CHAPTER 16

Ginkgophyta

KAEMPFER was the first European botanist to study the maidenhair tree. He observed it in cultivation in Japan in 1690 and later published a botanical description of the tree. Kaempfer proposed the name *Ginkgo,* and Linnaeus adopted this generic appellation in 1771, adding the descriptive specific epithet *biloba* as a reference to the deep notching that characterizes the lamina of the leaf on many specimens. Although there has been considerable difference of opinion regarding the etymology of the word "Ginkgo," there is, according to Li (1956), no justification for rejecting the name on the basis that it is a distortion of the word "Ginkyo." Li maintains that the maidenhair tree has been correctly designated as *Ginkgo* for nearly 250 years "and certainly will be known as such forever."

During the latter part of the nineteenth century, *Ginkgo biloba* was placed in the family Taxaceae under the order Coniferales because of the resemblance of its large fleshy seeds to the seeds of *Torreya* and *Cephalotaxus.* The discovery by Hirase (1896) of motile flagellated sperm in *Ginkgo* led to a complete reappraisal of the systematic position of *Ginkgo biloba,* which today is regarded as the only surviving representative of the Ginkgoales (Engler, 1954).

Like the cycads, *Ginkgo biloba* is a veritable "living fossil," and perhaps, as Arnold (1947) suggested, "may indeed be the oldest living genus of seed plants." Leaves very similar in form and venation to the leaves of the modern *Ginkgo* have been found as fossils in rocks deposited during the Mesozoic Era, when ginkgolike plants were apparently worldwide in distribution. For example, *Ginkgo digitata,* a Jurassic species, grew in such widely separated areas as western North America, Alaska, Australia, Japan, and England. Other fossil ginkgophytes are *Ginkgoites* and *Baiera.* The latter genus is particularly notable because its multilobed leaves resemble the deeply incised leaf blades often observed in seedlings and in coppice shoots of the living *Ginkgo.* According to Arnold (1947), many leaves of the form genus *Ginkgoites* so closely resemble *Ginkgo* as to be indistinguishable from those of the living species.

Following the Mesozoic, *Ginkgo* declined progressively in its distribution and, according to Seward (1938), "there can be no doubt that China was the last, if it is not the present, natural home of the maidenhair tree."

Whether *Ginkgo* still exists in the wild state in the more remote and poorly explored forests of China has been regarded an unsettled question by many writers. Some evidence has been produced in favor of the existence of native stands of *Ginkgo* trees, although many botanists contend that such

FIGURE 16-1 *Ginkgo biloba.* Young specimen illustrating dense foliage and characteristic excurrent habit of growth. This tree is vigorous and healthy despite its urban environment, which one might not expect to be favorable for its growth.

trees may represent the offspring of cultivated specimens. In a thorough discussion, however, Li (1956) presents evidence that *Ginkgo* still exists in the wild state in southeastern China, and that the last refuge of this living fossil is a mountainous area "along the northwestern border of Chekiang and southeastern Anhwei." From a broad evolutionary viewpoint, *Ginkgo* is to be regarded "as one of the wonders of the world; it has persisted with little change until the present through a long succession of ages when the earth was inhabited by animals and plants for the most part far removed, in kind as in time, from their living descendants. *Ginkgo* is one of a small company of living plants which illustrates continuity and exceptional power of endurance in a changing world" (Seward, 1938, p. 424).

Ginkgo biloba is widely cultivated as a park specimen or street tree in many temperate areas of the world (Figs. 16-1, 16-2). In accordance with the vitality that has enabled it to survive as a distinct organism for millions of years, the modern *Ginkgo* grows successfully amidst the smoke and gasoline fumes of modern cities. It is exceptionally resistant to the attacks of insects and parasitic fungi, except for the devastating fungus "Texas root-rot" or "Take-all" *(Phymatotrichum omniverum)*. The outer fleshy coat of the seed emits an odor like rancid butter, and for this reason the male or microsporangiate trees are preferable to female trees for park or street planting. Several cities have learned this lesson the hard way.

Although there is no known way of separating male from female trees on the basis of external morphological characters prior to the formation of reproductive structures, the work of Lee (1954) and Pollock (1957) suggests that it is possible to differentiate between chromosomal complements in the two sexes. If a study of chromosome morphology proves practical in distinguishing the sex of young *Ginkgo* plants, it would then be possible to eliminate potential female trees from street plantings.

The kernel of the seed (i.e., the female gametophytic tissue and the embryo) of *Ginkgo* is highly nutritious and is used as food in China and Japan. For 3,000 years, or more, an extract of the *Ginkgo* leaf has been recommended in Chinese medicine as being "good for the heart and lungs." Extracts have shown promise for treatment of asthma, toxic shock, Alzheimer's disease, and various circulatory disorders. Recently the compound ginkgolide B has been synthesized, which eventually could lead to its widespread use in treating various disorders.

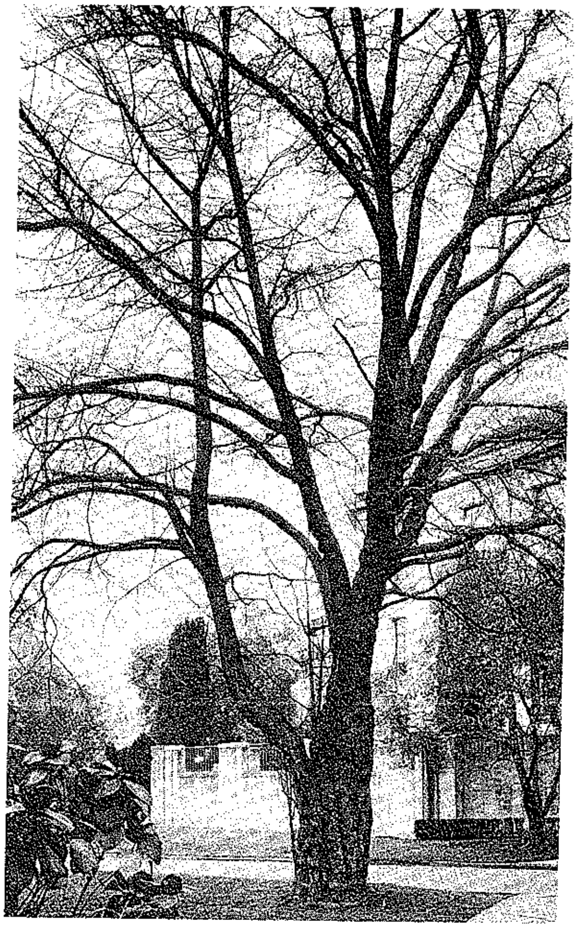

FIGURE 16-2 A large, microsporangiate specimen of *Ginkgo biloba* in leafless condition, on the campus of the University of California, Berkeley. Note very irregular pattern of branching.

Vegetative Organography and Anatomy

Habit

Young *Ginkgo* trees have a pronounced excurrent habit of growth, resembling that of many conifers (Fig. 16-1). With increasing age, the crown becomes broad and irregular and the pattern of branching variable (Fig. 16-2). Exceptionally robust trees, such as those found near certain temples and shrines in China and Japan, may attain a height of 30 meters.

