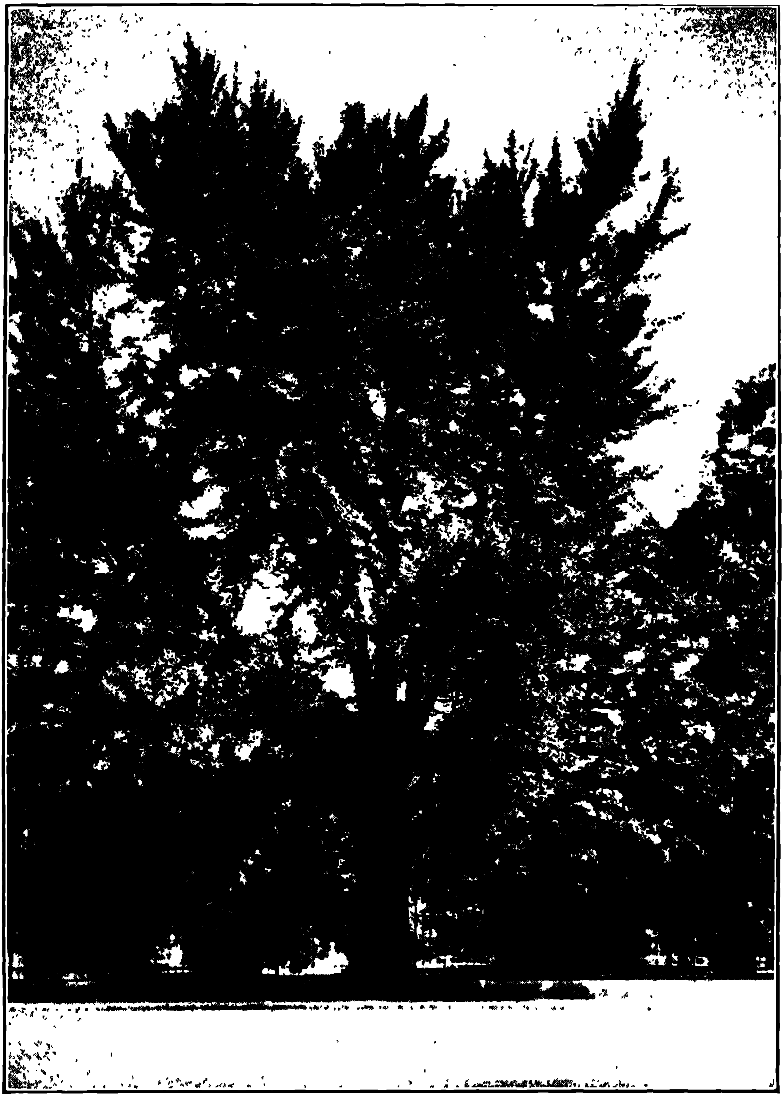

Fig. 283. A large tree of *Ginkgo biloba* on the grounds of the White House, Washington, D.C.

tribution (Fig. 258). The most important Mesozoic genera were *Baiera* and *Ginkgo* itself, both represented by many species.

Sporophyte. *Ginkgo* is a tree with the general habit of a conifer (Fig. 283). It is excurrent when young, becoming round-topped in old age. Under favorable conditions, it may reach a height of 30 m. There are two kinds of branches: long branches of unlimited growth bearing scattered leaves, and short branches of limited growth bearing a few leaves in a cluster. The leaves are deciduous. They have a long petiole and a broadly wedge-shaped blade (Fig. 284). The blade is typically bilobed but may be entire or each lobe may be partially divided into several narrow segments. The leaves are highly variable, even on the same tree. They exhibit dichotomous venation.

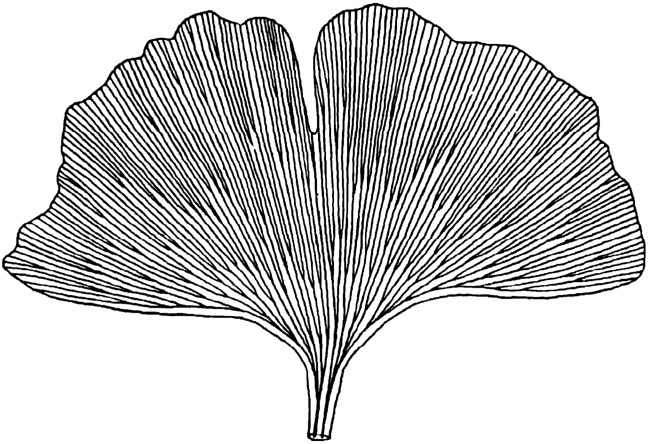

FIG. 284. Leaf blade of *Ginkgo biloba*, showing dichotomous venation, natural size.

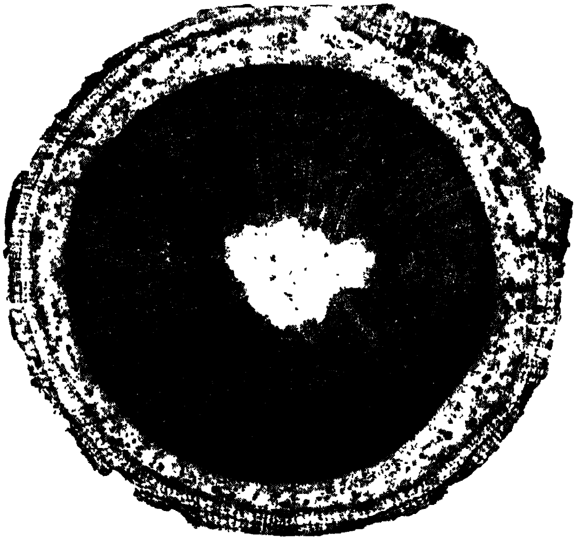

FIG. 285. Cross section of long stem of *Ginkgo biloba*, showing small pith, thick vascular cylinder, and thin cortex, ×15.

The stem of *Ginkgo* is an ectophloic siphonostele. The long stems have a small pith, a thick vascular cylinder, and a thin cortex, as in the Conifcrales (Fig. 285). The dwarf branches, on the other hand, have a large pith, a thin vascular cylinder, and a thick cortex, as in the Cycadales. The leaf traces are double and pass directly into the petiole. Mesarch bundles occur only in the cotyledons, those in all other parts of the plant being collateral and endarch. The tracheids of the secondary xylem have bordered pits in one or two rows.

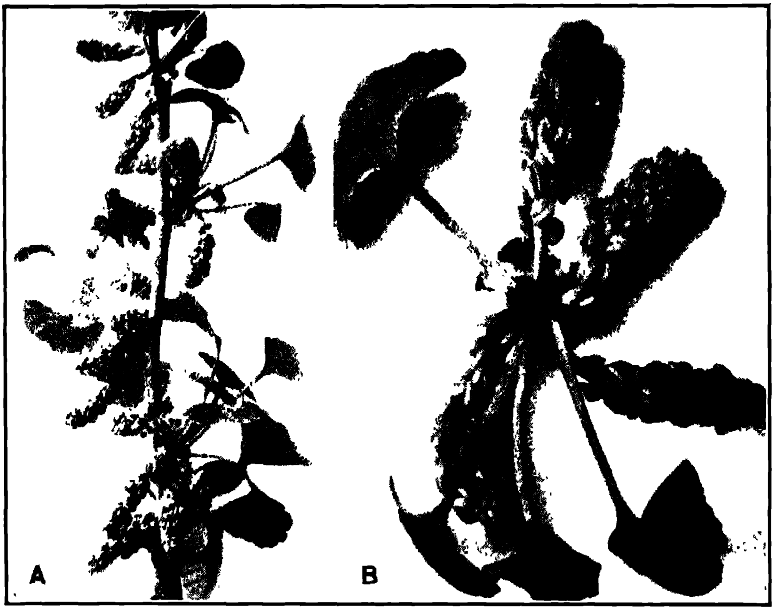

FIG. 286. Staminate strobili of *Ginkgo biloba*. *A*, clusters of strobili borne on dwarf shoots, two-thirds natural size; *B*, enlarged view of a dwarf shoot with young leaves and four strobili.

The strobili of *Ginkgo* are monosporangiate and dioecious, as in the Cycadales. They are borne at the end of the dwarf shoots, each in the axil of a leaf.

Staminate Strobilus. The staminate strobili are composed of a central axis bearing many spirally arranged microsporophylls (stamens) forming a loose, catkin-like cluster (Fig. 286). There are no sterile bracts among the sporophylls. The microsporophyll consists of a long stalk ending in a knob that bears two, or occasionally three or four pendent microsporangia. The knob is a reduced blade. *Ginkgo* has continued the "epaulet" type of stamen found among the Cycadofilicales. The microsporangium is eusporangiate in development, the initial being single and hypodermal. The wall consists of four to seven layers of cells, the tapetum being derived from the outermost layer of sporogenous tissue. Dehiscence occurs by means of a longitudinal slit.

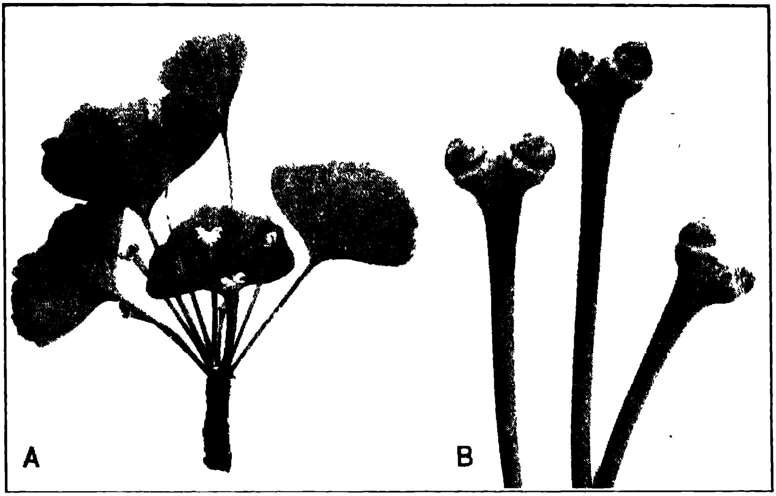

FIG. 287. Ovulate strobili of *Ginkgo biloba*. *A*, dwarf shoot bearing cluster of young leaves and ovulate strobili, two-fifths natural size; *B*, enlarged view of three strobili, each bearing two ovules.

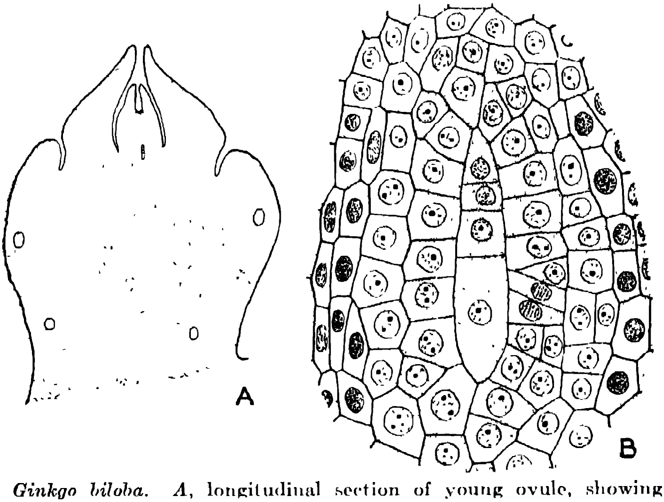

FIG. 288. *Ginkgo biloba*. *A*, longitudinal section of young ovule, showing "collar," integument, nucellus, and spore tetrad, ×15; *B*, enlarged view of tetrad of megaspores surrounded by nutritive tissue, ×400.

Ovulate Strobilus. The ovulate strobili are greatly reduced. Each consists of a long stalk that bears mostly two terminal ovules, only one of which ordinarily matures as a seed (Fig. 287). At the base of each ovule is a peculiar "collar." This probably represents a vestigial megasporophyll, since in rare instances it may become leaf-like. Sometimes three or four ovules may be borne on the same stalk. The ovule is characterized by a single massive integument. As in the Cycadales, this is three-layered, consisting of an outer fleshy, a middle stony, and an inner fleshy layer. A prominent nucellar beak and pollen chamber are present (Fig. 288*A*). Vascular strands are present in the outer fleshy layer, the inner set being suppressed. The megaspore mother cell is deep-seated but may be easily recognized, as it becomes invested with a glandular digestive tissue. A linear tetrad is formed and only the innermost megaspore is functional (Fig. 288*B*).

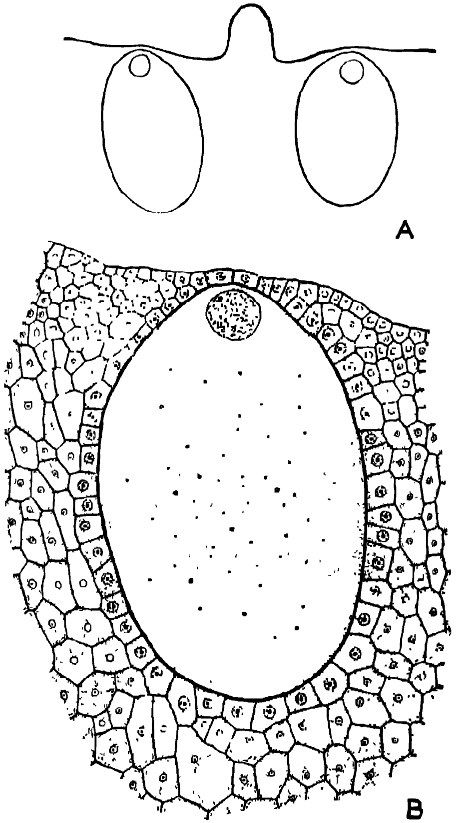

Fig. 289. Archegonium of *Ginkgo biloba*. *A*, micropylar end of female gametophyte, showing two archegonia, ×40; *B*, median longitudinal section of archegonium surrounded by tissue of the female gametophyte, showing central cell and two neck cells, × 100.

Female Gametophyte. As in the Cycadales, the development of the female gametophyte is initiated by free-nuclear division, but the nuclei are parietally placed from the beginning. Wall formation is centripetal. A remarkable condition is seen in that the vegetative tissue of the female gametophyte develops chlorophyll and becomes bright green. As it develops, it encroaches upon the nucellar tissue and destroys nearly all of it. As a rule, only two archegonia appear, developing as in the cycads, except that a small ephemeral ventral canal cell is formed. A prominent beak arises between the archegonia, a feature also of the Cordaitales (Fig. 289).

Male Gametophyte. The development of the male gametophyte begins with the cutting off of two prothallial cells, of which the first is ephemeral, the second persistent. The remaining large cell divides unequally to form the generative and tube cells. This is the shedding condition of the pollen. The further development of the male gametophyte takes place as in the Cycadales. The pollen tubes are extensively branched and function as haustoria. The generative nucleus gives rise to the stalk and body nuclei, but these are not separated by a cell wall. A body cell is organized and divides to form two sperm mother cells, within each of which a large swimming sperm is formed. The sperm has a band of cilia like that of the cycads.

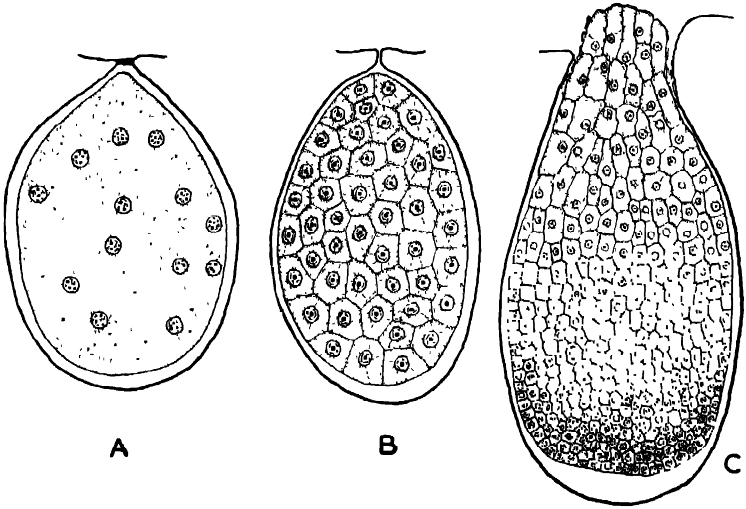

FIG. 290. Early embryogeny of *Ginkgo biloba*, ×75. *A*, free-nuclear stage; *B*, cellular stage; *C*, later stage with meristematic tissue at lower end.

