CHAPTER 15

Pteridospermophyta (Seed Ferns), Cycadeoidophyta (Cycadeoids), and Cycadophyta (Cycads)

IN this chapter we will discuss the living and extinct representatives of the cycadophyte lines of gymnosperm evolution. The cycadophytes are distinguished in general by their large, pinnately compound leaves, columnar or sparingly branched trunks, and manoxylic secondary xylem. The only surviving cycadophytes are the modern cycads, Cycadophyta, which will receive the major attention in this chapter. First, however, we will consider the extinct Pteridospermophyta, or "seed ferns," and later in the chapter we will discuss the extinct Cycadeoidophyta. Both of these taxa are of exceptional evolutionary interest. The seed ferns provide important clues about the nature of the seed in ancient gymnosperms. The Cycadeoidophyta, although sharing some features in habit and anatomy with modern cycads, appear to represent a separate "blind end" in cycadophyte evolution, although they have been cited periodically as the progenitors of angiosperms.

Pteridospermophyta

Pteridospermales

The Paleozoic pteridosperms extended from the Carboniferous into the Permian. They combined in a most remarkable way, the general habit and foliage of ferns with the formation of gymnosperm-type seeds (Figs. 15-1, 15-3, 15-4). The demonstration by Oliver and Scott (1905) that many of the presumed "ferns" of the Carboniferous were in reality seed-bearing plants was an outstanding achievement in the history of paleobotany and much study has been devoted subsequently to the comparative morphology and systematics of these interesting plants.

This book discusses two families in the order Pteridospermales — the Lyginopteridaceae and the Medullosaceae. A more thorough treatment of these families is beyond the scope of our discussion.