Burls

In very old cultivated specimens of *Ginkgo,* formations resembling stalactites, called *burls*—known as "chichi" (nipples) to the Japanese—hang downward from the lower sides of many of the larger branches. These peculiar burls may occur either singly or in clusters and, according to Fujii (1895), may attain a length of 2.2 meters and a diameter of 30 centimeters. If one of these strange growths reaches the ground, it may take root and form leaves. Fujii's anatomical study revealed that a chichi, near its point of attachment to the parent branch, contains a central, deeply imbedded, spur shoot together with its associated buds. These buds keep pace with the secondary growth of the burl and appear as small protuberances on the outer surface of the thick cylinder of xylem. Although Fujii concluded that the chichi of *Ginkgo* represent a pathological formation, he provided no explanation of the causal factors responsible for their origin and unusual mode of development.

Shoot Dimorphism

During the development of a *Ginkgo* tree, a marked distinction becomes increasingly evident between two types of shoots: *long shoots,* distinguished by their widely separated nodes and leaves, and the more slowly growing short shoots, also called *spur shoots,* which are characterized by short, crowded internodes and the annual expansion of only a few leaves. Spur shoots begin their development as buds, which arise in the leaf axils of long shoots, and may continue their sluggish pattern of vegetative growth for many years (Fig. 16-5, A). Anatomical studies have shown that the zonal structure of the apical meristem is similar in the terminal buds of both long and spur shoots (Fig. 16-15); the histogenetic difference between the two shoot types is the result of the longer duration of cell division and cell elongation in the primary stem tissues derived from the terminal meristem of the long shoots (Foster, 1938).

It is interesting physiologically that the pattern of growth in the two types of shoots is reversible: a spur shoot may abruptly poliferate into a long shoot, and, conversely, the terminal growth of a long shoot may be greatly retarded for several seasons, thus simulating the growth pattern of a lateral spur shoot. The physiological basis for shoot dimorphism in *Ginkgo* has not been fully explained, although there is experimental evidence that auxin—produced in an elongated long shoot—inhibits the expansion of the axillary buds into long shoots but does not prevent the formation of spur shoots (Gunckel, Thimann, and Wetmore, 1949).

Leaves

One of the most distinctive morphological characters of *Ginkgo* is the foliage leaf, which consists of a petiole and a fan-shaped dichotomously veined lamina (Fig. 16-3). Although Linnaeus' specific epithet *biloba* correctly describes the form of the lamina of many *Ginkgo* leaves, there is an enormous range of variation, with respect to the *degree* of lobing and dissection, among the leaves of a single tree. Critchfield (1970) has studied "heterophylly" in *Ginkgo* and has shown that the form of the lamina correlates with the position of a given leaf or leaf series in the shoot system of the tree. On spur shoots and the basal region of long shoots, the leaf blades are either entire or divided by a distal notch into two lobes. Leaves of this type are present in a partly developed stage in the winter buds and complete their growth during bud expansion the following spring. In contrast, most of the leaves found on the upper part of long shoots are initiated and complete their development during the same season; the lamina of such leaves is always divided by a very deep sinus into two major lobes, each of which in turn is further dissected into segments. Critchfield suggested that auxin may control the extended period of growth of long shoots and the correlated formation of multilobed leaves.

The regular dichotomous pattern of venation in the lamina is one of the striking morphological characters of the leaf of *Ginkgo.* Two leaf traces, derived from separate sympodia of the stele, extend through the petiole and give rise to two systems of dichotomously branched veinlets which vascularize

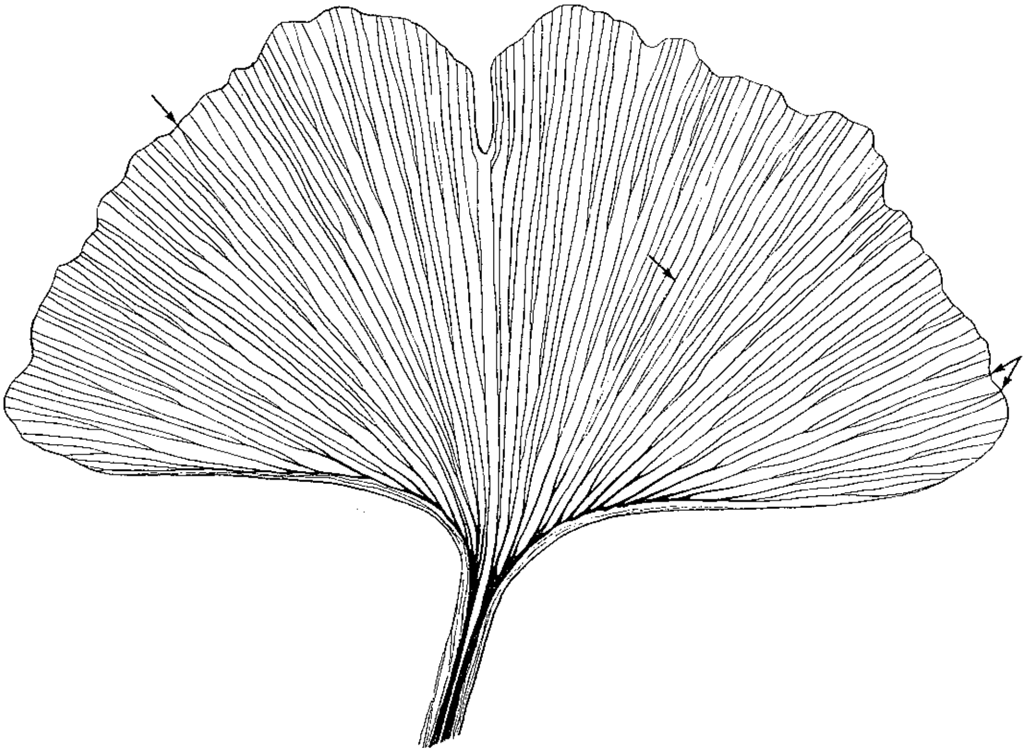

FIGURE 16-3 Cleared leaf illustrating the dichotomous pattern of venation. The arrows indicate vein anastomoses. See text for further explanation. [From Arnott, *Amer. Jour. Bot.* 46:405, 1959.]

the two halves of the lamina (Fig. 16-3). This distinctive type of venation was also present in the leaves of many of the extinct members of the Ginkgoales (Florin, 1936; Arnold, 1947).

The literature on the morphology of *Ginkgo* describes its dichotomous venation as "open" in type —i.e., devoid of vein unions. Arnott's (1959) detailed survey of more than 1,000 leaves of *Ginkgo biloba* revealed that there are various types of anastomoses. Approximately 10 percent of the leaves that he studied showed one or more anastomoses; the largest number of vein unions observed in a single lamina was five (Fig. 16-3).

Ginkgo is deciduous, and before the leaves are shed in the autumn, they turn a beautiful golden yellow. During the leafless period (See Fig. 16-2), the dormant buds of the spur and long shoots are protected by a series of tightly imbricated bud scales.