Embryo. In the development of the proembryo of *Ginkgo*, the first stage is one of free-nuclear division, 256 nuclei being formed (Fig. 290*A*). This is followed by a stage of wall formation, the entire egg becoming filled with tissue (Fig. 290*B*). The lower third of the proembryo now becomes meristematic, while the upper two-thirds remains dormant (Fig. 290*C*). The growing region gives rise to a short massive suspensor and a terminal embryo, the latter developing two cotyledons. On the whole, the embryo of *Ginkgo* is primitive. The ripe seed of *Ginkgo* is brownish yellow and about 2.5 cm. in diameter.

Summary. *Ginkgo biloba* is the sole survivor of an order that was widespread and abundant during the Mesozoic. It has retained the primitive reproductive features of its ancestors, its advance being wholly in vegetative characters. The stem is an endarch siphonostele, almost all traces of mesarch structure having disappeared. The pith is not large. Characters that the Ginkgoales have in common with the Cordaitales include the branching habit, thick vascular cylinder, venation of the leaves, structure of the stamens, ovule structure, and swimming sperms. The distinctive features of the Ginkgoales include the form of the leaves and the structure of the strobili. The ovulate strobili and megasporophylls are greatly reduced, the microsporophylls less so. The Ginkgoales may have been derived from the Cordaitales, but are themselves a blindly ending line.

6. Coniferales

The Coniferales constitute the largest order of living gymnosperms, including 6 families, 40 genera, and over 500 species. They are distributed throughout the North and South Temperate Zones, with only a few representatives in the tropics, where they occur at high altitudes. Conifers have been found as fossils as far back as the Permian, having probably been derived from the Cordaitales (Fig. 258). During the Mesozoic they became numerous and diversified into as many families as are represented today. As a group, the Coniferales reached their climax during the Lower Cretaceous.

Families. In the following outline, all the genera occurring in North America are named, together with several others of particular interest.

1. *Abietaceae.* This is a family almost entirely confined to the Northern Hemisphere. It comprises 9 genera and about 230 species. The largest genus is *Pinus*, with 90 species. Other important genera are *Cedrus, Larix, Picea, Tsuga, Pseudotsuga,* and *Abies.* Of the foregoing, all but *Cedrus* are represented in North America.

2. *Taxodiaceae.* Here belong 9 genera and 16 species, nearly all growing in the Northern Hemisphere. Only *Sequoia* and *Taxodium* are found in North America. *Metasequoia,* formerly known only in the fossil state, has recently been discovered growing in western China.

3. *Cupressaceae.* This family includes 10 genera and approximately 120 species. It is represented in both hemispheres. The following genera are found in North America: *Libocedrus, Thuja, Cupressus, Chamaecyparis,* and *Juniperus.* The largest genus, *Juniperus,* has 60 species.

4. *Araucariaceae.* This family has only 2 genera. Both *Agathis,* with 20 species, and *Araucaria,* with 12 species, are of wide distribution in the Southern Hemisphere.

5. *Podocarpaceae.* This family belongs almost exclusively to the

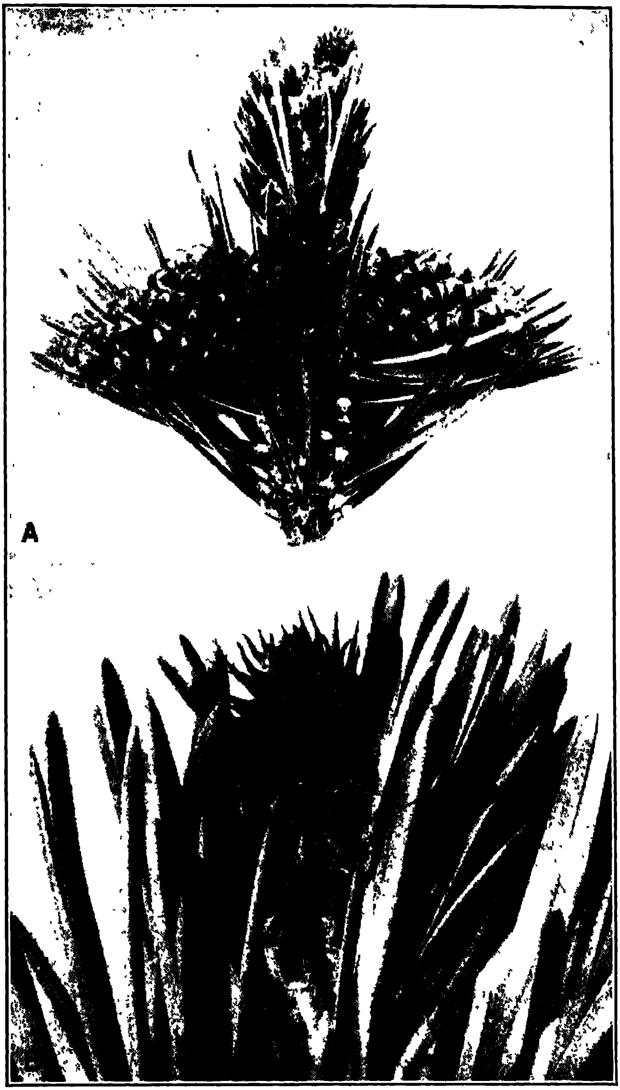

FIG. 291. Ovulate strobili of *Pinus contorta*. *A*, portion of leafy shoot with young cone and two one-year-old cones, three-fourths natural size; *B*, young cone at time of pollination, twice natural size.

Southern Hemisphere. It includes 6 genera and approximately 100 species. The largest genera are *Podocarpus*, with 70 species, and *Dacrydium*, with 20.

6. *Taxaceae*. Here belong 4 genera and 14 species, mainly occurring in the Northern Hemisphere. There are only two genera in North America, *Taxus* and *Torreya*.

Sporophyte. Almost all conifers are trees, but a few are shrubs. Typically they display the excurrent habit, with a tall straight trunk giving rise to numerous wide-spreading branches. Nearly all conifers are evergreen, retaining their leaves for from 3 to 10 years. The only deciduous forms in North America are *Larix* and *Taxodium*. The largest conifers are the two species of *Sequoia*, both native to California. *Sequoia sempervirens*, the redwood of the coastal region, sometimes reaches a height slightly in excess of 100 m., a diameter of 6 m.,[1] and an age of 1,300 years. *Sequoia gigantea*, the big tree of the Sierra Nevada, attains a maximum height of somewhat less than 100 m., a diameter of 8 m.,[1] and an age of about 3,500 years. This species is regarded by some botanists as distinct enough to constitute a separate genus, *Sequoiadendron*.

In almost all genera only stems of unlimited growth and with scattered leaves are present. In *Pinus*, *Cedrus*, and *Larix*, however, both long and dwarf (spur) shoots occur. In *Pinus* the long shoots bear scale-like leaves and in the axil of each arises a spur shoot bearing needle-like foliage leaves (Fig. 291). Only *Pinus monophylla* produces one leaf on a spur; most species have either two or three leaves; *Pinus quadrifolia* has four; and some species have five. In *Cedrus* and *Larix* foliage leaves are borne both on the long and dwarf shoots and the number of leaves on the latter is much larger than in *Pinus*, being usually 30 to 50. In *Pinus* the entire spur falls away with the leaves, but in *Cedrus* and *Larix* only the leaves drop off, new ones appearing on the old spur, as in *Ginkgo*.

The leaves of conifers are small and always simple. Their arrangement is spiral, except in the Cupressaceae, where it is cyclic. The needle-like type of leaf, as seen in *Pinus* and the other Abietaceae, is the dominant one throughout the order (Fig. 291), but other types are also found. Broad, flat leaves occur in *Agathis* and in many species of *Podocarpus* and *Araucaria*. Scale-like leaves are characteristic of nearly all the Cupressaceae (Fig. 292). Where the adult foliage is scale-like, often the juvenile leaves, appearing on seedlings, are needle-like. The flat leaves of conifers have several or many parallel veins, while the needle-like and scale-like leaves have but a single vein.

A pine leaf is adapted to endure severe environmental conditions (Fig. 293). On the outside is a single-layered epidermis with heavily cutinized cell walls and deeply sunken stomata. Beneath the epidermis are one or more hypodermal layers also with thick walls. The mesophyll is compact and peculiar in that the cells have infolded walls. It generally contains a number of resin ducts. The central tissue of the leaf, enclosed by an endodermis, contains one or two vascular bundles, the number depending on the species. The xylem and phloem, nearly equal in amount and

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[1] These diameters are measured at a height of about 3 m. above the greatly swollen base.

FIG. 292. Leafy branch of *Cupressus macrocarpa* with ripe cones, about one-half natural size.

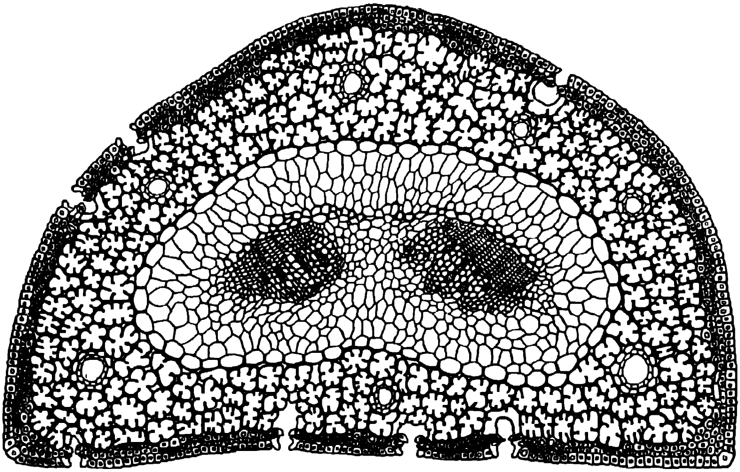

FIG. 293. Cross section of a leaf of *Pinus nigra*, ×75. The thick-walled epidermal and hypodermal layers surround the mesophyll, with infolded cell walls, and containing several resin ducts. The endodermis encloses the transfusion tissue and two vascular bundles, in which the xylem lies below the phloem.

largely secondary in origin, show a collateral arrangement. They are enclosed by a zone of "transfusion tissue."

The stem of the Coniferales is an ectophloic siphonostele and exhibits an advanced type of vascular anatomy (Fig. 294). It has a small pith, a thick vascular cylinder, and a thin cortex. The organization of the conducting tissues is collateral and endarch. Only traces of mesarch structure remain, as in the cotyledons of certain genera. There is a great development of secondary wood, which consists almost entirely of tracheids. The tracheids have bordered pits, those of the Araucariaceae being mostly in two or three rows, instead of in a single row as in the other conifers. In *Taxus* the tracheids bear spiral thickenings in addition to the bordered pits. The phloem of conifers consists chiefly of sieve tubes. There are no companion cells. The leaf traces may be double, as in the Abietaceae, or single, as in the Cupressaceae. The conifers are characterized by the presence of resin canals, which are long intercellular cavities lined with resin-secreting cells. They commonly occur in all parts of the plant, being especially abundant in the leaves and in the cortex of the stem. In *Pinus* and many other genera they may also be present in the wood. In *Taxus* resin canals are lacking.

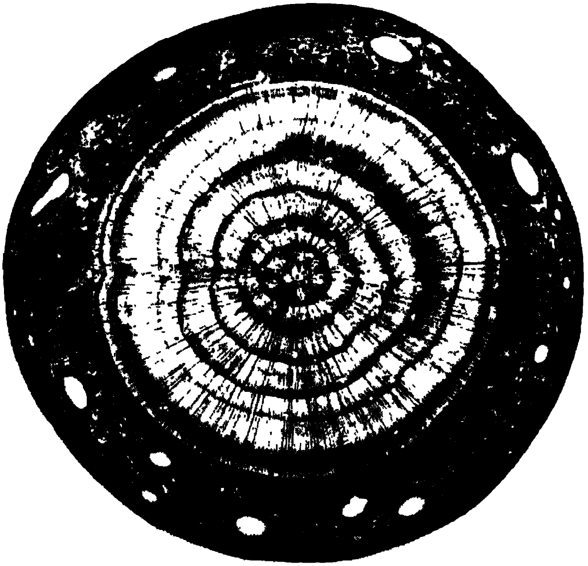

FIG. 294. Cross section of a six-year-old stem of *Pinus monophylla*, showing small pith, thick vascular cylinder, and thin cortex, × 11. The phloem occupies a narrow zone outside the xylem, the latter showing radiating vascular rays and numerous resin ducts.

The strobili are normally monosporangiate. The majority of conifers are monoecious, but some are dioecious, *e.g.*, *Juniperus*, *Araucaria*, *Podocarpus*, the Taxaceae, and a few others. The arrangement of the sporophylls follows that of the leaves, being cyclic in the Cupressaceae and spiral in the other families.

Staminate Strobilus. In all the Coniferales the staminate strobilus is simple, with few to many microsporophylls arising directly from the cone axis (Fig. 295*A*). Bracts are not present. The stamen is a reduced structure, generally consisting of a slender stalk and an expanded sterile tip. The microsporangia are abaxial and most commonly borne in pairs (Fig. 295*B*, *C*). Each stamen bears 2 microsporangia in the Abietaceae and Podocarpaceae, 2 to 5 in the Taxodiaceae, 2 to 6 in the Cupressaceae, 6 to 15 in the Araucariaceae, and 4 to 8 in the Taxaceae. In the Araucariaceae and Taxaceae the microsporangia are pendent on a peltate stamen, as in *Ginkgo*. The microsporangia of conifers are eusporangiate, developing either from a single hypodermal initial or from a layer of initials. The wall is composed of several layers of cells, the innermost layer forming the tapetum.

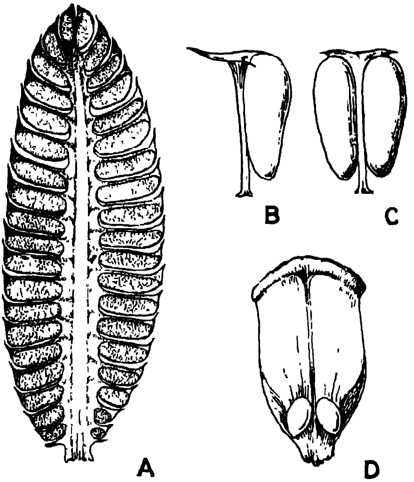

FIG. 295. *Pinus nigra*. *A*, longitudinal section of staminate strobilus, each microsporophyll bearing a pair of abaxial microsporangia, ×4, *B*, side view of a microsporophyll, ×10; *C*, abaxial view of same; *D*, ovuliferous scale, showing two adaxial ovules, natural size.

Ovulate Strobilus. A definite ovulate cone is present in all the families of Coniferales except the Podocarpaceae and Taxaceae, where it is greatly reduced, in some of the Podocarpaceae to one or two ovules and in most of the Taxaceae to one. The ovulate strobilus differs from the staminate in being compound, that is, the ovules are borne on secondary axes, as in the Cordaitales. The main axis of the cone bears a number of bracts and in the axil of each is an "ovuliferous scale" (Figs. 295*D* and 296*A*). The bract is homologous with the microsporophyll of the staminate cone, but the nature of the scale is puzzling. The view most generally held is that it represents a greatly reduced axillary shoot bearing a pair of leaves that are fused along their margins. In fact, in abnormal cones the ovuliferous scale is sometimes replaced by a spur shoot bearing two leaves. In the Abietaceae the bract and scale are free, being united only at the base. Although in the mature cone the bract is usually smaller than the scale and inconspicuous, in some cases, as in *Pseudotsuga* and species of *Larix* and *Abies*, it is large and very prominent. In the Taxodiaceae, Cupressaceae, and Araucariaceae the bract and scale are coalescent.

In families having a well-developed ovulate strobilus, this nearly always becomes dry and woody at maturity but, in some genera, as in *Juniperus*, the ripe cone is berry-like. In the Abietaceae each cone scale bears two basal ovules on the adaxial side (Fig. 295*D*), but in the other families the number is variable, being two to seven in the Taxodiaceae, one to many in the Cupressaceae, and only one in the Araucariaceae. The ovules are inverted in the Abietaceae, Araucariaceae, and almost all the Podocarpaceae; they are erect in the Cupressaceae, Taxaceae, and almost all the Taxodiaceae.

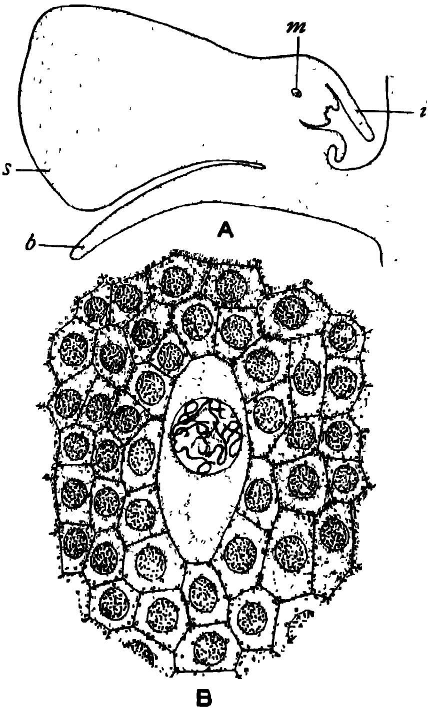

Fig. 296. *Pinus nigra*. *A*, longitudinal section of young ovule, showing integument (*i*), ovuliferous scale (*s*), bract (*b*), and megaspore mother cell (*m*), deeply embedded in the nucellus, ×25; *B*, megaspore mother cell surrounded by nucellar tissue, its nucleus in prophase of the first reduction division, ×400.