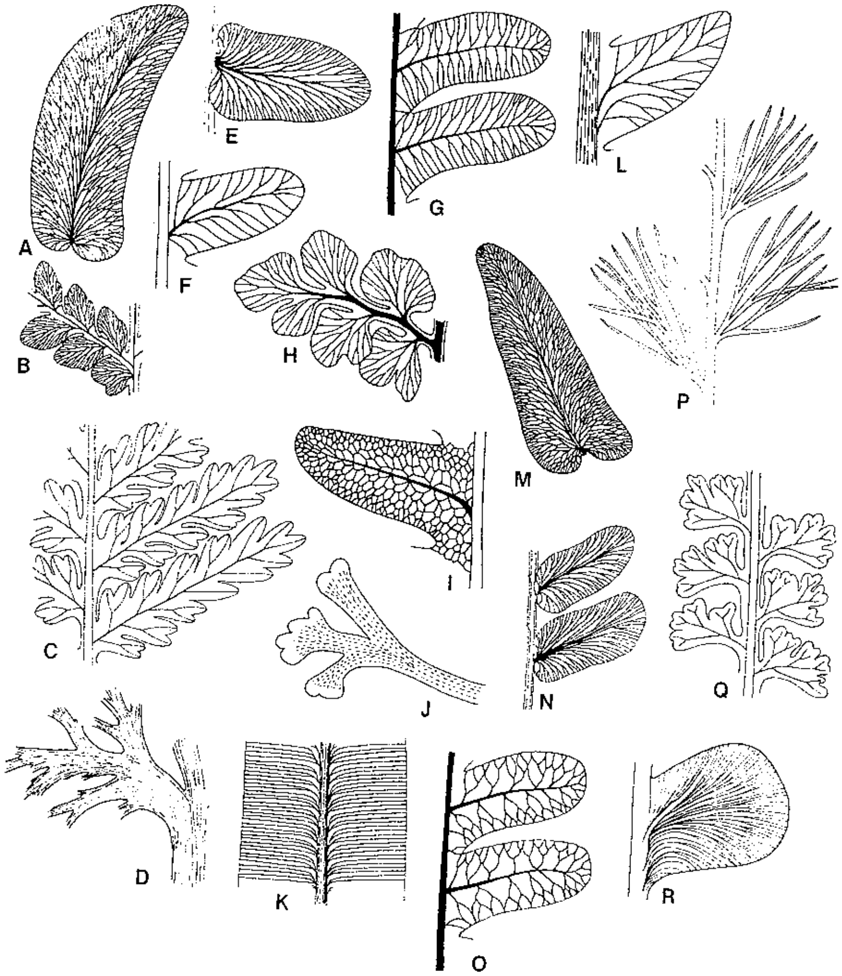


FIGURE 15-1 Representative examples of Paleozoic foliage, many of which have been shown to be the pinnules of seed-fern fronds. A, *Linopteris;* B, *Mariopteris;* C, *Sphenopteris;* D, *Aphlebia;* E, *Mixoneura:* F, *Pecopteris;* G, *Alethopteris;* H, *Eusphenopteris;* I, *Lochopteris;* J, *Kankakeea;* K, *Taeniopteris;* L, *Lescuropteris;* M, *Reticulopteris;* N, *Neuropteris;* O, *Lochopteridium;* P, *Rhodea;* Q, *Alloiopteris;* R, *Odontopteris.* [From *Paleobotany: An Introduction to Fossil Plant Biology* by T. N. Taylor. McGraw-Hill, New York. 1981.]

Therefore, we will adopt the type-method approach to describe vegetative and reproductive structures.

Lyginopteridaceae

Lyginopteris was established as a form genus for stems from the Carboniferous Coal Measures of Britain and Europe but now applies to an entire plant. *Lyginopteris* is thought to have been somewhat vinelike with large fronds, and probably supported by surrounding vegetation. The stem was from 3 to 4 centimeters in diameter and was eustelic; the primary xylem strands were mesarch in development, comparable to progymnosperms (see p. 337). Tracheids of the relatively small amount of manoxylic xylem was formed with multiseriate bordered pits on the radial walls of tracheids. The outer cortex consisted of a network of fibrous strands (Fig. 15-2). The microsporangiate structures were borne on laminar segments or were grouped terminally on axes of otherwise planated fronds; the sporangia were fused to form synangia (Fig. 15-3C). Microspores, often referred to as "prepollen," were trilete and resembled those of certain ferns. Ovules of *Lyginopteris,* assigned to the form genus *Lagenostoma,* were small—5.5 millimeters long by 4.4 millimeters in diameter. An interesting feature was the development of a *cupule* around the ovule (Fig. 15-3, D). The cupule was divided distally into eight to ten vascularized lobes. Capitate glands were present on the outer surface of the cupule which may have served to attract insects. The single integument was vascularized and fused with the nucellus except at the distal end, much like living gymnosperms. There was a central column of nucellar tissue, surrounded by the so-called lagenostome or *salpinx* (Greek, meaning "trumpet"), also of nucellar origin; the space between the two was the pollen chamber in which spores of the trilete