Stem

Compared with cycads, the pith and cortex of young stems of *Ginkgo* are relatively small. The pith and cortical zones of spur shoots are larger than the corresponding tissue zones in the stems of long shoots. The stems in both types are eustelic, but vascular cambial activity is vigorous and sustained in long shoots and produces pycnoxylic secondary xylem with well-defined growth rings. Vascular cambial activity persists in spur shoots, but only a small amount of manoxylic secondary xylem is produced.

The Reproductive Cycle

Phenology

The series of events that culminates in the production of ripe seeds in *Ginkgo* takes approximately fourteen months, according to the detailed investigations of Favre-Duchartre (1956) in the area of Paris, France. As is shown diagrammatically in Fig. 16-4, pollination, the maturation of the male and female gametophytes, and fertilization occur in one season (April to September), and embryogeny is not completed until the spring of the following year. In Fig. 16-4, the upper part of the solid black spiral line represents the period during which the development of the female gametophyte (♀) takes place and the dotted line depicts the period of association between the developing male gametophyte (♂) and the megagametophyte within the ovule. The reader will find frequent reference to Fig. 16-4 helpful in connection with the detailed descriptions of sporogenesis, gametogenesis, and embryogeny that follow.

Microsporangiate and Megasporangiate Structures

Ginkgo is dioecious, and when the reproductive stage has been reached, the pollen-forming organs and the ovules are produced on separate trees. A distinctive feature is the restriction of the microsporangiate and ovuliferous structures to the spur shoots, where they are evident in the spring in the axils of the inner bud scales and the foliage leaves (Fig. 16-5).

THE MICROSPORANGIATE STROBILUS. A strobilus arises in the axil of a bud scale or foliage leaf on a spur shoot. It is a loose, pendulous, catkinlike structure, consisting of a main axis to which are attached numerous appendages, each of which bears two (sometimes three or four) pendant microsporangia at its tip (Fig. 16-5, A). Although it is not yet clear whether the microsporangia originate from superficial or hypodermal initials, the general plan of development is eusporangiate as in the cycads. A nearly mature microsporangium has a wall of several layers of cells (including the tapetum) that encloses a central group of microsporocytes. These microsporocytes, by meiotic division, produce numerous tetrads of haploid microspores.

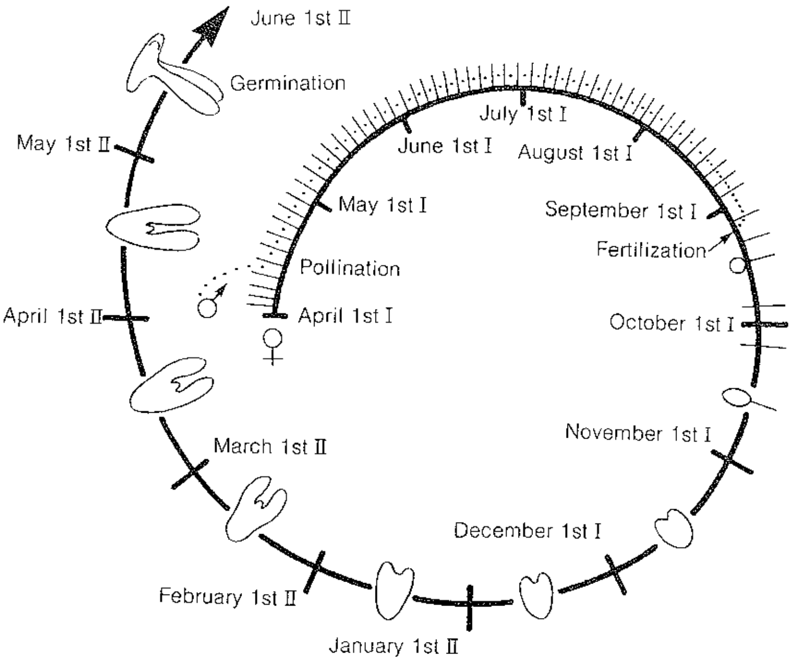

FIGURE 16-4 Diagrammatic representation of the cycle of reproduction in *Ginkgo biloba*. See text for explanation. [Adapted from Favre-Duchartre, *Phytomorphology* 8:377, 1958.]

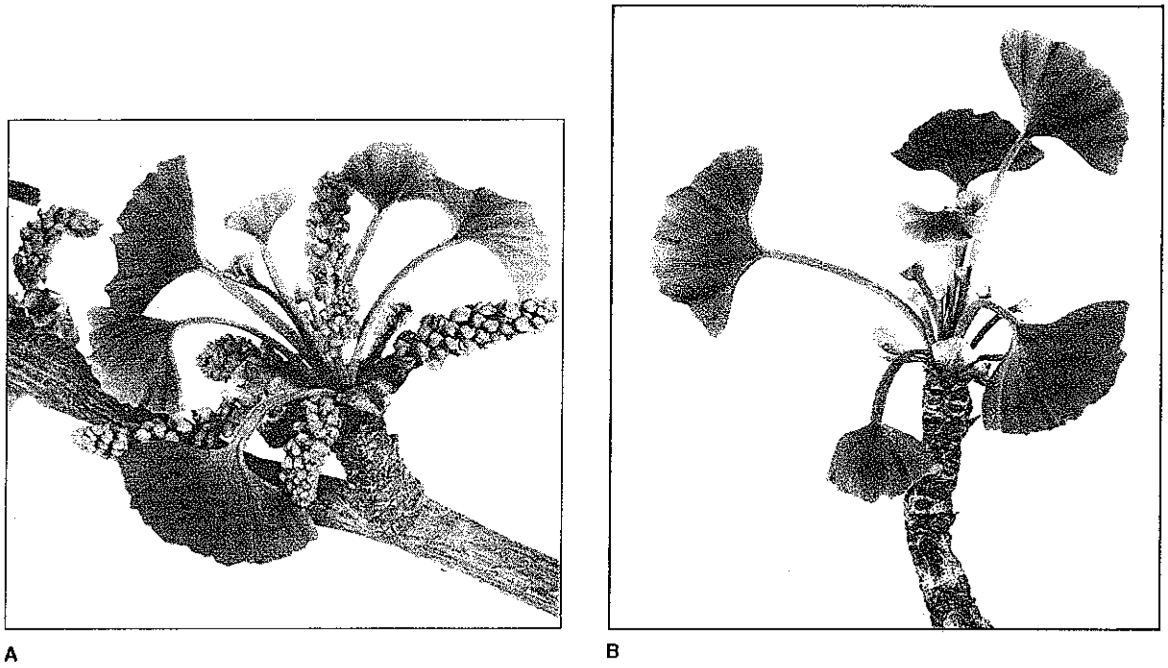

FIGURE 16-5 *Ginkgo biloba.* A, spur shoot with expanding leaves and microsporangiate strobili; B, spur shoot with young leaves and pairs of ovules borne on slender stalks.