The ovule has a single integument (Fig. 297*A*). In the Abietaceae the integument is fused to the nucellus below but is free at the apex, while in the other families, with few exceptions, the integument and nucellus are either entirely free or slightly united below. The ovule of the Coniferales does not develop a nucellar beak and pollen chamber, their absence being related to the fact that swimming sperms are not produced. The integument consists of an outer fleshy layer, a middle stony layer, and an inner fleshy layer. The outer layer is thin and usually disappears as the seed ripens. Both inner and outer sets of vascular strands have been eliminated. The megaspore mother cell is solitary and deep-seated (Fig. 296*B*). It forms a linear tetrad. As in other gymnosperms, the innermost megaspore alone is functional.

In the Podocarpaceae and Taxaceae an outer fleshy covering grows up around the ovule, uniting with it in *Podocarpus* and *Torreya*, but remaining separate in *Taxus*. This fleshy structure has been interpreted by some botanists as a second integument, by others as the ovuliferous scale.

Female Gametophyte. As in the Cycadales and Ginkgoales, the development of the female gametophyte involves several stages, as follows (1) free-nuclear division accompanied by the formation of a large central vacuole that results in parietal placing of the nuclei; (2) wall formation

(3) centripetal growth until the gametophyte is cellular throughout. A deeper region of nutritive tissue is usually differentiated from a micropylar region of smaller cells in which the archegonia develop. The number of archegonia is highly variable. In the Abietaceae it is usually 2 to 5, but in the other families the number may be much higher, reaching 200 in extreme cases.

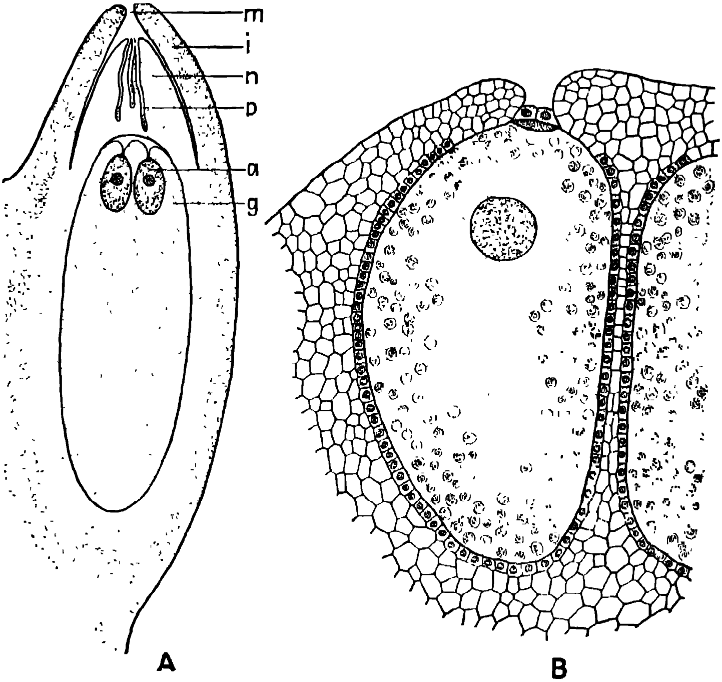

FIG. 297. Ovule and archegonium of *Pinus lambertiana*. *A*, longitudinal section of ovule, showing female gametophyte with two archegonia, ×10, *B*, mature archegonium with two neck cells, a small ventral canal cell, and a large egg with a conspicuous nucleus and many small food bodies, ×85; *m*, micropyle, *i*, integument; *n*, nucellus; *p*, pollen tube; *a*, archegonium; *g*, female gametophyte.

Archegonial development follows the same pattern as in the Cycadales. Sometimes only two neck cells are formed but generally there are many more, the number varying from 4 cells in one tier to about 12 or more in several tiers. In the Abietaceae a definite ventral canal cell is formed that soon disorganizes (Fig. 297*B*). In the other families there is only a ventral canal nucleus. In *Torreya* it is doubtful whether even this is present, the nucleus of the central cell apparently functioning directly as the egg nucleus. A special feature of the Taxodiaceae and Cupressaceae is the formation of an "archegonium complex," an organization of several archegonia in contact with one another and enclosed within a common jacket.

Male Gametophyte. The amount of vegetative tissue arising in the male gametophyte varies according to the family. The most primitive condition is seen in the Araucariaceae and Podocarpaceae, where two prothallial cells are cut off, these soon dividing to form a tissue of many cells. In the Abietaceae two prothallial cells are formed but both of them are ephemeral (Fig. 298*A*–*C*). Finally, in the Taxodiaceae, Cupressaceae, and Taxaceae, no prothallial cells are formed. The generative and tube cells are nearly always differentiated before the pollen is shed (Fig. 298*D*). All the conifers are wind-pollinated. In the Abietaceae, with the exception of a few genera, *e.g.*, *Larix*, *Tsuga*, and *Pseudotsuga*, the pollen grains develop a pair of wings that grow out from the wall (Fig. 298). The Podocarpaceae (except *Dacrydium*) also have winged pollen grains, but those of the other families are wingless.

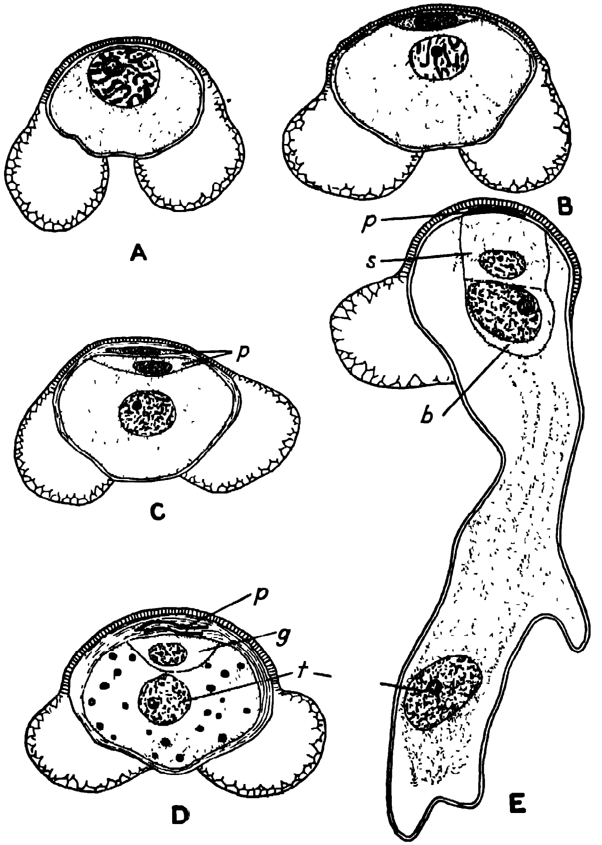

FIG. 298. Male gametophyte of *Pinus nigra*, ×600. *A*, microspore; *B*, *C*, *D*, successive stages in development of the pollen tube; *E*, pollen tube; *p*, prothallial cells; *t*, tube nucleus; *g*, generative cell; *s*, stalk cell; *b*, body cell. (*After Coulter and Chamberlain.*)

The young ovulate cone is ready for pollination soon after emerging from the bud (Fig. 291). Its scales separate slightly and a pollination droplet exudes through the micropyle of each ovule. This droplet catches some of the pollen grains and, upon evaporating, draws them down into contact with the nucellus. Following pollination, the scales close and the cone begins a long period of growth. The pollen grains soon germinate. The apical end of each pollen tube grows downward into the nucellus, not laterally as in the cycads.

The tube nucleus moves into the pollen tube, while the generative cell, remaining at its basal end, soon gives rise to the stalk cell and body cell (Fig. 298*E*). These pass into the tube and considerably later the body cell divides to form two male cells that are usually equal in size and are always nonciliated (Fig. 299*A*). In the Abietaceae the two male nuclei are surrounded by cytoplasm derived from the body cell but are without a cell wall. They remain inside the body cell until just before the time of fertilization.

The pollen tube comes in close contact with the archegonium and the tip ruptures, discharging its contents into the egg. One of the male nuclei approaches the egg nucleus and the two come together (Fig. 299*B*). If the second male nucleus also enters the egg, it soon disintegrates. The cytoplasm surrounding the male nucleus mingles with the egg cytoplasm. In conifers with highly organized male cells, after entering the egg, the protoplast escapes from the cell wall and the cytoplasm remains in contact with the male nucleus, finally forming a conspicuous sheath around the fusing nuclei. The male and female nuclei do not fuse in the resting condition, but each forms a group of chromosomes that become arranged on a common spindle (Fig. 299*C*, *D*). Completion of the mitosis gives rise to the first two nuclei of the proembryo.

In *Pinus* and *Juniperus* the interval between pollination and fertilization is slightly more than a year, but in most other conifers it is less, sometimes only a month or two. During this time the development of the female gametophyte and the growth of the pollen tube take place.

Embryo. In *Pinus* four free nuclei are formed within the fertilized egg as a result of two successive mitotic divisions (Fig. 300*A*, *B*). These nuclei move to the base of the egg, where they become arranged in a horizontal plane. Each nucleus divides and walls come in, forming two tiers of four cells each (Fig. 300*C*, *D*). The cells of the upper tier, which remain open above, divide again and then the cells of the lower tier divide. The proembryo now consists of four tiers of cells with four cells in each tier (Fig. 300*E*, *F*). The lowest tier gives rise to four embryos; the next tier forms the primary suspensor cells; the next one constitutes the "rosette tier," which may later give rise to four embryos also; while the four upper cells are part of the general cytoplasm of the egg, which serves as a large food reservoir. The nuclei of the upper cells soon disintegrate.

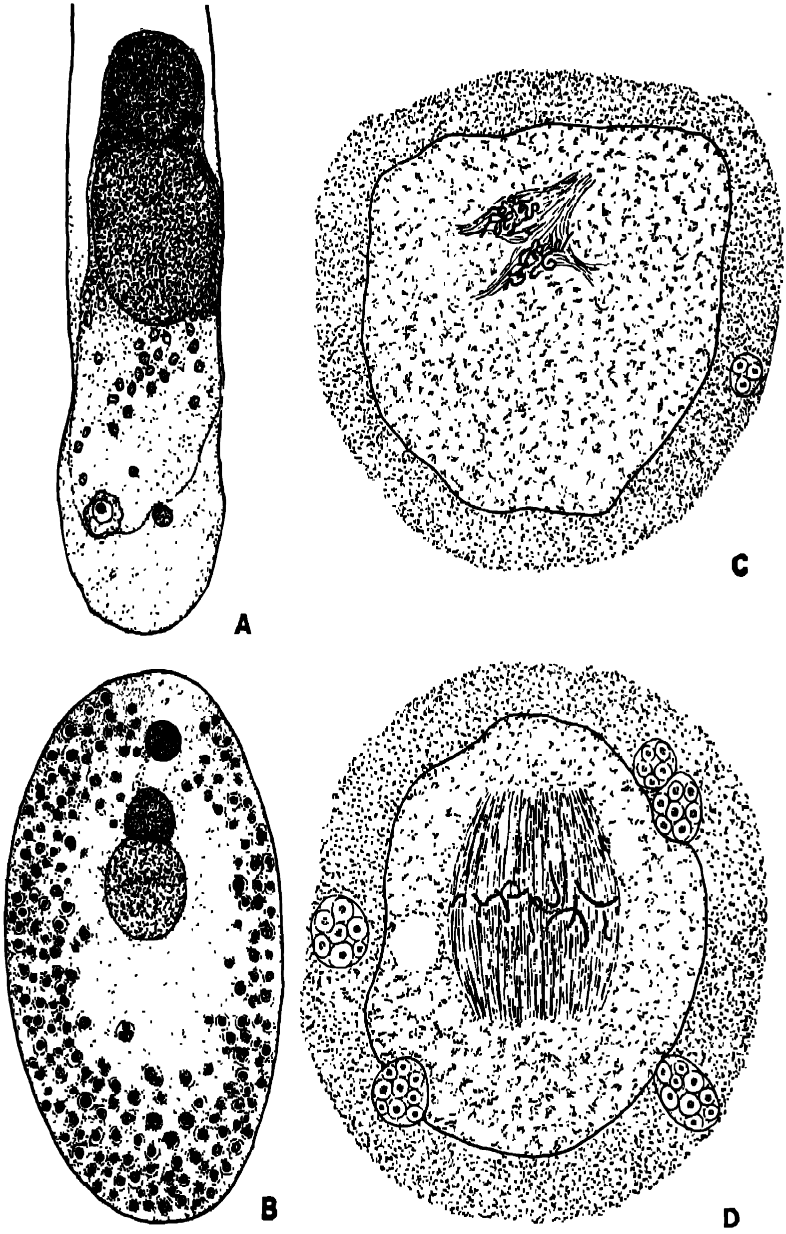

Fig. 299 Fertilization in *Pinus*. *A*, lower end of pollen tube, showing small tube nucleus, stalk cell, and two large male nuclei, ×250; *B*, two male nuclei within the egg, the larger one in contact with the egg nucleus, ×95; *C*, male and female chromatin groups inside egg nucleus; ×360; *D*, chromosomes derived from male and female nuclei on a common spindle, ×360. (*From Haupt.*)

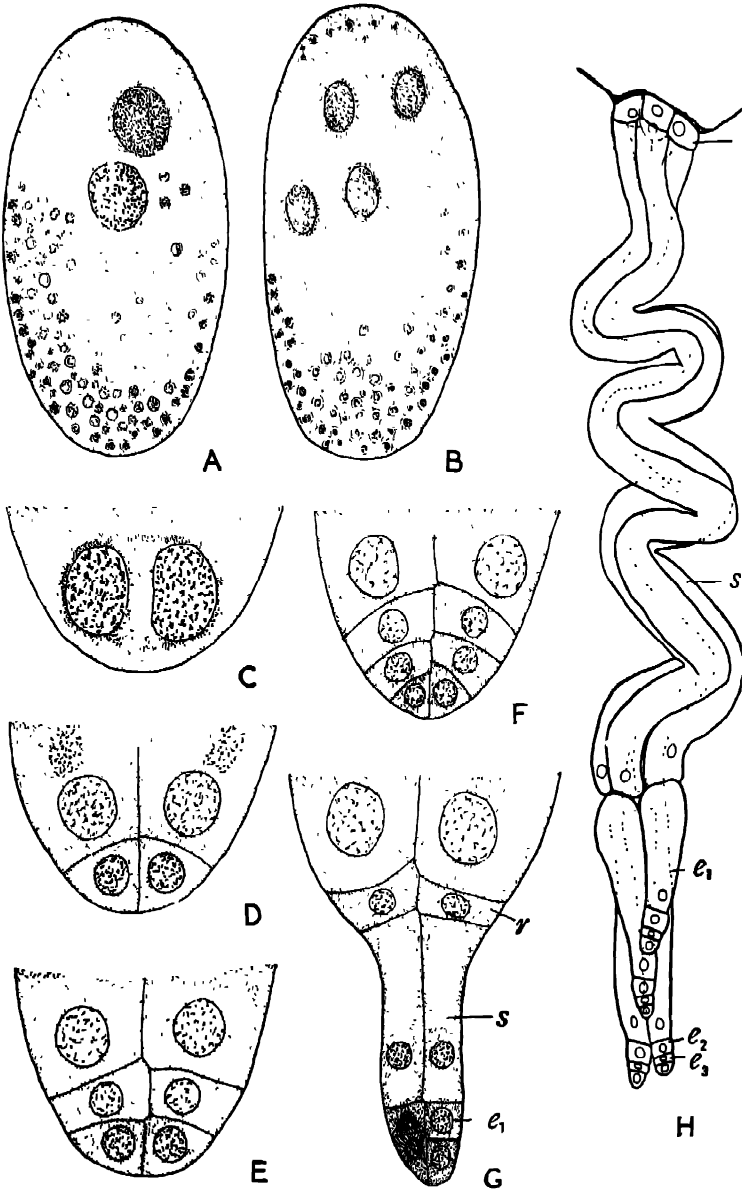

FIG. 300. Early embryogeny of *Pinus monophylla*. *A*, 2-nucleate proembryo; *B*, 4-nucleate stage; *C*, two of the four nuclei at base of egg; *D*, 8-celled proembryo; *E*, three tiers of four cells each, *F*, four tiers of four cells each; *G*, cells of suspensor tier elongating; *H*, later stage of *Pinus banksiana*, the four proembryos separating; *r*, rosette cells; *s*, primary suspensor cells; e_1, e_2, e_3, secondary suspensor cells; *A* and *B*, ×75; *C* to *G*, ×125; *H*, ×90. (*H*, *after Buchholz*.)