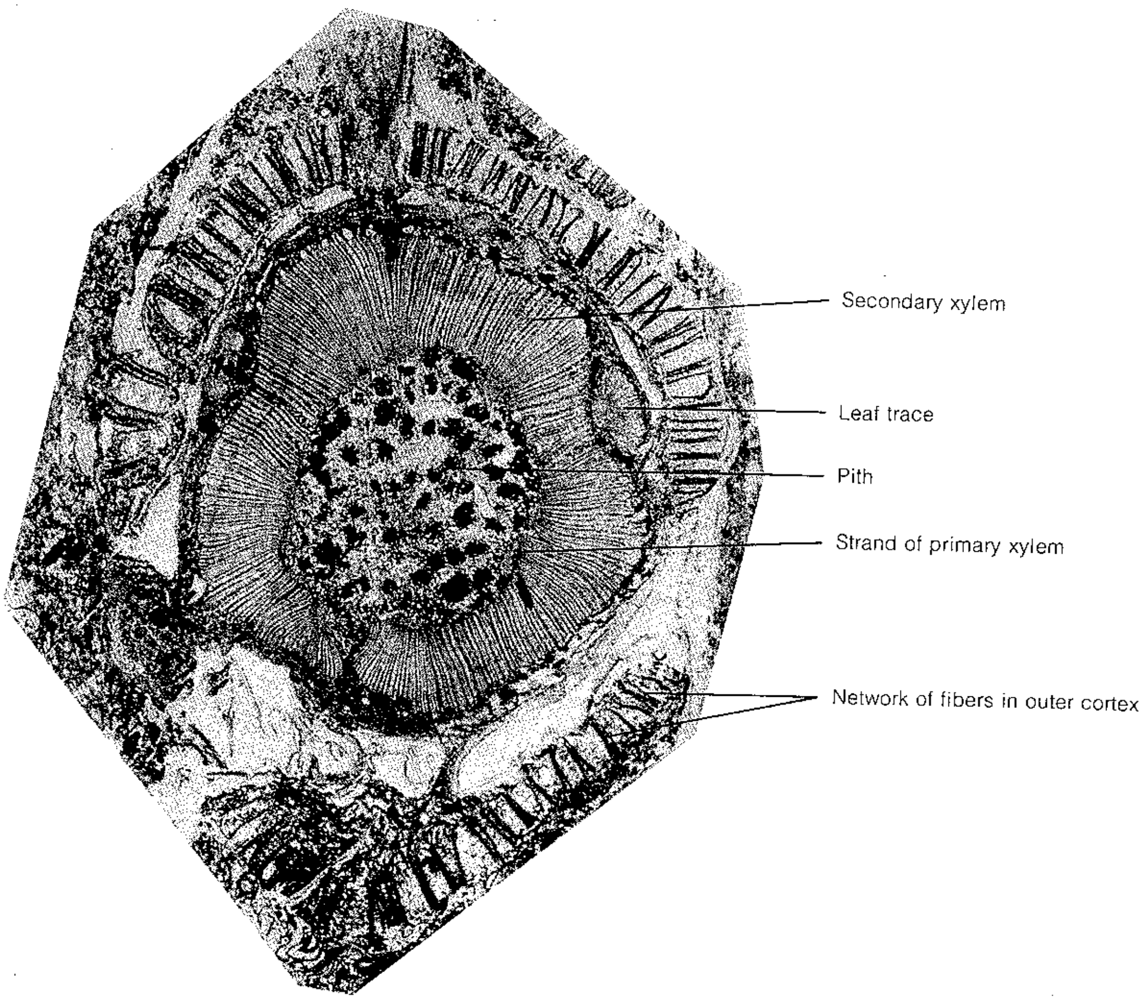


FIGURE 15-2 Transection of stem of *Lyginopteris oldhamia,* showing primary vascular strands, leaf traces, and the well-developed cylinder of secondary xylem. Note the characteristic network of fibrous strands in the outer cortex. [From *An Introduction to the Study of Fossil Plants* by J. Walton. Adam and Charles Black, London. 1953.]