THE OVULIFEROUS STRUCTURE. In striking contrast to the megasporophylls of the cycads, each of the ovuliferous organs of *Ginkgo* arises in the axil of a leaf of the spur shoot and consists of a stalk or "peduncle" that bears at its tip two (occasionally three or more) erect ovules (Figs. 16-5, B; 16-13). Each ovule is subtended, below the point of divergence of the integument from the nucellus, by a rimlike outgrowth that was termed the "collar" by Chamberlain (1935). The so-called collar has been interpreted as a vestigial sporophyll and the entire ovuliferous structure as a strobilus. The histogenetic studies of Pankow and Sothmann (1967) provide no support for this speculative interpretation. They found that the collar originates as a rim of tissue *after* the integument of the ovule is well advanced in its ontogeny. This fact — coupled with the absence of any vascular tissue in the collar — led them to conclude that the ovules of *Ginkgo* are cauline and terminal on lateral axes, and that the assumed "foliar" nature of the collar is highly questionable, at least from an ontogenetic point of view (Figs. 16-6; 16-13).

The relatively extensive free portion of the nucellus of the ovule of *Ginkgo* is enclosed by a single integument which becomes anatomically differentiated into a thick outer fleshy layer, a more compact and thinner inner fleshy layer, and a hard stony middle layer; the latter constitutes the "shell" of the mature seed (Fig. 16-7). In contrast to the ovules of cycads, the vascular system of the ovule of *Ginkgo* is weakly developed and consists of two bundles which are restricted to the inner fleshy layer of the integument (Favre-Duchartre, 1956).

The Male Gametophyte (Pollen Grain)

The early ontogeny of the male gametophyte of *Ginkgo* resembles that typical for the cycads except that two prothallial cells — rather than one — are developed. After the second prothallial cell has been formed, the meristematic initial divides and produces the generative cell and the tube cell (see Fig. 17-31). At this four-celled stage, the young male gametophyte, enclosed within the wall of the

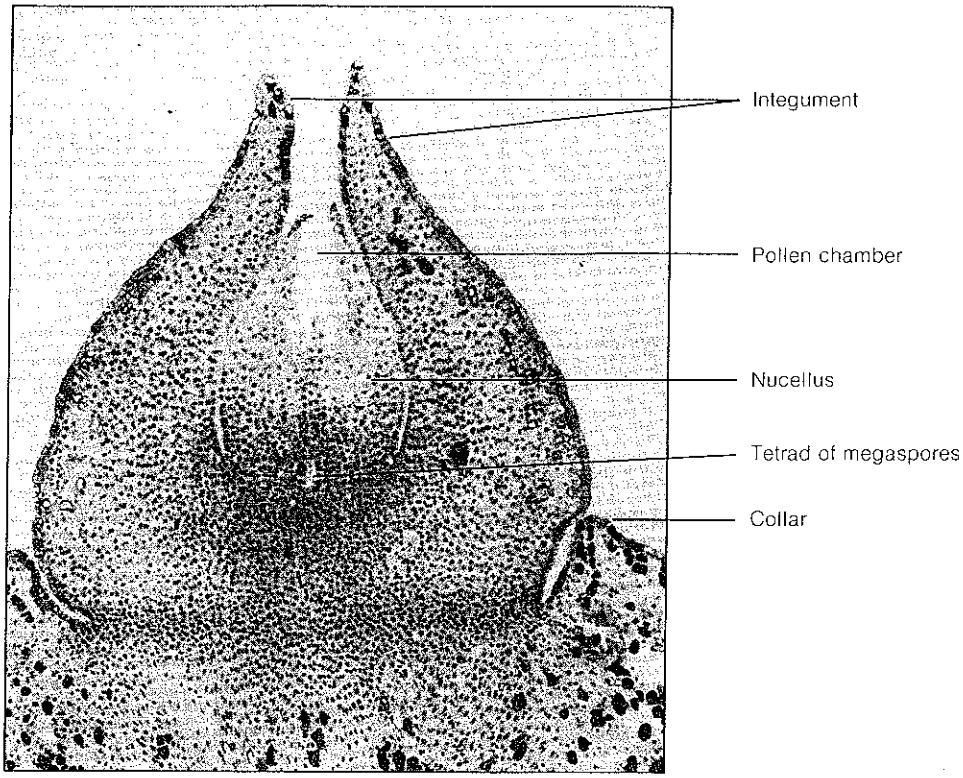

FIGURE 16-6 Median longisection of an ovule of *Ginkgo*, showing nucellus with conspicuous pollen chamber, enclosed by the single integument. Megasporogenesis has occurred and a linear tetrad of megaspores is present in the basal region of the nucellus. Note sectional view of the "collar" below the point of divergence of the ovular integument.

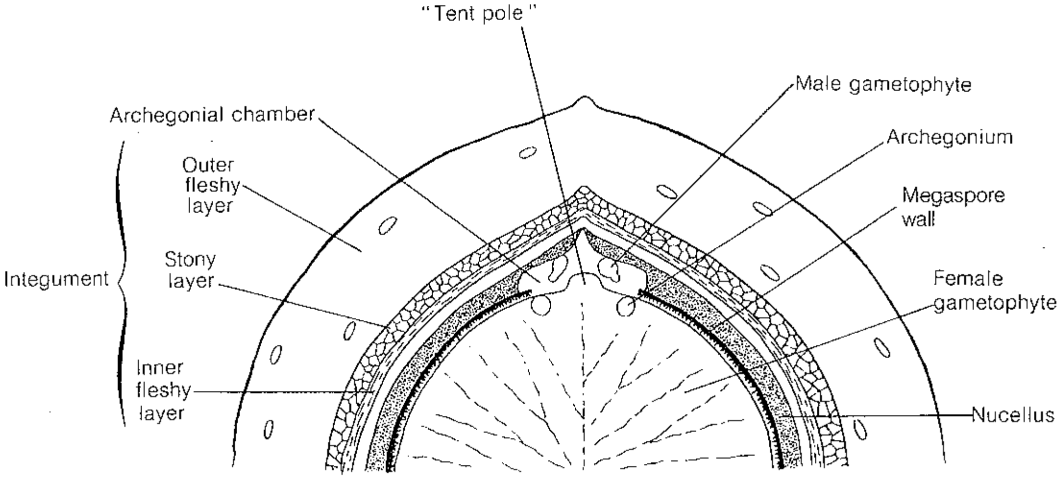

FIGURE 16-7 Longitudinal section (diagrammatic) showing the structure of the upper part of a mature ovule of *Ginkgo*. See text for further explanations. [Redrawn from Favre-Duchartre, *Rev. Cytol. Biol. Veg.* 17:1, 1956.]

pollen grain, is released into the air by the dehiscence of the microsporangium wall.

The pollen is carried to the megasporangiate tree by wind currents and adheres to the mucilaginous pollination droplet which exudes from the micropyles of the ovules. Retraction of this droplet brings the pollen into the pollen chamber where the formation of a much branched, rhizoidlike haustorial pollen tube (Fig. 16-8, A, B; Friedman, 1987) and the final stages in the development of the male gametophyte take place (see Fig. 16-4 for the approximate date of pollination).