Following the establishment of the embryonal, suspensor, and rosette tiers, the four cells of the lowest tier divide and interpose another tier between them and the primary suspensor cells, thus forming secondary suspensor cells (embryonal tubes). This behavior may be repeated once or twice again. The primary suspensor cells elongate and thrust the lower cells into the female gametophyte tissue. The four rows of lower cells now separate and the secondary suspensor cells elongate. Elongation of the suspensors, both primary and secondary, continues to such an extent that they become coiled and twisted (Fig. 300*H*).

Each of the four terminal cells gives rise to a separate embryo. Meanwhile one or more cells of the rosette tier may divide to form a rosette embryo. These ordinarily do not develop very far, however, before they disintegrate. As a result of receiving unequal amounts of food, the four primary embryos grow at different rates. The largest finally survives and the others become aborted. Thus the mature seed, with rare exceptions, has only one embryo.

In the Abietaceae, Taxodiaceae, and Cupressaceae four free nuclei are formed in the egg before walls appear. In the other families a larger number of nuclei are produced—as many as 32 or 64 in the Araucariaceae. After the appearance of walls, the proembryo, as a rule, consists of four tiers of cells in the Abietaceae, but of only three tiers in the Taxodiaceae, Cupressaceae, and Araucariaceae. In many conifers the cells of the lowest tier of the proembryo do not separate to form four embryos, as they do in *Pinus*, but remain together to form a single embryo, while the cells of the rosette tier collapse instead of giving rise to rosette embryos. In these conifers several embryos usually begin to develop in the same ovule, but each comes from a different fertilized egg.

Thus polyembryony in the Coniferales is of two types: (1) *cleavage polyembryony*, where multiple embryos arise from the splitting of a single embryo; and (2) *simple polyembryony*, where more than one fertilized egg in the same ovule gives rise to an embryo. Each type is characteristic of particular genera. In the Abietaceae, for example, cleavage polyembryony is a feature of *Pinus*, *Cedrus*, and *Tsuga*, while simple polyembryony is characteristic of *Larix*, *Picea*, *Pseudotsuga*, and *Abies*. In both types of polyembryony only one embryo in each seed reaches maturity, the others degenerating.

When mature, the conifer embryo consists of a hypocotyl terminating in a radicle at the suspensor end and a minute plumule at the opposite end, the plumule being surrounded by two or more cotyledons (Fig. 301). The number of cotyledons ranges from 2 to 18, but more conifers are dicotyledonous than polycotyledonous. The Abietaceae show the largest number and the greatest variability. The ripe seed of conifers is generally brown. The outer and inner fleshy layers of the integument become very thin, the outer one often disappearing entirely. Thus the seed coat consists essentially of the middle stony layer. The embryo goes into a condition of dormancy in which it usually remains for many months, although the seeds of many conifers will germinate without undergoing a resting period. As in the cycads and *Ginkgo*, food is stored in the vegetative tissue of the female gametophyte, generally designated as *endosperm*. In germination the entire embryo emerges from the seed coat, which is carried out of the ground on the tips of the cotyledons.

Summary. The Coniferales were probably derived from the Cordaitales during the Paleozoic and represent a parallel line of evolution to the Ginkgoales, which seem to have had a similar origin. These three orders, comprising the coniferophytes, constitute a line of descent as old as the cycadophytes. The Coniferales have retained fewer primitive reproductive features than the Ginkgoales, their chief advance being in ovule structure and the loss of swimming sperms. In both orders the stem, freely branching, is an endarch siphonostele with almost no mesarch structure left. Moreover, the pith is small and the vascular cylinder thick. The leaves of conifers are characteristically small and without dichotomous venation. Although the microsporophylls are grouped to form a simple strobilus, the ovulate strobilus, except where greatly reduced, is compound, a feature also of the Cordaitales.

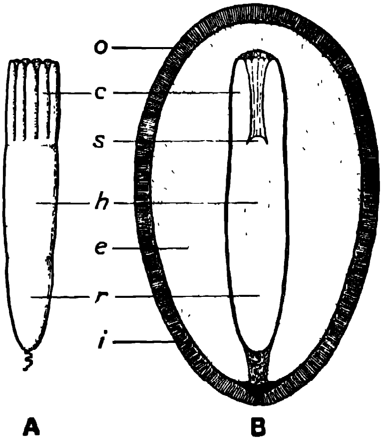

FIG. 301. Embryo (*A*) and longitudinal section of the seed (*B*) of *Pinus edulis*, ×4; *o*, outer seed coat; *i*, inner seed coat; *c*, cotyledons; *s*, stem tip; *h*, hypocotyl; *r*, root tip; *e*, endosperm.

The six families of conifers represent various degrees of progress from a common ancestry. Their advance has been in different directions, as follows:[1] (1) The arrangement of leaves and sporophylls is spiral in all the families except the Cupressaceae, where it is cyclic. (2) All families have distinct ovulate cones except the Podocarpaceae and Taxaceae. (3) The bract and scale in the ovulate cone are separate in the Abietaceae but united in the other families. (4) Winged pollen grains are present only in the Abietaceae and Podocarpaceae. (5) A considerable amount of vegetative tissue is present in the male gametophyte of the Araucariaceae and Podocarpaceae. Two ephemeral prothallial cells are formed in the Abietaceae, none in the three other families. (6) A ventral canal cell is formed in the Abietaceae, only a ventral canal nucleus in the other fami-

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[1] In each case the condition to be regarded as primitive is stated first.

lies. (7) An archegonium complex is present only in the Taxodiaceae and Cupressaceae. This is an advanced character.

The oldest families of conifers are the Abietaceae and Araucariaceae. Although it is uncertain which is the more ancient, much evidence from the vascular anatomy of both living and extinct forms indicates that the Abietaceae are the ancestral stock of conifers. The Araucariaceae seem to have given rise to the Podocarpaceae and Taxaceae. The Taxodiaceae and Cupressaceae are younger than the other families and have probably sprung from the Abietaceae.

7. Gnetales

This is the highest order of gymnosperms. It includes 3 peculiar genera of diverse habit and distribution. *Ephedra*, with about 35 species, inhabits arid parts of the Mediterranean region, tropical and temperate Asia, and western North and South America. *Welwitschia*, with a single species, is found only in arid parts of western South Africa. *Gnetum*, with 30 species, occurs in the tropics of South America, Asia, and Africa. The fossil record of the Gnetales is very fragmentary and does not extend beyond the Tertiary.

Sporophyte. The species of *Ephedra* are low, much-branched shrubs, seldom exceeding 2 m. in height, with long-jointed green stems bearing opposite or whorled scale-like leaves (Fig. 302*A*). Some of the species are trailing. *Welwitschia* is a large turnip-shaped plant with a tuberous stem about 1 m. in diameter and about one-third as tall (Fig. 303). It bears a single pair of terminal, elongated, strap-shaped leaves with parallel venation. They trail along the ground, reaching a length of 3 m. or more and becoming split into numerous segments. Except for the cotyledons, these are the only leaves the plant ever has. Most of the species of *Gnetum* are woody vines, but a few are shrubs or small trees. They have oval, leathery, opposite leaves that are net-veined and 5 to 8 cm. long (Fig. 304*A*). All three genera are cyclic in the arrangement of their leaves and sporophylls.

The most distinctive feature of the vascular anatomy of all three genera is the occurrence of true vessels (tracheae) in the secondary wood. These are present in addition to tracheids. Resin canals are absent. The endarch condition prevails throughout the plant body, all traces of mesarch structure apparently having been eliminated.

The strobili of *Ephedra* and *Gnetum* are usually monosporangiate and, as a rule, the two kinds occur on separate plants. The strobili of *Welwitschia* are also functionally monosporangiate but, in the staminate strobilus, each set of stamens surrounds an abortive ovule, thus indicating an ancestral bisporangiate condition (Fig. 305*C*). In all three genera both kinds of strobili are compound, the sporophylls arising on secondary axes borne in the axils of bracts.

Staminate Strobilus. The staminate strobilus consists of an axis bearing a series of bracts arranged in opposite pairs. These are connate in

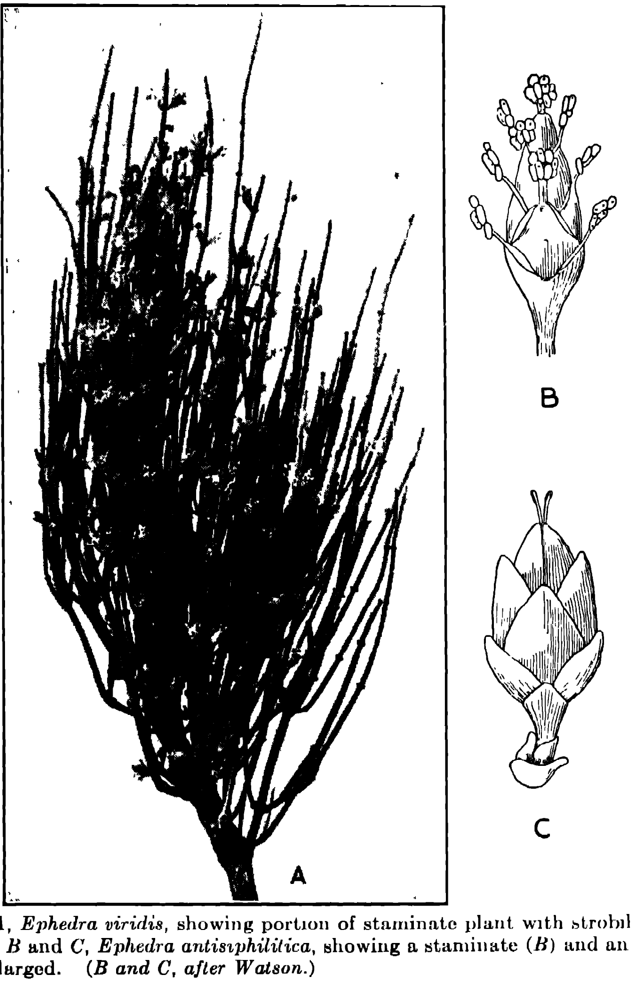

Fig 302. *A*, *Ephedra viridis*, showing portion of staminate plant with strobili two-fifths natural size; *B* and *C*, *Ephedra antisiphilitica*, showing a staminate (*B*) and an ovulate (*C*) strobilus, enlarged. (*B and C, after Watson.*)

Gnetum and imbricate in the two other genera. In the axil of each bract, except the lower ones, is a "staminate flower," representing a simple strobilus. This consists, in *Ephedra* and *Gnetum*, of a stalk bearing two (or, in *Ephedra*, up to six or eight) terminal microsporangia and a pair of basal scales (Figs. 302*B* and 304*C*). In *Welwitschia* the staminate flower is composed of two opposite pairs of basal scales investing a whorl of six united stamens that surround a sterile ovule (Fig. 305*A*, *C*). Each stamen bears three terminal microsporangia forming a synangium. In all three genera the scales at the base of each staminate flower are sometimes designated as a "perianth."

Ovulate Strobilus. The ovulate strobilus of *Ephedra* is simpler than that of either of the other genera, consisting of an axis bearing several opposite pairs of bracts and an erect terminal ovule or, in some species, of two or more ovules (Fig. 302*C*). In *Welwitschia* and *Gnetum* the strobilus has a long axis with many ovules borne in the axils of bracts (Figs. 304*E* and 305*B*). In each genus an "ovulate flower" includes a single ovule invested by a pair of scales that constitute a "perianth." The ovule has two integuments, the inner one forming a long tubular micropyle (Figs. 305*D* and 306*A*). The outer integument has an outer fleshy layer and an inner stony layer. There is a set of vascular strands in the fleshy layer of the outer integument. In *Ephedra* a pollen chamber is formed by the breaking down of some of the nucellar tissue but there are no swimming sperms. In *Gnetum*, but not in *Welwitschia*, there is a slight tendency toward the formation of a pollen chamber.

FIG. 303. *Welwitschia mirabilis.* Female plant in foreground; male plant in background. (*From a photograph furnished by the Chicago Natural History Museum.*)

Female Gametophyte. The female gametophyte differs greatly among the three genera of Gnetales. In *Ephedra* it develops as in the Coniferales, with free-nuclear division followed by the formation of compact, small-celled, nutritive tissue (Fig. 306). The archegonia, usually numbering two or three, appear in the micropylar region. They have many tiers of neck cells. A ventral canal nucleus is cut off but a wall does not separate it from the egg nucleus.

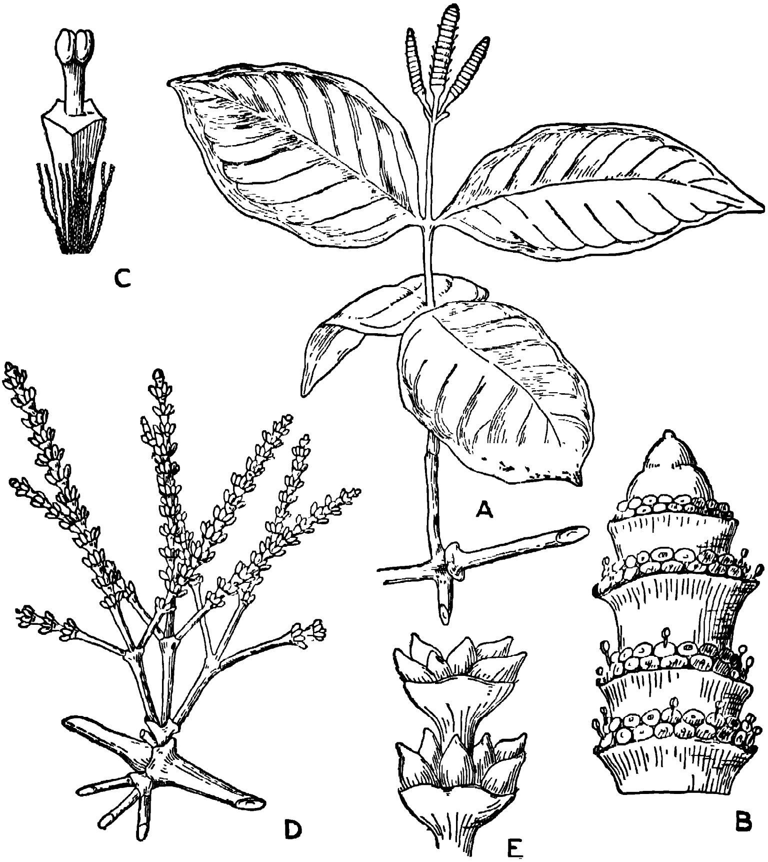

FIG 304. Strobili of *Gnetum latifolium* *A*, leafy branch with staminate strobili, natural size; *B*, part of staminate strobilus, enlarged; *C*, an expanded staminate "flower," ×5; *D*, branches with ovulate strobili, natural size, *E*, part of ovulate strobilus, enlarged. (*After Blume.*)

In *Welwitschia* the development of the female gametophyte proceeds as far as the formation of walls, but this is incomplete and the cells are multinucleate. Nuclear fusions are said then to occur in most of the cells until they become uninucleate. No archegonia are formed. The cells in the micropylar region are multinucleate and become free eggs, sending out tubes into which their nuclei pass. These tubes penetrate the nucellus, where they meet the pollen tubes. Then an egg nucleus fuses with one of the male nuclei, after which it passes back into the female gametophyte. The cells in the lower region, after becoming uninucleate, continue to multiply, even after fertilization has taken place. They form a nutritive tissue.