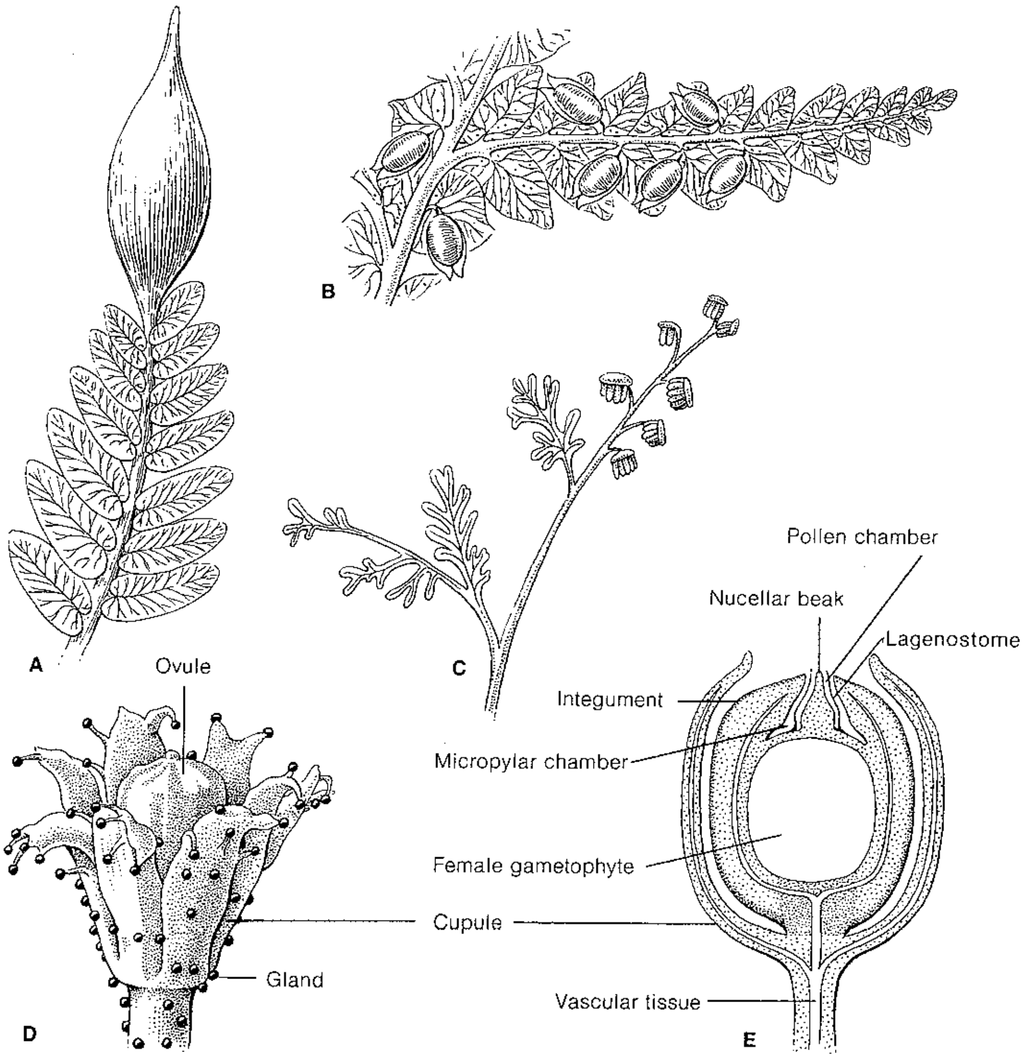


FIGURE 15-3 Reproductive structures in seed ferns. **A**, pinna with terminal seed of *Neuropteris heterophylla:* **B**, *Emplectopteris triangularis*, seeds attached to subdivisions of leaf; **C**, portion of fertile leaf of *Crossotheca* bearing clusters of pendant microsporangia; **D**, reconstruction of the ovule and cupule of *Lagenostoma lomaxi:* **E**, longisection of ovule of *Lagenostoma* showing details of internal structure. [**A** redrawn from *Textbook of Paleobotany* by W. C. Darrah. Copyright D. Appleton-Century Co., New York, 1939, by permission Appleton-Century-Crofts, Inc; **B** redrawn from *Ancient Plants and the World They Lived In* by H. N. Andrews. Comstock, New York. 1947; **C** and **D** from *Les Plantes Fossiles dans leurs Rapports avec les Végétaux Vivants* by L. Emberger. Masson et Cie, Paris. 1944; **E**, adapted from *An Introduction to Paleobotany* by C. A. Arnold. McGraw-Hill, New York. 1947.]

type have been found (Fig. 15-3, E). (Additional information can be found in Taylor and Millay, 1981.)

Medullosaceae

Members of this family, known from the Lower Carboniferous to the Permian, are generally depicted as rather tall trees (3 to 8 meters high) with alternately arranged compound leaves, resembling modern tree ferns (Fig. 15-4). Leaves are referable to two or more form genera (e.g., *Alethopteris, Neuropteris;* Fig. 15-1). *Medullosa* was used originally as a form genus for stem remains, but is now generally used for the entire plant. A transection of

FIGURE 15-4 Reconstruction of a specimen (3.5 to 4.5 meters high) of *Medullosa noei.* [Redrawn from Stewart and Delevoryas, *Bot. Rev.* 22:45, 1956.]

a medullosan stem may reveal the presence of two or more vascular cylinders, each consisting of primary xylem surrounded by a cylinder of manoxylic secondary xylem (Fig. 15-5, A, B). For many years each of these seemingly separate cylinders were termed "steles," and the stem was said to be "polystelic." According to a now more generally accepted concept, the stem is not polystelic, but rather has evolved in the course of evolution from the dissection of a single protostelic vascular cylinder. The individual vascular cylinders are defined as vascular *segments,* not "steles." All of the vascular segments, collectively, comprise a *eustele. Sympodia* are represented by protoxylem strands in the vascular segments rather than by the vascular segments themselves (Fig. 15-5, A, B). Steps in the possible evolution of the *Medullosa*-type eustele are shown in Fig. 15-5, C–E. Leaf gaps are absent. It should be noted, however, that the eustele in progymnosperms, gymnosperms, and angiosperms lack the formation of secondary xylem toward the pith.