Megasporogenesis and Pollen Chamber Development

According to Favre-Duchartre (1956), megasporogenesis in *Ginkgo* occurs toward the end of April. The single megasporocyte is a cell deeply situated in the ovule approximately at the level of separation of the integument from the nucellus (Fig. 16-6). Meiosis occurs, producing a row of four (or sometimes three) cells, the lowermost of which develops into the female gametophyte. In their study of the ultrastructure of the megaspore mother cell

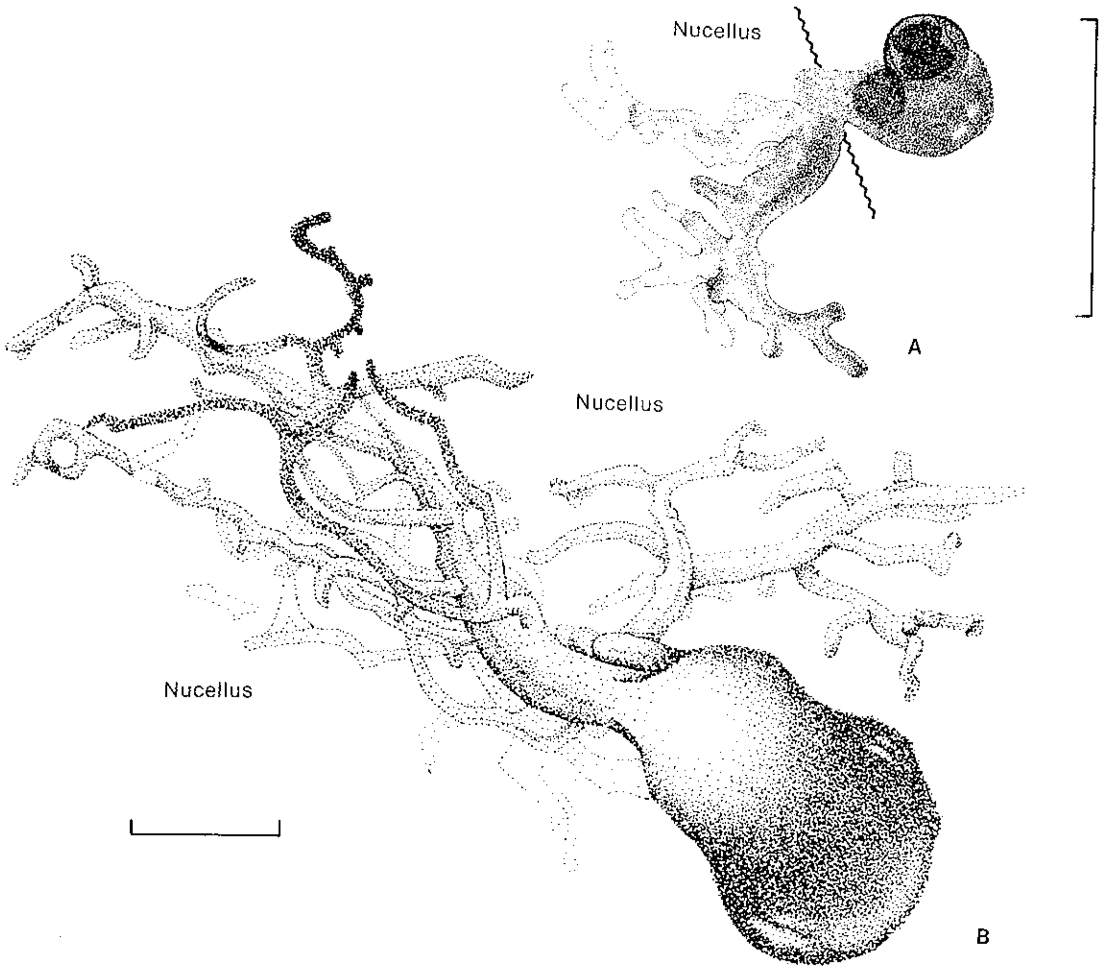

FIGURE 16-8 A, B, reconstructions of stereo computer images of the male gametophyte of *Ginkgo*, based on serial histological sections; note hyphal-like outgrowths of the pollen tube. Two ontogenetic stages are shown. Scale bars = 100 micrometers. [Courtesy of Dr. W. E. Friedman.]

in *Ginkgo*, Stewart and Gifford (1967) made the interesting observation that following meiosis I, *all* the plastids and mitochondria present at the chalazal end of the sporocyte become segregated in the lower dyad cell that is destined to produce the functional megaspore.

The investigations of Favre-Duchartre (1956) and DeSloover-Colinet (1963) have shown that megasporogenesis and the formation of the *pollen chamber* in the upper part of the nucellus are synchronized events. A group of internal cells, at the micropylar end of the nucellus, enlarge and then begin to degenerate, creating a cavity that is the beginning of the pollen chamber. The breakdown of nucellar tissue continues; finally the nucellar epidermis, which lies over the cavity, ruptures, and a large open pollen chamber is formed (Fig. 16-6).

The Female Gametophyte

As in the cycads, the development of the female gametophyte in *Ginkgo* begins with the *coenocytic* stage, characterized by extensive free nuclear divisions, and is followed by the *cellular stage*, during which the coenocyte becomes converted by wall formation into a cellular gametophyte bearing archegonia at its micropylar end. These two phases in the development of the megagametophyte may now be considered in more detail.

COENOCYTIC STAGE. This phase in development results from the enlargement of the functional megaspore accompanied by a succession of free nuclear divisions which occur in the peripheral cytoplasm situated between the megaspore wall and the large central vacuole. Favre-Duchartre (1958) reported that as the result of thirteen successive mitotic divisions, approximately 8,000 free nuclei are produced. He found that the free nuclear divisions are not synchronized but rather proceed from the chalazal to the micropylar end of the coenocyte. During the coenocytic phase, the megaspore wall becomes progressively thicker.

CELLULAR STAGE. Cellularization of the female gametophyte is similar to that of cycads. Chapter 15 (Fig. 15-27) presented the details of female gametophyte development in most gymnosperms. At the close of the period of free nuclear divisions, the nuclei are connected by microtubules (Fig. 15-27, A). Anticlinal walls begin to form between the nuclei, from the periphery of the coenocyte toward the central vacuole (Fig. 15-27, C). The six-sided *alveoli* that are produced are long tubular uninucleate cells that for some time are "open," i.e., devoid of internal walls. As seen in surface view, the developing gametophyte resembles a honeycomb of six-sided tubular cells (Fig. 15-27, B). Precociously formed "pyramidal cells" may be formed before many of the alveoli meet in the center of the gametophyte (Fig. 15-27, C). A wall then forms across their open ends, transforming them into complete cells. The closed alveoli divide by the formation of periclinally oriented walls, creating files of cells that are oriented radially with respect to the megaspore wall (Fig. 15-27, D). As the young cellular gametophyte increases in volume, anticlinal divisions also occur which disrupts the previous regular alignment of the files.

One would assume that all nuclei of the female gametophyte would have the haploid content of DNA. However, Avanzi and Cionini (1971) made the interesting observation that during the *early* phase of cellularization most of the nuclei are not haploid, but undergo an increase in DNA content by endoreduplication or amplification to the diploid level or higher. However, at gametophytic maturity the bulk of the cells have the haploid amount of DNA except for cells of the archegonial jacket, some of which undergo an increase in DNA content. This may be related to a high metabolic activity involved in the transfer of nutrients to the archegonia from the stored reserves in the surrounding gametophytic tissue (Cionini, 1971).