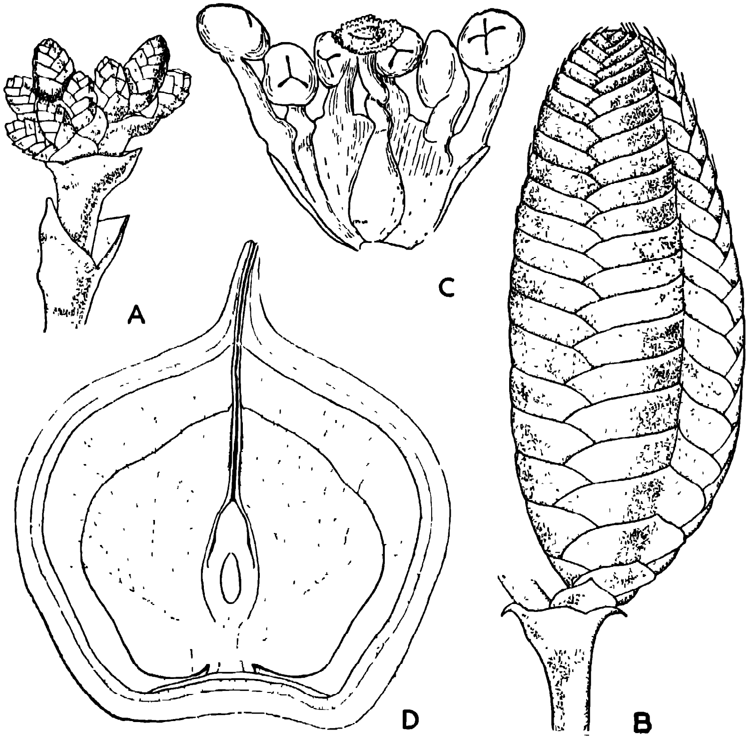

FIG. 305. *Welwitschia mirabilis* *A*, young staminate strobili, natural size; *B*, ovulate strobilus, natural size; *C*, staminate "flower" with bracts removed, showing the six stamens united below and the sterile ovule with a long twisted micropylar tube, ×8; *D*, longitudinal section of ovule, showing inner integument forming micropylar tube and outer integument forming a wing, ×3. (*A*, *B*, *C*, *after Hooker*; *D*, *after Church*.)

In *Gnetum* the female gametophyte begins its development with free-nuclear division. However, there is no wall formation except, in some species, in the basal region, where a small-celled nutritive tissue is formed. Each nucleus in the micropylar region is a potential egg nucleus, several usually becoming organized as eggs but only one being fertilized. After fertilization, the gametophyte becomes cellular throughout. At first the cells are multinucleate but later become uninucleate, as in *Welwitschia*.

Male Gametophyte. In *Ephedra* the microspore cuts off two prothallial nuclei but only the first is organized as a cell (Fig. 307). These are persistent. The generative nucleus and tube nucleus are differentiated, the former giving rise to the stalk and body nuclei. These are not formed as cells. In this condition the pollen grain is shed. In the pollen tube two male nuclei are formed. The pollen grains of *Gnetum* and *Welwitschia* contain an ephemeral prothallial nucleus, a tube cell, and a generative cell. A stalk cell and body cell are not formed, but later the nucleus of the generative cell gives rise directly to two male nuclei, as in angiosperms.

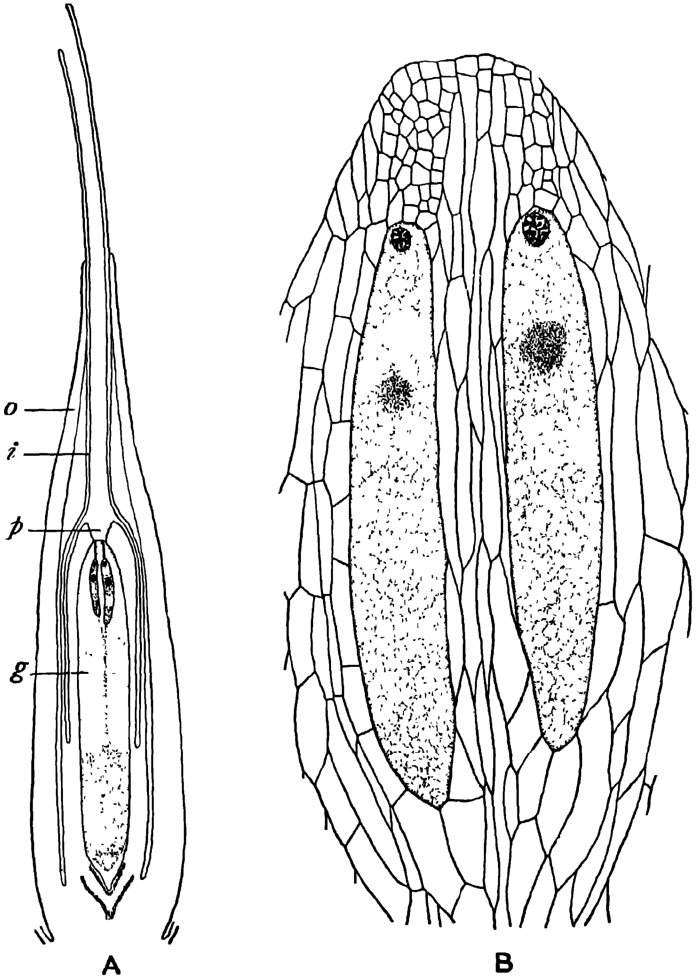

FIG. 306. *Ephedra trifurca*. *A*, longitudinal section of an ovule, showing outer integument (*o*), inner integument (*i*) forming a long micropylar tube, pollen chamber (*p*), and female gametophyte (*g*) with two archegonia, ×42; *B*, two archegonia just before division of the central-cell nucleus, ×112. (*After Land.*)

Embryo. In all three genera of the Gnetales the embryo is dicotyledonous but its development varies. In *Ephedra* the division of the fertilized egg nucleus results in the formation of eight free nuclei, around each of which there is organized a cell that becomes an independent proembryo (Fig. 308*A*). Only one or, rarely, two of these reach maturity. The proembryo sends out a suspensor tube, at the tip of which a cell is cut off. This gives rise to the embryo (Fig. 308*B*). In *Welwitschia* and *Gnetum* the fertilized egg behaves as one of the proembryonal cells of *Ephedra*, the embryo arising from the fertilized egg without any free-nuclear division. This condition is characteristic of angiosperms.

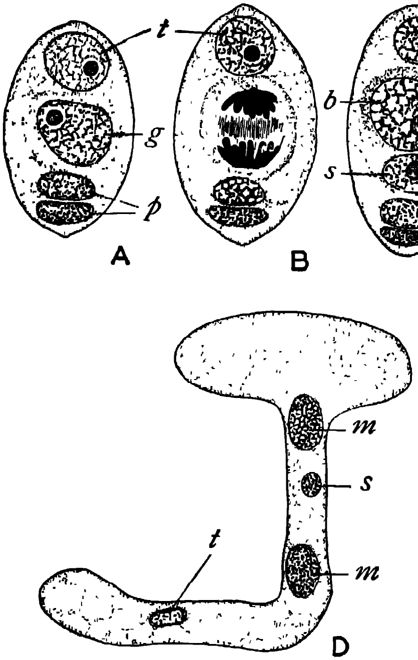

FIG. 307. Male gametophyte of *Ephedra trifurca*. *A*, pollen grain with two prothallial nuclei (*p*), generative nucleus (*g*), and tube nucleus (*t*), *B*, division of generative nucleus, *C*, shedding condition with two prothallial nuclei, stalk nucleus (*s*), body nucleus (*b*), and tube nucleus; *D*, pollen tube with tube nucleus (*t*), stalk nucleus (*s*), and two male nuclei (*m*); *A*, *B*, *C*, ×1,500; *D*, ×500. (*After Land.*)

Summary. The occurrence of vessels in the secondary wood, of compound staminate strobili, and the prolongation of the inner integument of the ovule into a micropylar tube are unique features that distinguish the Gnetales from all other gymnosperms. The presence of true vessels is an angiosperm character. Others include the elimination of archegonia and formation of free eggs (except in *Ephedra*), the elimination of free-nuclear division in the embryogeny (except in *Ephedra*), the formation of two male nuclei directly from the generative nucleus (except in *Ephedra*), and the presence of compound strobili with simple strobili ("flowers") bearing a "perianth." Such strobili suggest the inflorescences of certain angiosperms. The origin of the Gnetales is unknown. They are not

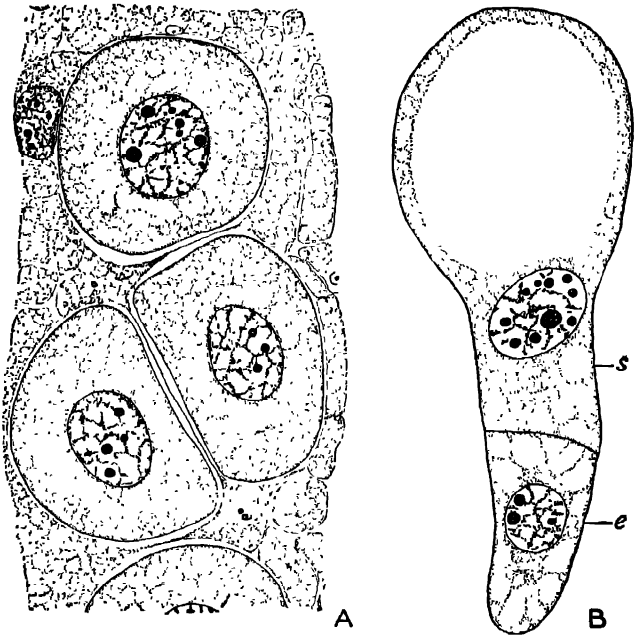

Fig. 308. Proembryonal cells of *Ephedra trifurca*, ×440. *A*, three of the eight free proembryonal cells; *B*, a proembryonal cell in which the embryo initial cell (*e*) is differentiated from the suspensor cell (*s*). (*After Land.*)

closely related to any of the other gymnosperms, while any direct relationship to the angiosperms is very doubtful, although both groups may have had a common ancestry. The three genera do not seem to be closely related to one another and may have had a separate origin. *Ephedra* shows certain resemblances to the Cordaitales that suggest its derivation from that group.

CHAPTER IX

SPERMATOPHYTA (CONTINUED)

2. ANGIOSPERMAE

The angiosperms are the largest and most conspicuous group of modern plants, numbering about 195,000 species. They are also the youngest group, and are thought to have been derived from the gymnosperms, or possibly to have had an independent origin from the pteridophytes. They appeared in the Lower Cretaceous and from the Upper Cretaceous to the present time have been the dominant group of land plants (Fig 258). Angiosperms are found in practically all terrestrial habitats where plants may exist. Some occur in fresh water and even in the sea, the aquatic habit being secondarily acquired. A relatively few forms, having little or no chlorophyll, are saprophytic or parasitic.

Although many angiosperms are woody, the majority are herbaceous. The woody condition is considered to be the more primitive, and the herbaceous one to have been derived from it. The seeds of angiosperms are borne in a closed vessel, the ovary, and not, as in gymnosperms, on the exposed face of an open carpel (or equivalent structure). The ovary represents the basal portion of a single closed carpel or of two or more united carpels. It ripens to form a fruit, which contains the seeds. Angiosperms are often called "flowering plants," as the presence of flowers is one of their most outstanding features.

The two great groups (subclasses) of angiosperms are the Dicotyledoneae and the Monocotyledoneae, distinguishable on the basis of the following combination of characters, but with individual exceptions to each: The dicotyledons have seeds with two cotyledons, stems with a hollow cylinder of vascular tissue and with a functioning cambium, leaves with netted veins forming an open system, and floral parts chiefly in fours or fives. The monocotyledons have seeds with one cotyledon, stems with scattered vascular bundles and without a functioning cambium, leaves with parallel veins forming a closed system, and floral parts typically in threes.

The Dicotyledoneae include 240 families and approximately 155,000 species, the Monocotyledoneae 45 families and about 40,000 species. The Dicotyledoneae comprise the Archichlamydeae, whose flowers are naked, apetalous, or choripetalous, and the Metachlamydeae, whose flowers are sympetalous. The Archichlamydeae include some members having floral parts more or less spirally arranged, while the flowers of the Metachlamydeae are all definitely cyclic. The Archichlamydeae are generally regarded as the ancestral stock from which both the Metachlamydeae and the Monocotyledoneae have been derived.

Vegetative Organs

The sporophyte of angiosperms presents an enormous diversity in size and habit, ranging from tiny herbs to tall trees 100 m. in height. Most angiosperms grow erect upon the ground, but some are trailing, climbing, or epiphytic. Their stems are usually branched, but may be unbranched; they are generally aerial, but may be subterranean. As in gymnosperms, branching of the stem is lateral, never dichotomous. The leaves are typically broad and thin, but display extreme variation in size, shape, and other features. Their arrangement on the stem may be either spiral or cyclic. They may be simple or divided into leaflets (compound), petiolate or sessile, net-veined or parallel-veined, deciduous or evergreen. In net-veined leaves the veins form an obvious reticulum and their ultimate veinlets end freely to form an open system. In parallel-veined leaves the larger veins run parallel to one another and, if connected by cross veinlets, these form a closed system.

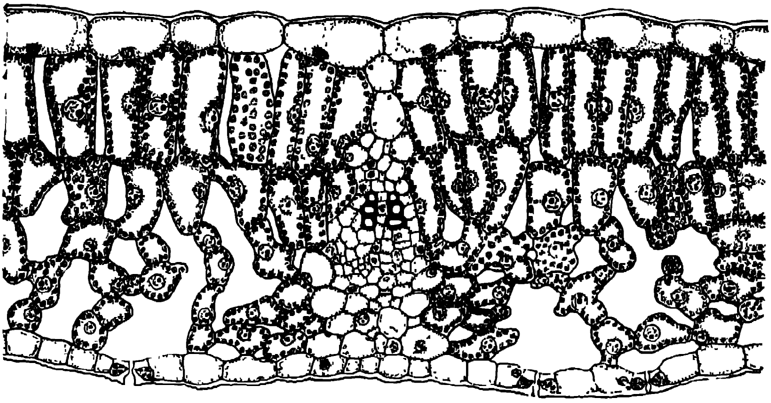

FIG 309. Cross section of a leaf of lilac (*Syringa vulgaris*), ×250 Beginning at the top, the tissues are the upper epidermis, the palisade layer, the spongy tissue with numerous intercellular spaces, the lower epidermis in which three stomata are seen, and, in the center, a small vein.

Leaf Structure. In spite of their diversity in external features, the leaves of angiosperms are rather uniform in structure. Leaves arise as lateral outgrowths from the embryonic region of a stem tip and develop by intercalary growth. A cross section of a typical mature leaf reveals the following tissues (Fig. 309): the *epidermis*, usually a single external layer of colorless cells with cutinized outer walls and containing numerous stomata; the *palisade tissue*, generally comprising one or two layers of green cells, vertically elongated, and lying beneath the upper epidermis; the *spongy tissue*, a loose region of green cells and large intercellular spaces; the *veins*, vascular bundles that traverse the spongy tissue. The arrangement of the conducting tissues in the veins is collateral, the xylem lying above the phloem. Cambial activity, if present, is weak. The mesophyll, including the palisade and spongy tissues, is the photosynthetic tissue of the leaf.

Root Tip. The root tip comprises the rootcap, embryonic region, region of elongation, and region of maturation. The rootcap is a protective sheath. The embryonic region includes the apical meristem, of very limited extent, characterized by active cell division. In the region of elongation the newly formed cells increase in length, while in the region of maturation they become differentiated to form permanent tissues. In many roots three or four distinct growing regions, or *histogens*, can be recognized (Fig. 310). The outermost layer of cells, nearly continuous around the embryonic region, is the *dermatogen*, which gives rise to the epidermis. Inside the dermatogen is the *periblem*, consisting of several layers that form the cortex. In the center of the root tip is the *plerome*, which produces the stele. In the monocotyledons a *calyptrogen* forms the rootcap and lies just behind it.

The plerome arises from a group of initials situated at its very tip. Just beyond lie another group of initials, often constituting a single layer. In the dicotyledons these form the periblem, while a third layer, beyond and in contact with it, gives rise to both the dermatogen and rootcap. In the monocotyledons the middle group of initials produce both the periblem and dermatogen, while the outermost layer of initials, the calyptrogen, independently forms the rootcap (Fig. 310).

Root hairs, arising in the region of maturation, are slender tubular extensions of the epidermal cells. They greatly increase the absorbing surface of the root. New ones are formed as the root increases in length. The older ones finally disappear.

Mature Root. The structure of the mature root is rather uniform throughout the angiosperms (Fig. 311). As in other vascular plants, the root represents a primitive type of vascular organization, being typically an exarch radial protostele. The stele is surrounded by an extensive cortex whose innermost cells, the endodermis, have more or less thickened walls. Lying immediately inside the endodermis is a layer of parenchyma, or occasionally several layers, forming the pericycle.

The process of lignification, progressing centripetally from the protoxylem strands, often does not reach to the center of the root, whose cells then remain parenchymatous and form a pith. Such a condition is common in monocotyledons, while in dicotyledons a pith is typically absent.