All medullosan microsporangiate structures ("pollen organs"), whether simple or complex, were synangiate and consisted of tubular sporangia. In *Codonotheca* each unit consisted of several sporangia fused at their bases (Fig. 15-6, A). In the form genus *Whittleseya* (attached to *Neuropteris*-type foliage) many sporangia were joined laterally, forming a bell-shaped structure (Fig. 15-6, B). In the compound synangiate pollen organ of *Dolerotheca formosa (Bernaultia formosa)* there were up to 1200 sporangia in the entire structure, which may be 4.5 cm in its maximum dimension (Rothwell and Eggert, 1986). Microspores in the Medullosaceae

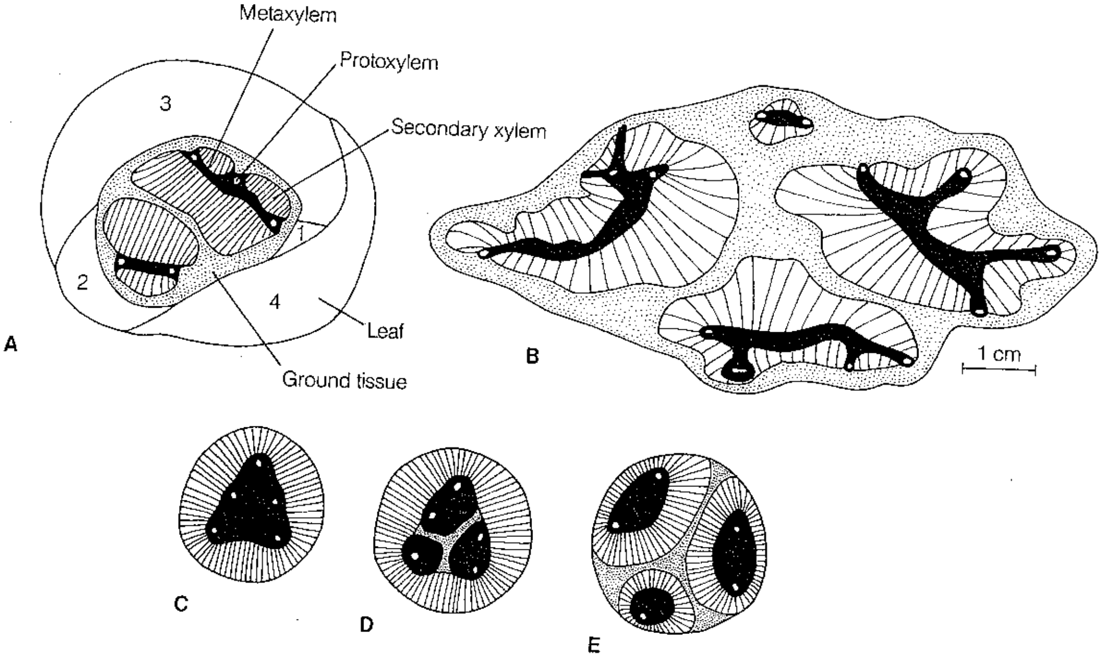


FIGURE 15-5 **A, B,** transverse sections of medullosan stems. **A,** *Medullosa noei.* At this level the vascular cylinder consists of two vascular "segments" and five sympodia (corresponding to five protoxylem poles) surrounded by ground tissue and four leaves (numbered 1 to 4); **B,** *Medullosa primavea.* Vascular cylinder comprising five vascular segments and thirteen sympodia; scale bar = approx. 1 centimeter. **C–E,** hypothetical sequence of how vascular segments could have been derived by dissection of the protostele. [A, B redrawn from Basinger, Rothwell, and Stewart, *Amer. J. Bot.* 61:1002–1015, 1974: C–E, redrawn from Stewart, *Birbal Sahni Institute of Paleobotany,* Lucknow, India, pp. 1–13, 1973.]