ARCHEGONIA. Although the number of archegonia varies from one to five, according to Favre-Duchartre (1956), the usual number is two (Fig. 16-9). Each archegonial initial is a superficial cell at the micropylar end of the gametophyte and, by means of periclinal division, forms a large *central cell* and a smaller *primary neck cell.* The latter soon divides anticlinally, forming a pair of neck cells. Coinciding with the enlargement of the archegonial central cell, a peculiar column of female gametophytic tissue— known as the "tent pole"— becomes elevated between the archegonia (Figs. 16-7; 16-9; 16-10). This column at first extends toward the part of the nu-

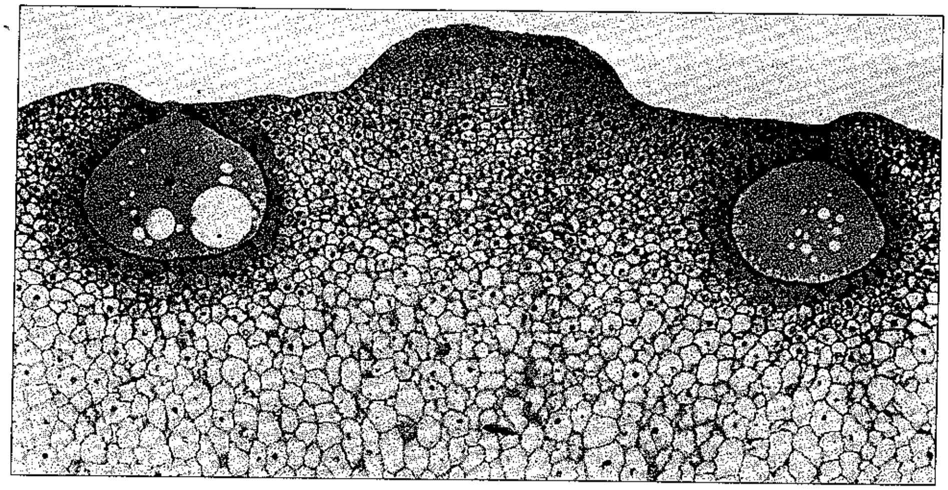

FIGURE 16-9 *Ginkgo biloba.* Longisection of upper portion of the female gametophyte showing "tent pole" and two archegonia. [Courtesy of Dr. W. E. Friedman.]

cellus lying below the pollen chamber. In late August, the nucellar tissue and the megaspore wall in this region become destroyed. This creates an *archegonial* or *fertilization chamber* surrounding the central tent pole (Fig. 16-7).

Fertilization

The final stages in development of the male gametophyte prior to fertilization, take place within the ovule. As mentioned previously, the pollen tube is haustorial, sending out delicate rhizoidlike processes between cells of the nucellus (Fig. 16-8, A, B). The basal end of the male gametophyte is freely suspended within the archegonial chamber (Fig. 16-10). The generative cell divides (commonly in July) giving rise to the sterile cell and the spermatogenous cell (Fig. 16-11) by a cell division similar to the first division of an antheridial initial in certain Filicales (Friedman and Gifford, 1988; see Chapter

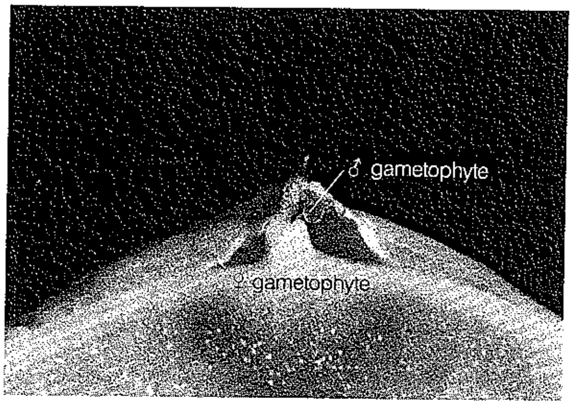

FIGURE 16-10 Integument removed from ovule of *Ginkgo* to reveal the suspended male gametophyte in the archegonial chamber and the "tent pole."

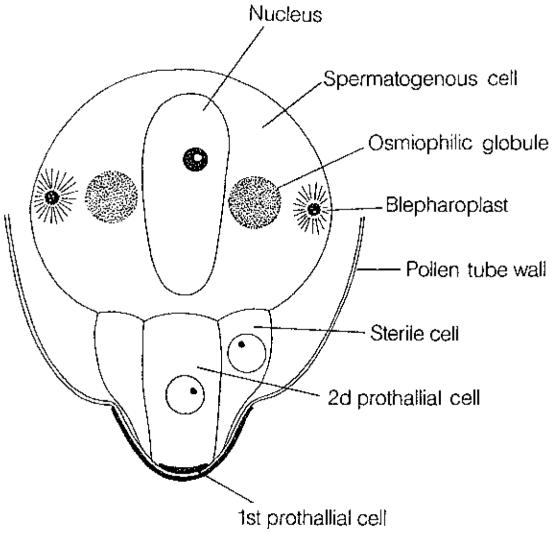

FIGURE 16-11 Schematic representation, basal portion of male gametophyte of *Ginkgo* prior to division of the spermatogenous cell.

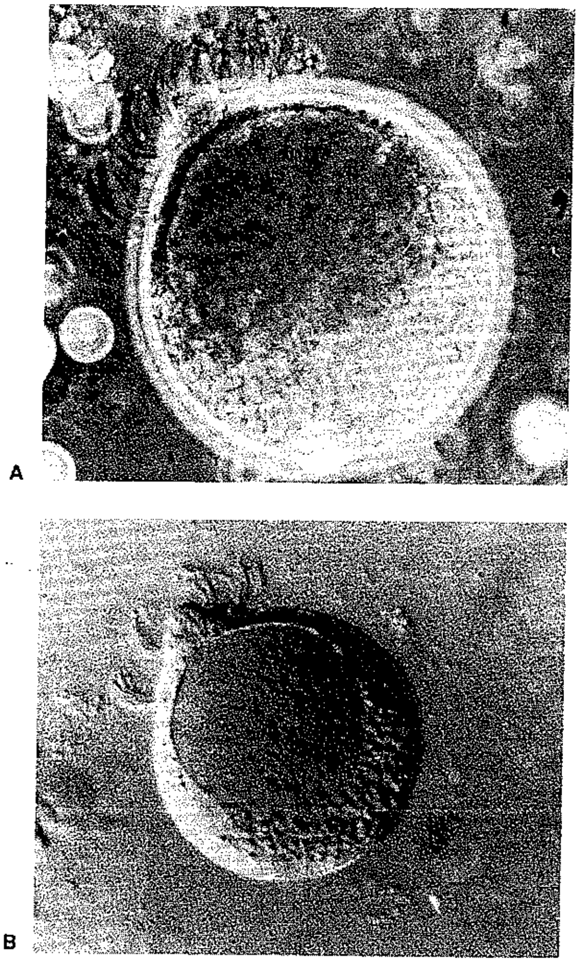

FIGURE 16-12 Sperm of *Ginkgo* seen with phase optics (A) and Nomarski optics (B). Note flagella at anterior end, and the globular nucleus (X ~ 500).