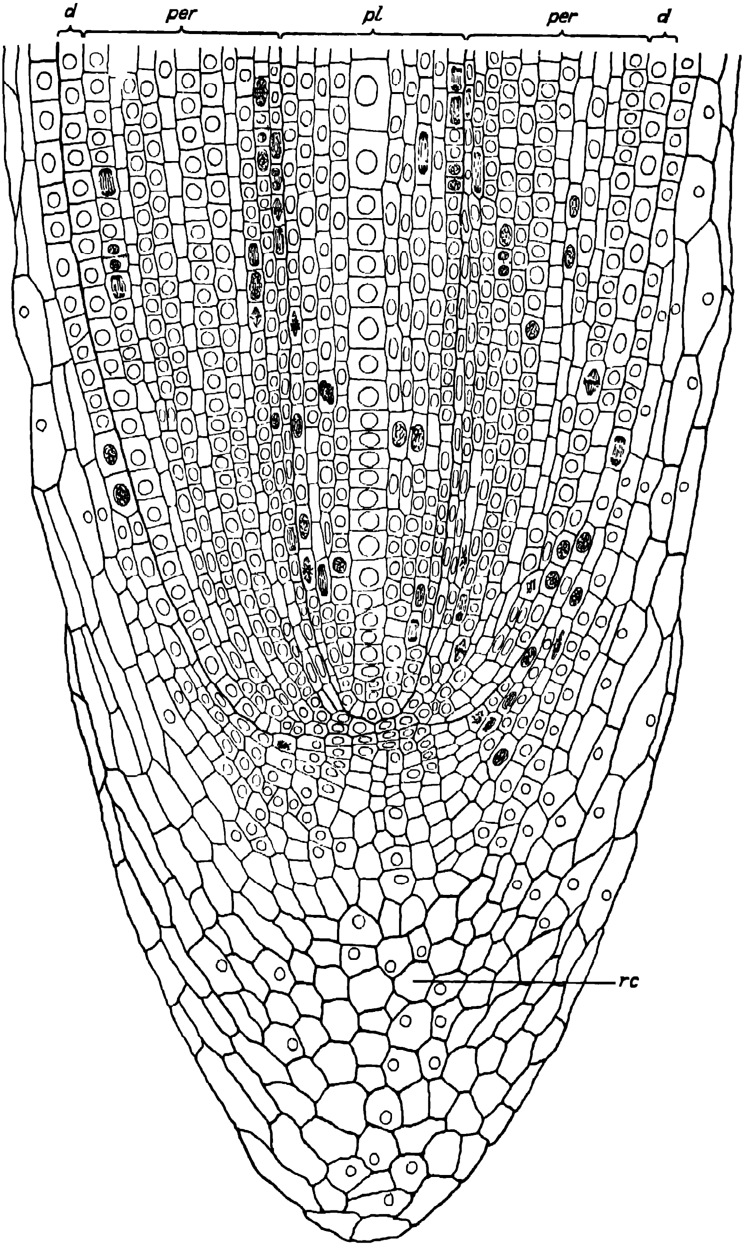

FIG. 310. Median longitudinal section of a root tip of onion (*Allium cepa*), showing histogens, × 170. *d*, dermatogen; *per*, periblem; *pl*, plerome, *rc*, rootcap At the tip of the plerome is a layer of cells that gives rise to the periblem and dermatogen. Below this layer is the calyptrogen, which produces the rootcap.

The primary wood that forms after the protoxylem is differentiated is metaxylem. In dicotyledons the number of protoxylem strands is commonly 4 or 5, while in monocotyledons it is generally more, often 15 or 20. Phloem occurs as separate strands lying between the groups of protoxylem elements. Branch roots arise in the pericycle directly opposite the protoxylem strands. They then grow outward through the cortex (Fig. 312).

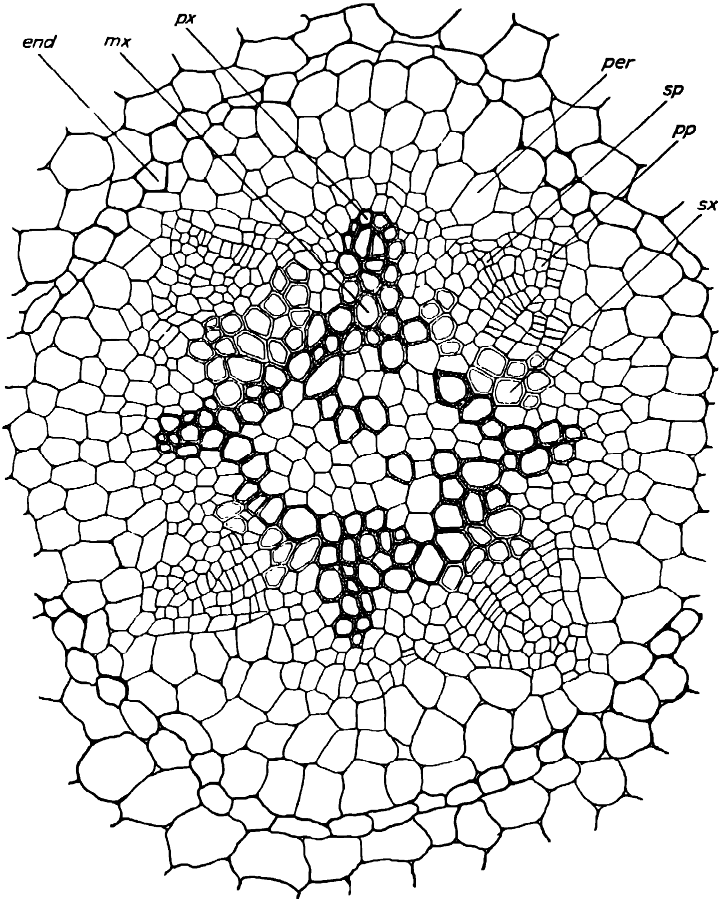

Fig. 311. Cross section of the central portion of a root of baneberry (*Actaea alba*), showing primary tissues and beginning of formation of secondary tissues by the cambium, which lies between the secondary xylem and phloem, ×200; *end*, endodermis; *per*, pericycle; *pp*, primary phloem; *sp*, secondary phloem, *px*, protoxylem; *mx*, metaxylem; *sx*, secondary xylem.

Except in fibrous roots, a cambium arises between the primary xylem and phloem and cuts off secondary vascular tissues—secondary xylem on the inside and secondary phloem on the outside (Fig. 311). Soon a more or less continuous cylinder of secondary vascular tissues is formed.

Stem Tip. An embryonic region, a region of elongation, and a region of maturation are present in a stem tip, but are more extensive and much less clearly defined than in a root tip, overlapping to a considerable extent. Immediately behind the apical meristem the leaf primordia arise superficially as lateral outgrowths and develop in acropetal succession (Fig. 313). A meristem may arise in the axil of each leaf primordium while it is still very small, giving rise to a lateral bud, or the meristem may not appear until later.

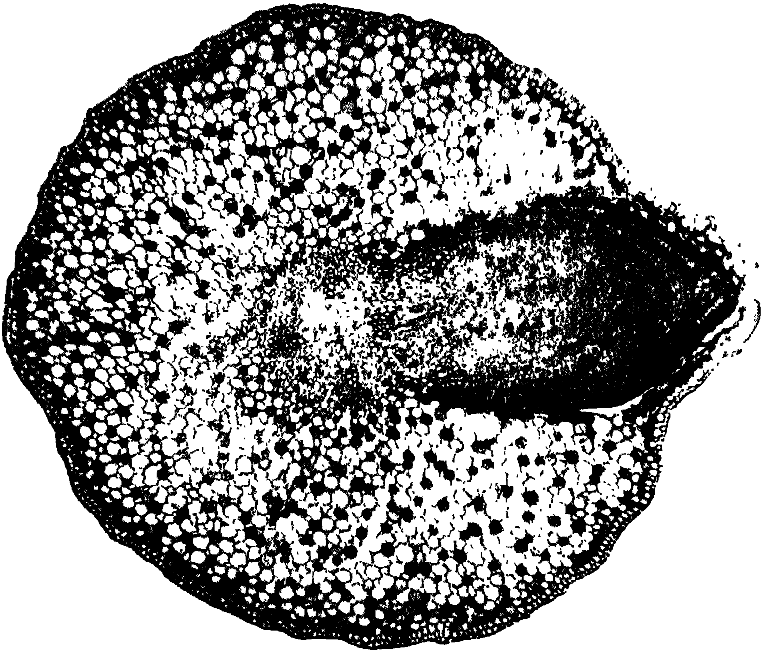

FIG. 312. Cross section of a root of willow (*Salix*), showing a branch root pushing outward through the cortex, ×55

Generally the dermatogen is clearly recognizable, but often the line of demarcation between the periblem and plerome is not. For this reason, and because it is usually difficult or impossible to relate the origin of the epidermis, cortex, and stele to distinct cell regions or "histogens," a newer and more satisfactory concept of the structure and growth of the stem apex is that it is made up of two distinct "growth zones." The outer zone, or *tunica*, consists of one or more (up to four or five) superficial layers of small uniform cells that divide anticlinally, so that each layer remains distinct. Periclinal divisions occur only in connection with leaf and bud formation. The inner zone, or *corpus*, comprises the central tissue, the cells of which are larger and divide in all planes and so are irregular in size and arrangement. Thus the two zones differ both in position and mode of growth. Surface growth predominates in the tunica, while volume growth is characteristic of the corpus. Frequently these zones are not clearly marked off from each other and vary considerably in form and relative extent. Moreover, the relative contributions of the tunica and corpus to the three regions of the mature stem are usually difficult to determine and differ according to the species.

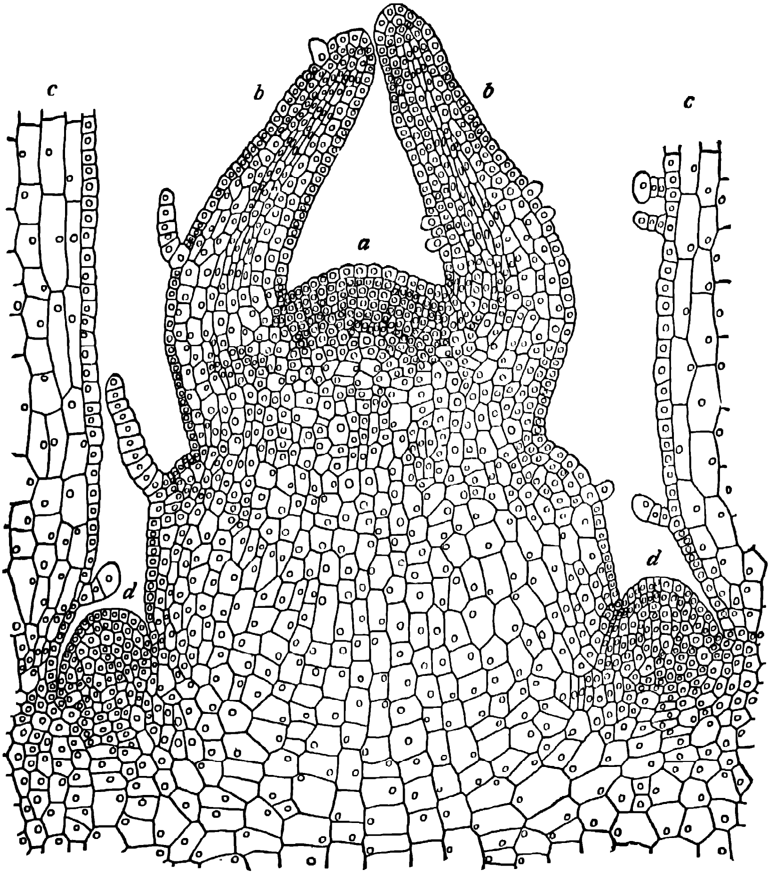

FIG. 313. Median longitudinal section of the stem tip of *Coleus blumei*, ×200. In the center is the apical meristem (*a*) with a leaf primordium (*b*) on either side. In the axil of each of the older leaves (*c*) is a lateral meristem (*d*) that will produce an axillary bud.

Mature Stem. As in the leaf, the epidermis of the young stem becomes cutinized and contains many stomata. The cortex consists mainly of green parenchyma, but sclerenchyma may be differentiated as development proceeds. In some stems a well-marked endodermis is present, but generally this layer is not clearly differentiated. In stems that increase in diameter a cork cambium or *phellogen* arises beneath the epidermis, forming cork tissue. This finally replaces the epidermis as a protective covering. Communication between the atmosphere and the living tissues beneath the cork is maintained through lenticels.

The stele is bounded externally by the pericycle, which usually consists of several layers of cells. Some of these may remain parenchymatous, while others become sclerenchymatous. The development of the primary xylem is endarch. Among gymnosperms, with the exception of the Gnetales, tracheids are the only conducting elements present in the xylem, but in angiosperms *vessels* are the chief elements. Tracheids are derived from single cells, vessels from a row of cells whose end walls break down. Both are lignified, the lignin being localized to form spirals, rings, an irregular network, or it may be so abundant that the walls are pitted (Fig. 314*C*–*E*). Spiral and annular elements are characteristic of protoxylem, reticulate and pitted elements of metaxylem and secondary xylem. In addition to vessels, the secondary xylem of angiosperms may consist, largely or in part, of tracheids, wood fibers, and wood parenchyma (Fig. 314*F*). The phloem is made up of sieve tubes, companion cells, and often

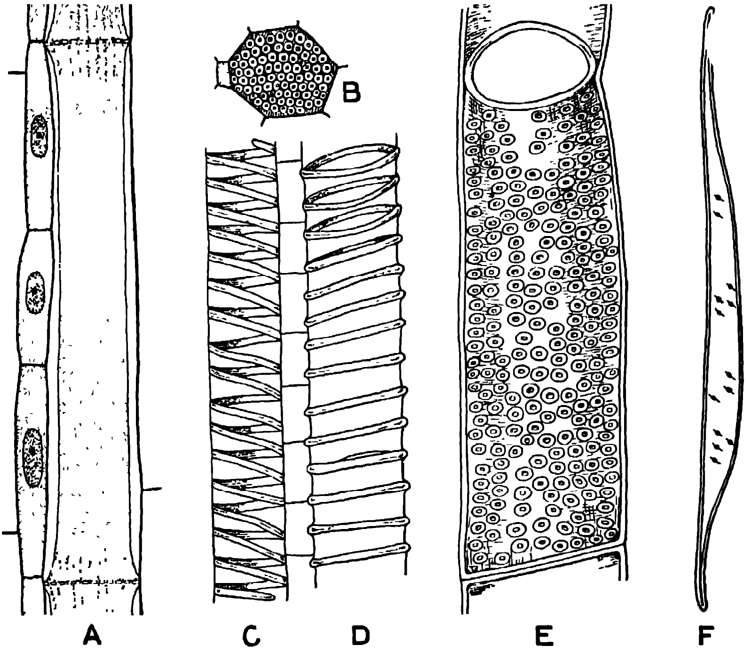

FIG 314. Conducting tissues, ×200. Phloem elements: a sieve tube and a row of companion cells from a squash stem, as seen in longitudinal (*A*) and transverse (*B*) sections. Xylem elements spiral (*C*), annular (*D*), and pitted vessels (*E*), and a wood fiber (*F*) from a stem of castor bean.

also of fibers and parenchmya (Fig. 314*A*, *B*). Companion cells do not occur in pteridophytes and gymnosperms. As in the Filicinae and gymnosperms, leaf gaps are formed in the vascular cylinder in connection with the departure of leaf traces.

Stelar Types. The stem of most woody dicotyledons is like that of gymnosperms in being an ectophloic siphonostele, the vascular tissues forming a nearly continuous cylinder enclosing the pith (Fig. 315). This cylinder, consisting of xylem and phloem in collateral arrangement, is traversed by numerous vascular rays. As in the root, the cambium, a meristematic layer of cells, arises between the primary xylem and phloem. Through cambial activity, the stems of woody dicotyledons undergo a great deal of secondary thickening, increasing in diameter from year to year.

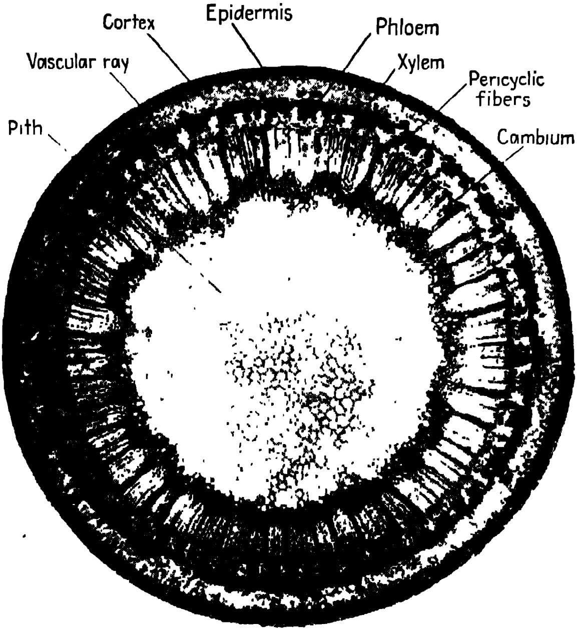

FIG. 315. Cross section of a young stem of magnolia (*Magnolia grandiflora*), showing vascular cylinder surrounded by the cortex and enclosing the pith, ×17.