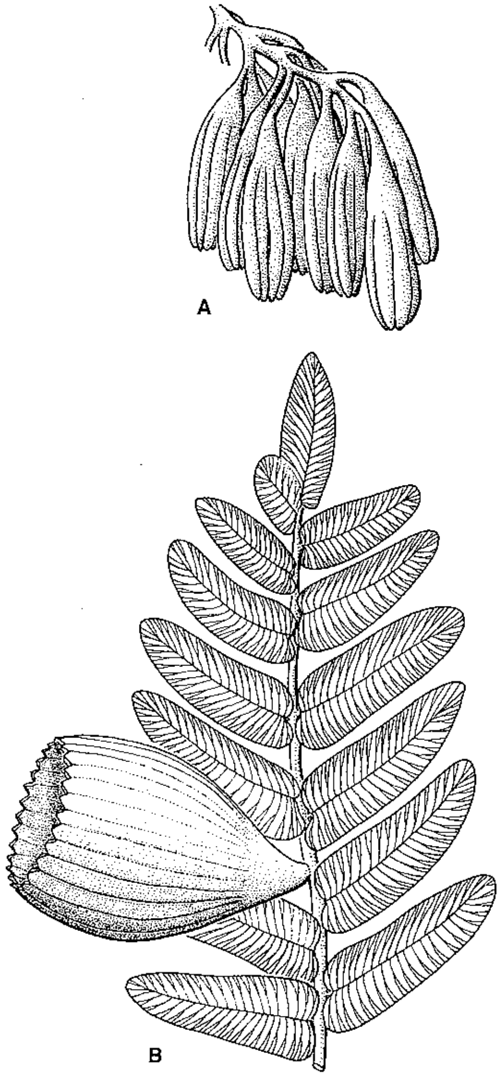


FIGURE 15-6 Representative medullosan pollen-producing structures. **A,** *Codonotheca* sp., cluster of synangia, each consisting of four partially fused, elongate microsporangia; **B,** synangium *(Whittleseya media)* attached to *Neuropteris*-type foliage; the synangium consists of numerous fused elongate microsporangia. [Redrawn from *Paleobotany and the Evolution of Plants* by Stewart. Cambridge University Press, Cambridge. 1983.]

were often monolete on the proximal surface, and germination probably occurred along this suture. The seeds were large, and, as illustrated by *Pachytesta,* the integument was completely free from the nucellus, unlike *Lagenostoma* (compare Figs. 15-3, E and 15-7). A vascular system was present in both the outer layer (sarcotesta) of the integument and the nucellus (Fig. 15-7, B).

Space does not permit a complete discussion of the Pteridospermales, but we should mention the interesting discovery of pollen grains in the family Callistophytaceae. Pollen was shed in an endosporic, multicellular condition, remarkably similar to pollen grains of living gymnosperms. Also, pollination-drops and pollen tubes have been identified (Rothwell, 1977; Millay and Eggert, 1974).

Mesozoic Seed Ferns

The two orders Caytoniales (Upper Triassic to Lower Cretaceous) and Glossopteridales (primarily of the Permian and Triassic) are rather enigmatic groups. Some paleobotanists align them with the Paleozoic seed ferns, others believe them to be of unknown affinity; still others consider them as possible preangiosperms or at least exhibiting angiospermlike reproductive characteristics.

Caytoniales

Plants assigned to the order Caytoniales had either pinnately or palmately divided leaves based upon compression-impression fossils. Very little is known about the internal structure of stems. Microsporophylls were generally branched, the sporangia aggregated on ultimate segments or fused into elongate, pendent synangia (Fig. 15-8, C, D). The discovery by Thomas (1925) of ovules enclosed in a cupulelike structure created quite a stir in botanical circles at the time. These cupules were borne along a bilaterally symmetrical megasporophyll (Fig. 15-8, A). Each cupule was recurved with a liplike opening near the stalk which became closed at maturity. Numerous small ovules were contained within the cupule (Fig. 15-8, B). Thomas originally described the lipped portion as a "stigmatic surface" comparable to the stigma of angiosperms, because pollen grains were observed on it. The cupule was interpreted as a "fruit." Subsequently, pollen grains were discovered inside the cupules, which detracted from the idea that a cupule was a fruit comparable to that of angiosperms. Nevertheless, the formation of cupules does represent a method whereby ovules could be enclosed and protected during development.