5, Fig. 5-5). The spermatogenous cell is of special interest. During August (in California) the spermatogenous cell consists of a large, discoid nucleus flanked by two "osmiophilic globules" (of unknown function) and two spherical organelles, the *blepharoplasts,* which arise *de novo* near the nuclear envelope (Fig. 16-11). Each blepharoplast appears to have been formed from a microtubule organizing center (Gifford and Lin, 1975; Gifford and Larson, 1980). Microtubules can be identified in the interior of the organelle and can also be seen extending into the cytoplasm. On the surface are about 1,000 centrioles or probasal bodies (Gifford and Lin. 1975). Concomitant with mitosis of the spermatogenous cell to form the two sperm, the blepharoplast breaks up, and the probasal bodies become aligned on a spiral, lamellar band becoming the basal bodies of flagella as in cycads. When the wall of the spermatogenous cell ruptures, the two sperm are released into the pollen tube. The basal end of the pollen tube then ruptures and the sperm are liberated, often forcefully, into the liquid of the archegonial chamber. The liquid would seem to come from the pollen tube and the breakdown of nucellar cells. The sperm swim in this liquid for some time before they enter an archegonium. The sperm aside from their smaller size, resemble those of cycads (compare Figs. 15-28 and 16-12).

During its passage between the swollen and reflexed cells of the archegonial neck, a sperm becomes greatly stretched, but the entire gamete, including the flagellated band, enters the cytoplasm of the upper part of the egg (Shimamura, 1937).

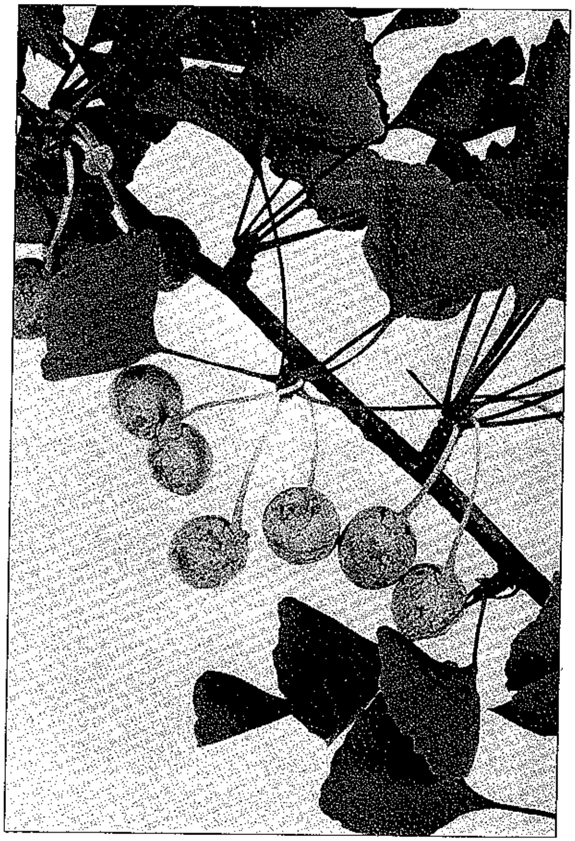

FIGURE 16-13 Portion of a branch of an ovulate tree of *Ginkgo biloba,* showing the attachment of the peduncles of the ripening ovules to the tips of the spur shoot.

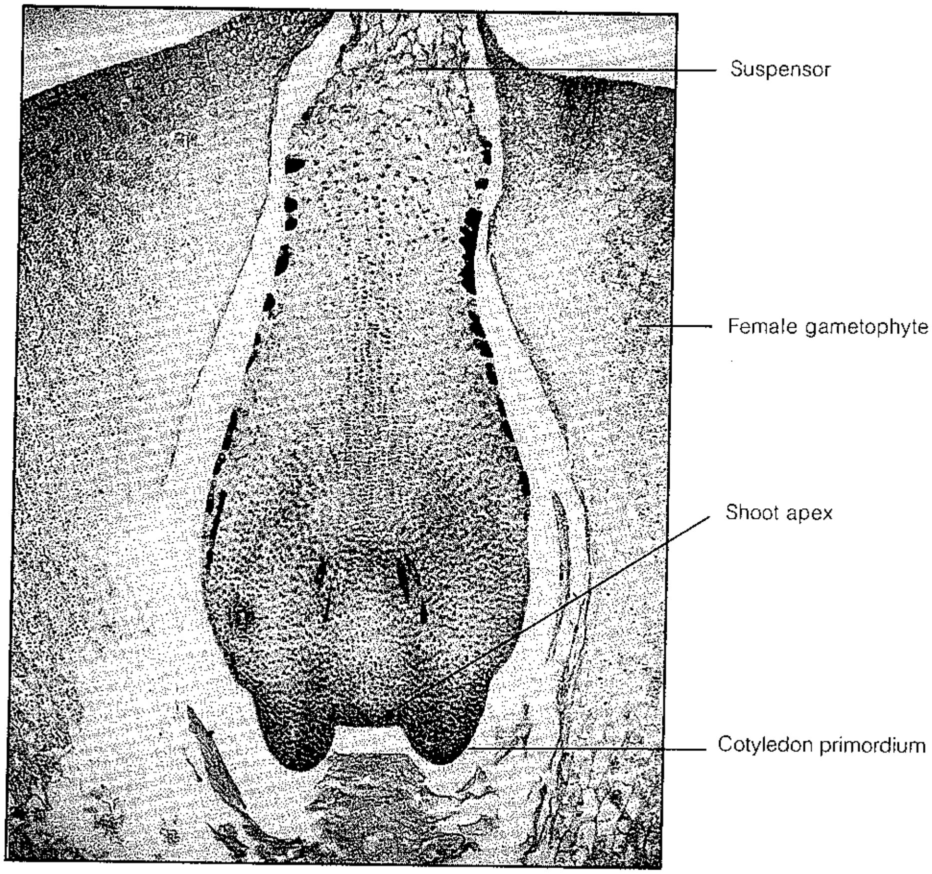

Figure 16-14 Longitudinal section of an advanced stage in the embryogeny of *Ginkgo biloba*. The future shoot apex region is flanked by a pair of developing cotyledon primordia. Note the poorly defined suspensor of the embryo and the adjacent food-storing tissue of the female gametophyte.

According to Lee (1955), usually only one of the two sperm produced by a pollen tube enters an archegonium; the other sperm, if it enters the same archegonium, soon degenerates and is eventually "absorbed." The nucleus of the functional sperm separates from the flagellated sheath and moves downward until it contacts the egg nucleus, forming a diploid zygote, which gives rise to the future embryo. Fertilization generally occurs in late August or early September.

Figure 16-13 illustrates the appearance of older ovules of *Ginkgo*, probably after fertilization had occurred. However, Eames (1955) confirmed earlier reports that fertilization and embryogenesis in *Ginkgo* may occur either on the tree or after the ovule has fallen to the ground. The latter possibility is of phylogenetic interest with reference to some of the Paleozoic gymnosperms (e.g., the Cordaitales) in which the embryo, like that of *Ginkgo*, may have only begun to develop after the ovules had been shed from the parent tree.