The stems of herbaceous dicotyledons are like those of woody dicotyledons except that the vascular tissues are greatly reduced in amount, either as a result of diminished cambial activity, resulting in a continuous but narrow vascular cylinder, or by the breaking up of the cylinder into separate bundles to form a dictyostele. In such stems the vascular bundles are at first separated by wide bands of parenchyma connecting the pith with the cortex. The cambium may extend across these "pith rays" and later give rise to secondary xylem and phloem, thus forming a continuous vascular cylinder, or it may produce only parenchyma between the bundles, which then remain separate. In many herbs the interfascicular cambium fails to develop at all, the secondary vascular tissues then being produced within the bundles.

Thus the stems of herbaceous dicotyledons illustrate various degrees of reduction from the more highly organized but more primitive condition seen in the stems of typical woody dicotyledons. This strongly indicates that the woody stem is the more ancient type from which the herbaceous stem has been derived, probably in response to climatic changes.

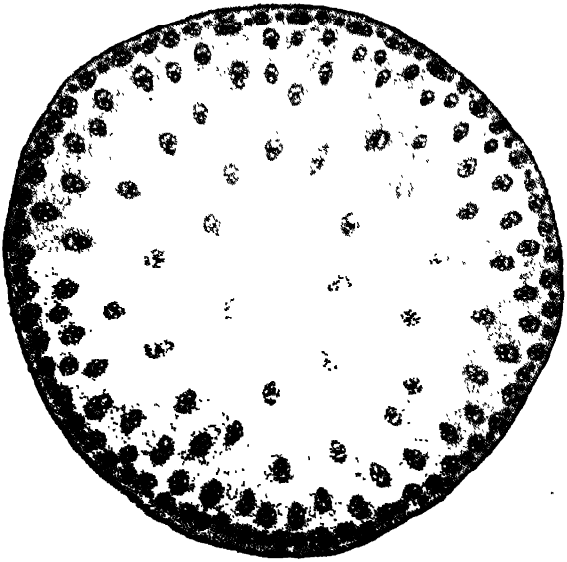

FIG 316 Cross section of a young stem of Indian corn (*Zea mays*), showing scattered vascular bundles, ×8.

The stems of most monocotyledons display a characteristic type of dictyostele with scattered vascular bundles (Fig. 316). With rare exceptions, a cambium is wanting, and so no secondary thickening ordinarily occurs. In a few monocotyledons, such as *Dracaena*, *Aloe*, and *Yucca*, a special kind of secondary thickening takes place. Here a cambium arises in the pericycle or inner cortex and forms a cylinder of new vascular tissues.

In most monocotyledons the arrangement of the conducting tissues in each vascular bundle is collateral, as in dicotyledons, but frequently it is *amphivasal*, the xylem surrounding the phloem (Fig. 317). The young stem of a monocotyledon is usually a siphonostele with collateral bundles. The monocotyledons represent, in their stem structure, the final stages in a reduction series that begins with the gymnosperms and woody dicotyledons and passes through the herbaceous dicotyledons, where every intermediate condition is seen. This reduction series indicates the general trend of evolution as it seems to have taken place in the spermatophytes.

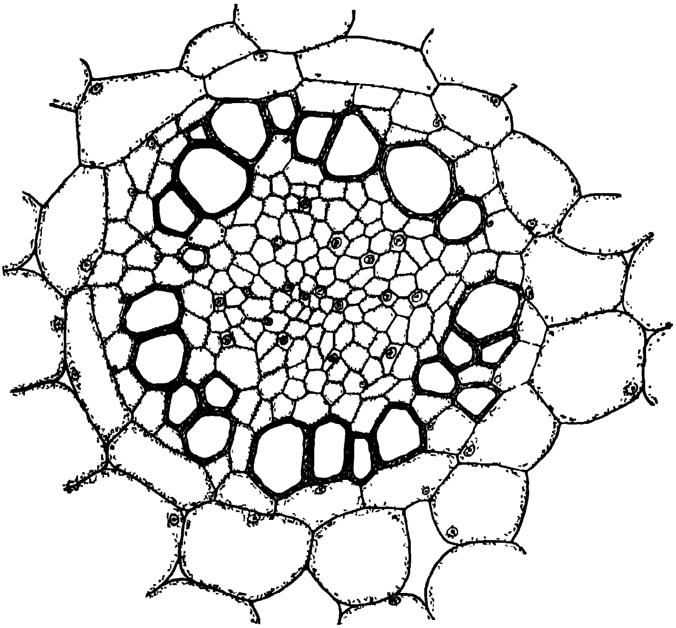

Fig. 317. Cross section of an amphivasal bundle from the rhizome of sweet flag (*Acorus calamus*), a monocotyledon, showing the xylem completely surrounding the phloem. × 500

The Flower

A strobilus is a group of sporophylls borne on a more or less elongated axis. A flower is essentially a strobilus in which the sporophylls (stamens and carpels) are usually borne on a shortened axis (receptacle) and are usually surrounded by a perianth. This distinction is untenable, however, because some flowers have an elongated receptacle and some have no perianth. For convenience, any organization of sporophylls may be designated as a strobilus in pteridophytes and gymnosperms and as a flower in angiosperms. Such a distinction is arbitrary. A flower and a strobilus are morphologically equivalent structures.

Practically all gymnosperms, except the Bennettitales, have monosporangiate strobili, while most angiosperms have bisporangiate ("perfect") flowers. In many cases the monosporangiate ("imperfect") condition has arisen by the suppression of stamens in the one kind of flower and of carpels in the other, the reduced organs often being represented by vestiges. The two kinds of flowers may occur on the same plant (monoecious condition) or on separate plants (dioecious condition).

The Perianth. In a typical flower the perianth consists of two differentiated sets of parts, the outer set being the *calyx* and the inner set the *corolla* (Fig. 318). The calyx is made up of *sepals*, the corolla of *petals*. Ordinarily the sepals are scale-like and green, while the petals are larger and either white or of some other color than green. Both may be small and inconspicuous, however, as in the rushes (*Juncus*), or large and showy, as in the lilies (*Lilium*). In some flowers the perianth consists of a single set of parts. These may be greenish and scale-like, as in the beet (*Beta*), or large and showy, as in the anemone. In either case the flower is said to be *apetalous* and the single whorl is arbitrarily designated as the calyx. This is based on the assumption that the corolla is the missing

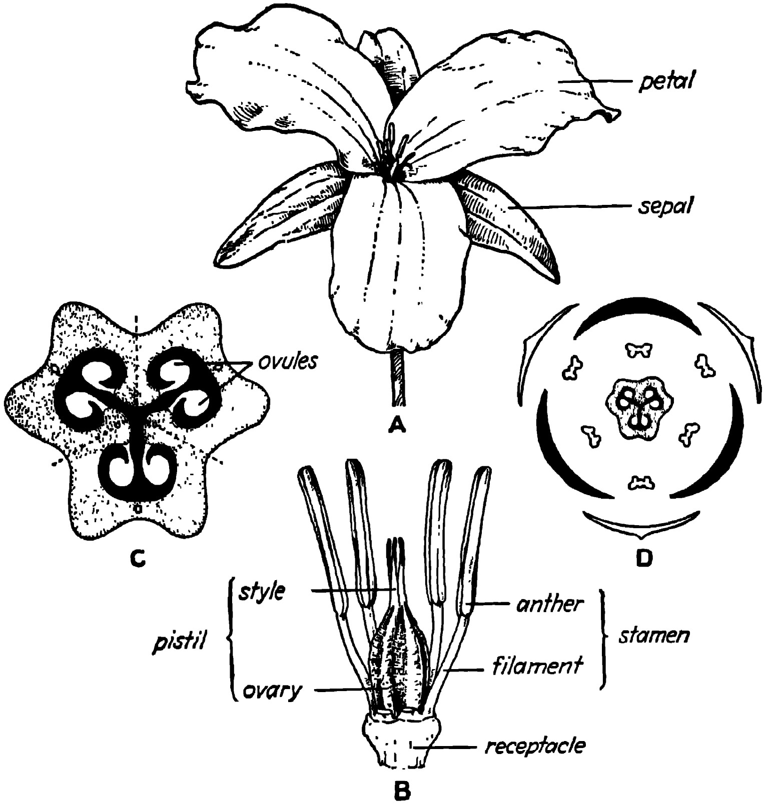

FIG. 318. Floral structure of the large-flowered trillium (*Trillium grandiflorum*). *A*, a single flower, two-thirds natural size; *B*, four of the stamens and the pistil, twice natural size; *C*, cross section of the ovary, the dotted lines indicating the junction of the carpels, ×10; *D*, the floral diagram.

set, which may or may not be true. In fact, the single whorl apparently often represents a perianth that has never become differentiated into a calyx and corolla. *Naked* flowers are those which are entirely without a perianth. It may have been lost through degeneration or may never have been developed.

Sepals and petals are leaf-like in both form and structure. Phylogenetically they may either have been derived by sterilization from sporophylls, may represent modified foliage leaves, or possibly, at least in some flowers, the sepals may have evolved from leaves and the petals from stamens. Often the foliage leaves and perianth parts intergrade, making it difficult to delimit the flower from the vegetative shoot that bears it. In some flowers, notably in the water lily (*Nymphaea*), the petals intergrade with the stamens.

FIG. 319. Flower of *Magnolia grandiflora*, a primitive type, with numerous stamens and carpels borne in spiral arrangement on an elongated receptacle, one-half natural size.

Most flowers have a regular (*actinomorphic*) corolla, composed of petals alike in size and shape, the flower as a whole exhibiting radial symmetry (Fig. 318). This represents a relatively primitive condition. Many flowers have an irregular (*zygomorphic*) corolla, with not all the petals alike, thus showing bilateral symmetry. This tendency reaches its highest expression in flowers having spurs, sacs, or pouches, as in the Leguminosae, Labiatae, and Orchidaceae.

Establishment of Whorls and Definite Numbers. Primitive flowers, like those of the magnolia and buttercup (*Ranunculus*), have a convex, elongated receptacle bearing indefinitely numerous stamens and carpels in spiral arrangement (Fig. 319). Such a condition is similar to that of a strobilus. In most flowers, however, the receptacle does not elongate but generally broadens at the apex, the floral parts arising from it in a series of whorls. The members of one whorl usually alternate with those of the next whorl (Fig. 318*D*). Commonly there are two whorls of perianth parts, two whorls of stamens, and one whorl of carpels. Such flowers are said to be *pentacyclic*. Where one whorl of stamens is wanting, this being nearly always the inner one, the flower is *tetracyclic*. With the establishment of a cyclic arrangement of floral parts, the members of each set are reduced to a definite number that is often the same in all whorls. In monocotyledons the number of parts in each whorl is generally three, while in dicotyledons it is usually five but often four. In many flowers the number of carpels is less than the number of parts in any of the other whorls.

Zonal Development. A striking feature of floral evolution has been the tendency for the members of the same whorl to develop as a single organ. Thus, in some flowers, the carpels are separate, each forming a simple pistil, while in most flowers the carpels are organized to form a compound pistil (Figs. 318*B*, *C*, and 326). Similarly, in many flowers, the petals are wholly or partly united to form a corolla tube and the sepals are united to form a calyx tube. Obviously a *syncarpous* flower (one with united carpels) is more advanced than an *apocarpous* one (one with separate carpels), and a *sympetalous* flower (one with united petals) is more advanced than a *choripetalous* one (one with separate petals). In some flowers the stamens are united to form a tube, but this condition is uncommon.

It should be understood that, in all flowers where members of the same set are united, the parts do not arise separately and later fuse, but originate together from a common meristem and develop as a single organ. There is a zonal development from the receptacle that involves all members of the same set, so that they are united from the beginning. Sometimes the primordia of the individual members arise separately but are soon carried upward by zonal development from below. This results in a compound pistil with separate styles or in a corolla tube with free tips.

Hypogyny, Perigyny, and Epigyny. In most sympetalous flowers the stamens are free above but are attached below to the corolla tube. Here zonation involves the members of two different sets. A still more advanced condition occurs where the receptacle enters into a zonal development with other floral sets. In *hypogynous* flowers all the sets arise independently from a more or less convex receptacle, the ovary being entirely free and situated above the place of attachment of the sepals, petals, and stamens (Fig. 320). In *perigynous* flowers the ovary is also free, but the receptacle is more or less concave, forming a disk-like or cup-like structure from the rim of which the sepals, petals, and stamens arise.

Here zonation involves the three outer floral sets. In *epigynous* flowers the upward growth of the receptacle involves the ovary as well as the other floral parts, so that the ovary is embedded in the receptacle and the sepals, petals, and stamens seem to arise from its summit. In hypogynous and perigynous flowers the ovary is *superior*, while in epigynous flowers it is *inferior*. Hypogyny represents the most primitive and most common condition, epigyny the most advanced. Perigyny is intermediate and least common.

In perigynous and epigynous flowers the structure surrounding the ovary and bearing the sepals, petals, and stamens on its rim is generally regarded as a zonal upgrowth of the receptacle because, in the development of the flower, such an upgrowth actually occurs. Another view, supported by evidence from vascular anatomy, is that the structure referred to is made up of the fused basal portions of the sepals, petals, and stamens, to which, in epigynous flowers, the carpels are also united. Although such fusion cannot be seen in floral development (ontogeny), it is assumed to have occurred during the course of floral evolution.

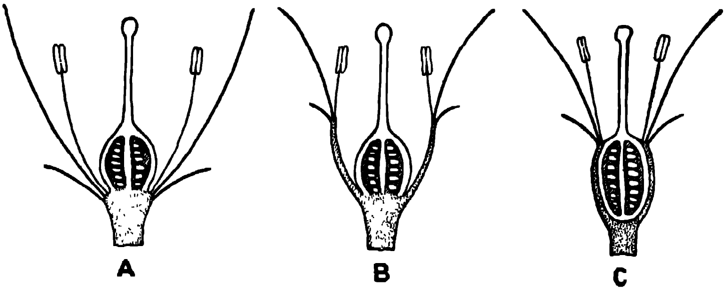

FIG. 320. Diagrams illustrating hypogyny (*A*), perigyny (*B*), and epigyny (*C*). In each flower the receptacle is stippled.

Floral Development. A longitudinal section through a very young flower bud reveals the fact that the floral parts arise at the tip of the receptacle as rounded protuberances of meristematic tissue. They arise in much the same way as foliage leaves from a vegetative stem tip. Ordinarily their appearance is acropetal, the sepals coming first, next the petals, then the stamens, and finally the carpels. This sequence is shown in the buttercup (*Ranunculus*), for example, a primitive flower that is apocarpous and hypogynous and one in which the stamens and carpels arise in spiral succession on an elongated receptacle (Fig. 321). As in all flowers, the apical meristem does not continue to grow indefinitely, but sooner or later becomes transformed into carpels.

The usual order of appearance of floral parts is modified in certain flowers, especially where one set is being suppressed. In the shepherd's-purse (*Capsella*), one of the Cruciferae, the petals appear after the other

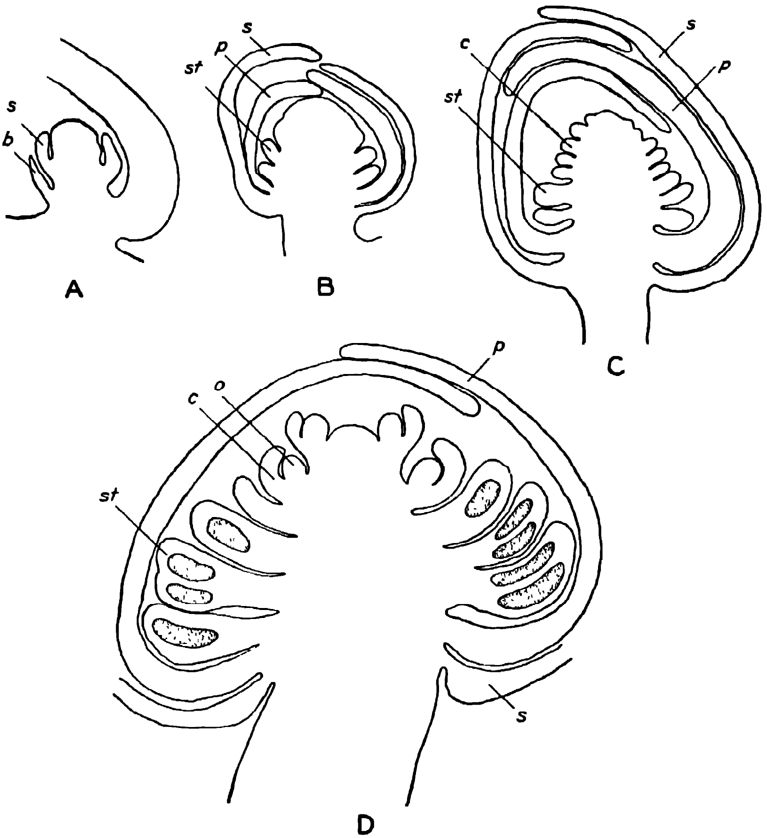

FIG. 321. Floral development in the buttercup (*Ranunculus*), ×50. *A* to *D*, successively older stages; *b*, bract; *s*, sepal; *p*, petal; *st*, stamen; *c*, carpel; *o*, ovule.

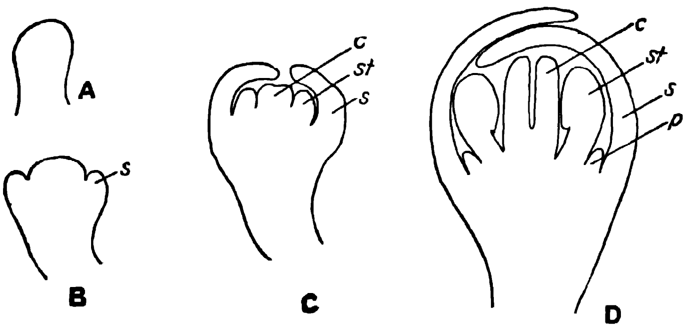

FIG. 322. Floral development in shepherd's-purse (*Capsella bursa-pastoris*), ×100. *A* to *D*, successively older stages; *s*, sepal; *st*, stamen; *c*, carpel; *p*, petal. The order of appearance differs from that of a typical flower in that here the petals appear last.

parts have arisen but, of course, in their proper place between the sepals and stamens (Fig. 322). This flower, when mature, has small petals. In the fleabane (*Erigeron*) and other members of the Compositae the sepals are the last members to appear. They remain vestigial. This flower shows the epigynous type of development (Fig. 323).

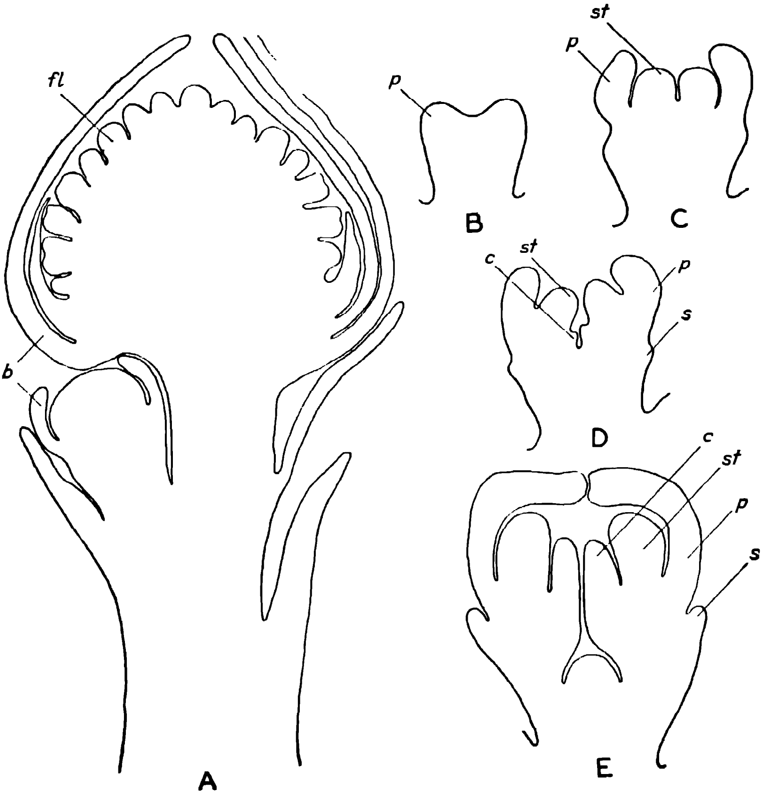

FIG. 323. Floral development in fleabane (*Erigeron*). *A*, very young and older inflorescence, the flowers arising on the convex receptacle, ×75; *B* to *E*, successive stages in the development of a single flower, ×200; *b*, bract; *fl*, flower; *p*, corolla; *st*, stamen; *c*, carpel; *s*, calyx.

The Stamen. The stamen of angiosperms is the same structure as in gymnosperms, a microsporophyll. Generally it is differentiated into a terminal, club-like, spore-bearing portion, the *anther*, and a slender stalk, the *filament* (Fig. 318*B*). A cross section of a young anther usually shows four microsporangia, but the number may vary among different angiosperms from one to many (Fig. 324*A*). As a rule, the microsporangia extend the entire length of the anther. Later, by the breaking down of the intervening tissue between each pair of microsporangia, two large cavities may be formed (Fig. 324*B*); or the four microsporangia may remain separate. When the stamen is mature, the microsporangia, regardless of their number, are called *pollen sacs.*

As in gymnosperms, the development of the microsporangia is eusporangiate. A very young anther is made up of uniform meristematic tissue

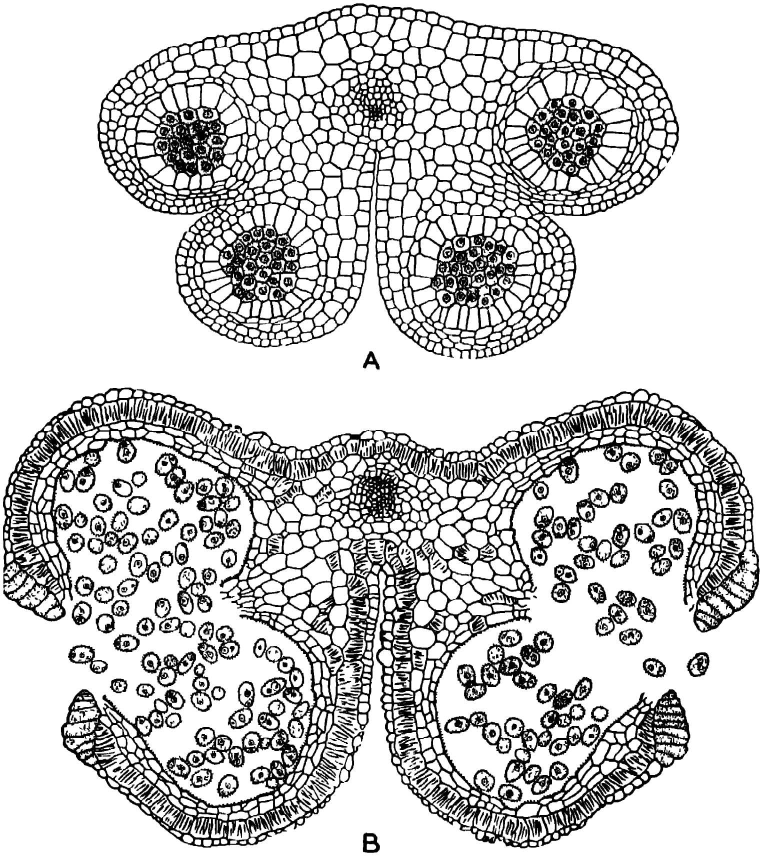

FIG. 324. Cross section of a young and of a mature anther of lily (*Lilium*). *A*, young anther, the four microsporangia with sporogenous tissue, ×60; *B*, mature anther with two pollen sacs containing pollen grains, ×30. The tapetum, surrounding the sporogenous tissue and conspicuous in *A*, has broken down in *B*, while the endothecium has developed bands of thickening. (*B*, *after Chamberlain*.)

surrounded by an epidermis. As seen in cross section, four lobes soon appear and a conducting strand becomes differentiated in the center. The cells forming the hypodermal layer are probably all potentially sporogenous but, as a rule, are actively so only in four regions, *viz.*, under the lobes. Only one longitudinal row of hypodermal cells may be differentiated under each lobe as sporangium initials, as in the Malvaceae and

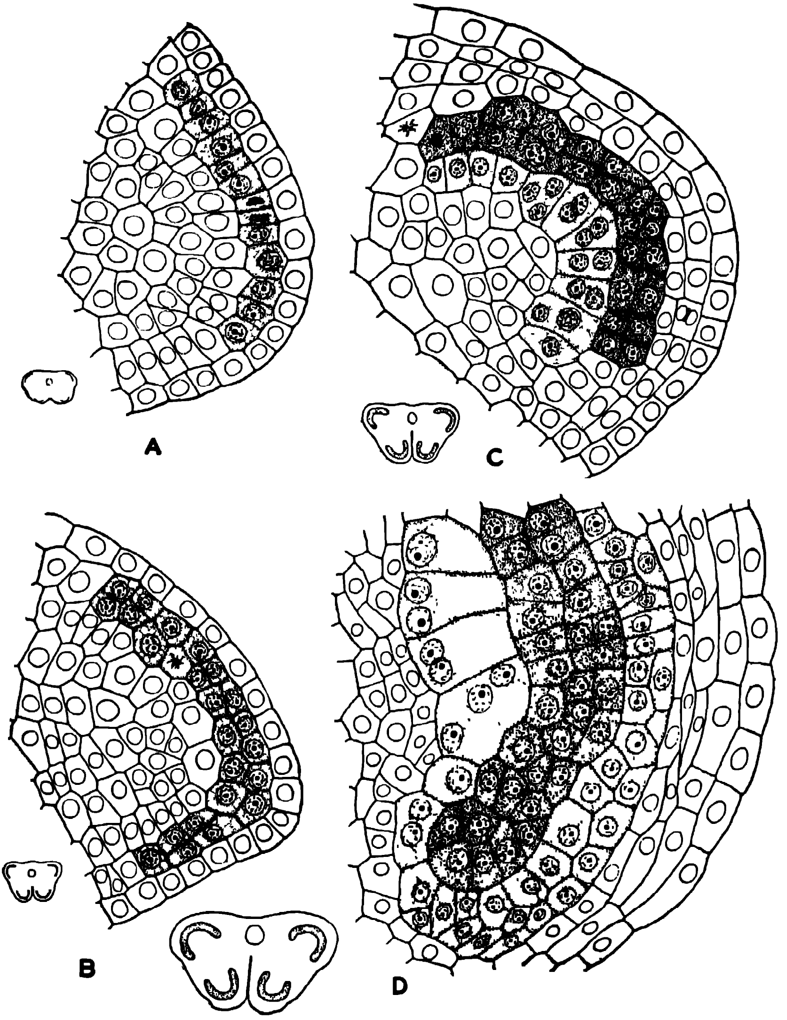

FIG. 325. Early development of the microsporangium of *Iochroma lanceolatum*, ×400. Each stage also shows outline of entire anther, ×32. *A*, cross section of portion of young anther with hypodermal initial cells (shaded); *B*, division of initials to form primary parietal cells (outer shaded layer) and primary sporogenous cells; *C*, later stage, showing two layers of parietal and of sporogenous cells (latter heavily shaded) and differentiation of inner portion of tapetum (lightly shaded); *D*, later stage, showing anther wall composed of epidermis, endothecium, and middle layers; also sporogenous tissue (heavily shaded) surrounded by tapetum (lightly shaded).

most members of the Compositae, but ordinarily a plate including several or many hypodermal cells appears (Fig. 325*A*).

In the development of a microsporangium, the formation of a periclinal wall in each initial separates the outer *primary parietal cells* from the inner *primary sporogenous cells* (Fig. 325*B*). The former, lying immediately beneath the epidermis, then undergo further periclinal divisions, usually forming about three to five layers of parietal tissue (Fig. 325*C*, *D*). The outermost parietal layer, lying next to the epidermis, is the *endothecium.* As a rule, by the development of fibrous bands of thickening, the endothecium becomes hygroscopic and assists in the dehiscence of the anther (Fig. 324*B*). The innermost layer of parietal tissue forms part of the tapetum, the rest of which is derived from the cells immediately in contact with the sporogenous cells on their inner side. Sometimes the tapetum becomes two- or three-layered. An interesting feature is the division of the tapetal nuclei to form two or more free nuclei in each cell (Fig. 325*D*). The middle layers and tapetum generally disappear before the maturing of the spores, the ripe sporangium wall usually consisting only of the epidermis and endothecium. A tapetal plasmodium, surrounding the microspores, is seen in several groups, such as the Compositae and Helobiales.

The cells forming the primary sporogenous layer generally undergo two or three divisions to form the microspore mother cells, which then greatly enlarge and assume a spherical form. The next two divisions, during which the number of chromosomes is reduced one-half, result in the formation of tetrads. At this time the tapetum disorganizes. The tetrads are mostly tetrahedral in dicotyledons and isobilateral in monocotyledons. A linear arrangement of microspores is rare, but occurs in the milkweeds (*Asclepias*) and a few other forms.

Upon separation from the tetrads, the microspores have developed a two-layered cell wall consisting of an outer *exine* and an inner *intine* (Fig. 334). Although commonly the exine is thickened, the cell wall usually has one or more thin places where the exine is not formed and through which the pollen tube may later emerge. Its outer surface usually bears warts or spines, or is variously sculptured. Ordinarily the microspores become free from one another at maturity, but in some angiosperms (*e.g.*, *Typha* and *Rhododendron*) the members of the tetrad do not separate, while in a few others, notably in the milkweeds (*Asclepias*) and certain orchids, all the spores in a sporangium cling together and escape as a mass, which is called a *pollinium.*

As a rule, the anther dehisces by means of two longitudinal slits (Figs. 318*B* and 324*B*), but sometimes by terminal slits or pores, by hinged valves, or irregularly.

The Carpel. The carpel of angiosperms is really a megasporophyll but, instead of bearing the ovules freely exposed, as in gymnosperms, it surrounds them. Where two or more carpels are wholly or partly united, forming a compound pistil, the flower is said to be *syncarpous.* Where the carpels are free, each constituting a simple pistil, the flower is *apocarpous.* The enlarged, hollow, lower portion of the pistil, the *ovary,* encloses one or more ovules (Fig. 318*B*). Generally a slender stalk-like *style* arises from the ovary. In some compound pistils the styles as well as the ovaries are united, while in others the styles are wholly or partly free (Fig. 326). The style may be hollow but usually is solid. The tip of the style, termed the *stigma*, is not a morphological unit, but merely an exposed and often expanded portion of the tissue that lines the ovarian cavity and extends upward through the style. In some flowers the stigmatic surface extends down the outside of the style.

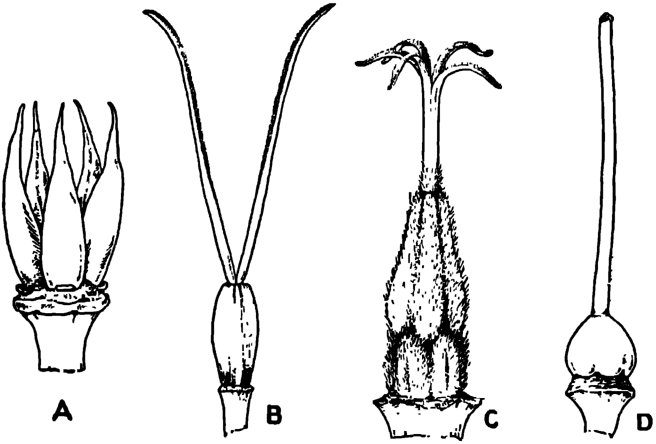

FIG. 326 Pistils showing various degrees of union between the carpels. *A*, five separate carpels in the flower of stonecrop (*Sedum*), ×3; *B*, pistil of garden pink (*Dianthus*) with two carpels having united ovaries and free styles, ×3; *C*, pistil of geranium (*Pelargonium*) with five united carpels having free stylar tips, ×6; *D*, pistil of nightshade (*Solanum*) with two completely united carpels, ×6.

An ovary may contain a single cavity (*locule*) or two or more cavities separated from one another by partitions. The ovules may be attached to the walls of the ovary or to the partitions between the locules, in either case being foliar in origin. In some cases the receptacle grows upward into the ovarian cavity and bears the ovules either terminally, laterally, or in both ways. Such ovules are cauline in origin.

The carpel of angiosperms is generally regarded as the equivalent of an infolded leaf bearing ovules along its fused margins. In fact, in many apocarpous flowers the carpel arises as an open structure that encloses the ovules as development proceeds. Although a foliar organ, the carpel is not a transformed foliage leaf. It is a sporophyll—an organ with its own evolutionary history reaching far back into a pteridophyte ancestry. Sporophylls and foliage leaves have undergone a parallel evolutionary development. Another view regarding the nature of the carpel is that it is a greatly reduced branch system. This theory is based on its supposed