Embryogeny

The early phase of embryogeny in *Ginkgo* is characterized by numerous free nuclear divisions, as in the cycads. After a series of about eight successive divisions (256 nuclei), centripetal wall formation begins and the young embryo becomes cellular throughout. In contrast with cycad embryogeny, no well-defined suspensor is formed. The lower end of the embryo, by means of active cell divisions, becomes a meristem from which the shoot apex and cotyledons are developed (Fig. 16-14); the cells immediately behind this portion ultimately differentiate into the primary root or radicle (Ball, 1956a, b). Usually there are two cotyledons, but occasionally three are developed. In addition to the cotyledons, the embryo of ripe seeds commonly contains the primordia of several additional foliar structures which, together with the shoot apex, constitute the first terminal bud of the plant.

The germination of the seed closely resembles that typical of cycads. The primary shoot and root emerge by the rupture of the micropylar end of the seed, but the tips of the cotyledons remain within the nutritive tissue of the female gametophyte. The original seed may still cling to the base of a seedling a year or more in age.

The apical meristem of both the long and spur shoots of *Ginkgo* has a characteristic zonal structure. As shown in Fig. 16-15, the subsurface zone of the shoot apex consists of a conspicuous group of enlarged, highly vacuolated, central mother cells from which the more actively dividing and smaller cells of the peripheral and rib-meristem zones take their origin. The type of zonation in the apical meristem of *Ginkgo* has been very helpful in the interpretation of the structure and growth of the shoot apex in the cycads and in certain genera of the coniferales. (See Foster, 1938; Johnson, 1951; Esau, 1965; Gifford and Corson, 1971.)

Fossil Ginkgophytes

Fossils presumed to be ginkgophytes were present in the Lower Permian. Ginkgophytes increased in number in the Jurassic, and declined in the Upper Cretaceous; the only surviving representative is the "living fossil" *Ginkgo biloba.* Many species of *Ginkgoites* (fossil leaves resembling those of *Ginkgo biloba*) have been described as having been distributed worldwide during the Mesozoic. However, rather than representing many different

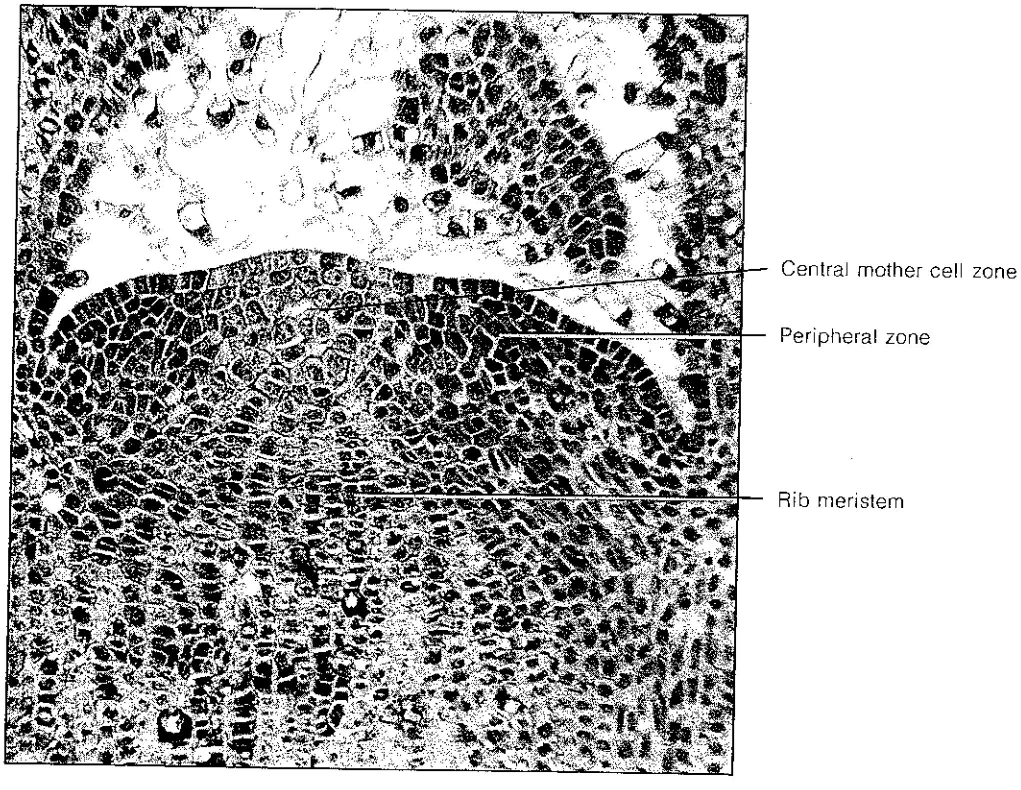

FIGURE 16-15 Median longisection of shoot apex of *Ginkgo biloba* showing typical zonal structure.

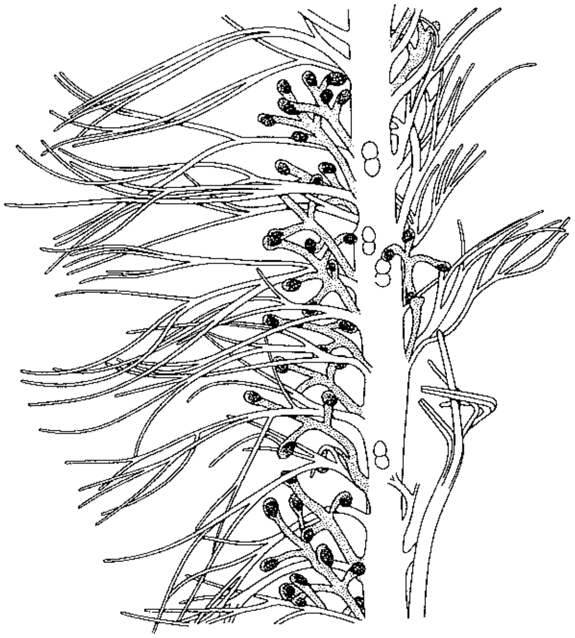

FIGURE 16-16 Reconstruction of *Trichopitys,* showing main axis and axillary, ovule-bearing shoots. [From *Studies in Paleobotany,* by H. N. Andrews, Jr., Wiley, New York. 1961.]

species, the fossils may instead represent only variations in leaf morphology similar to the variations found on the same tree of a living *Ginkgo biloba.* The fossil record of *Ginkgo* extends back to the Upper Triassic-Jurassic and is more extensive in the Lower Cretaceous. Convincing reproductive structures are known for ginkgophytes in the Jurassic-Cretaceous, some having a marked similarity to those of *Ginkgo biloba.* An older fossil, *Trichopitys,* from the Lower Permian indicates that the primitive type of ovuliferous structure in ginkgophytes probably consisted of a main axis with lateral branches bearing terminal ovules (Fig. 16-16). A fertile branch was axillary, similar to that of *Ginkgo biloba.* (For more information on the subject, see Stewart, 1983, and Taylor, 1981.)

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