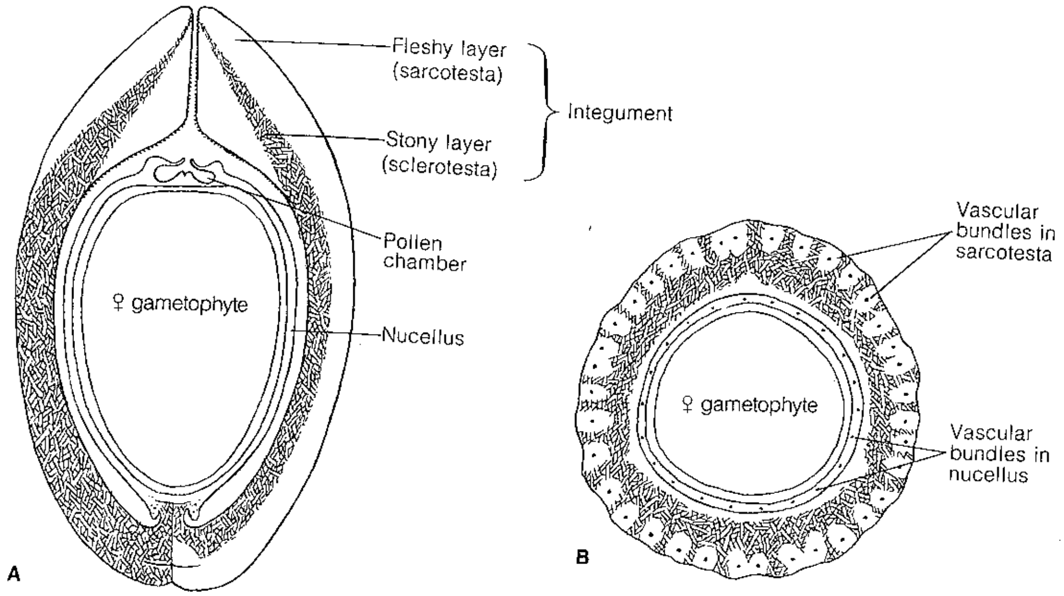
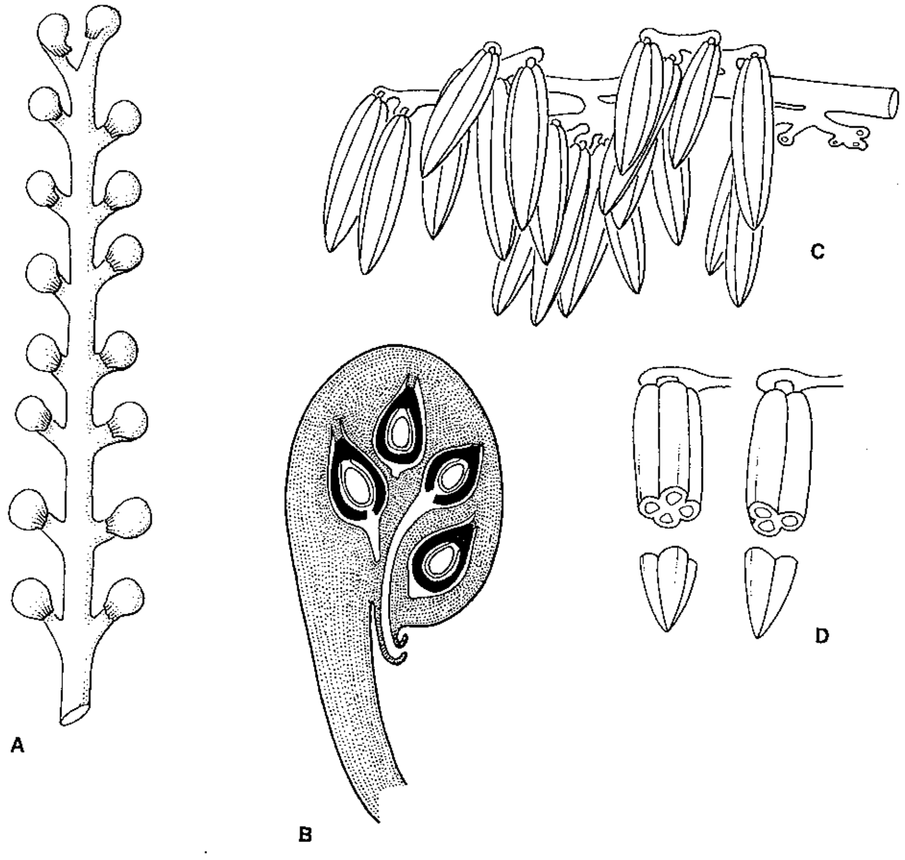


FIGURE 15-7 Reconstruction of the seed of *Pachytesta illinoensis* showing the absence of union between the integument and the nucellus. **A**, longitudinal view; **B**, transectional view. Note numerous vascular bundles in both the integument and the nucellus. [Redrawn from Taylor, *Palaeontographica* 117(B):1, 1965.]



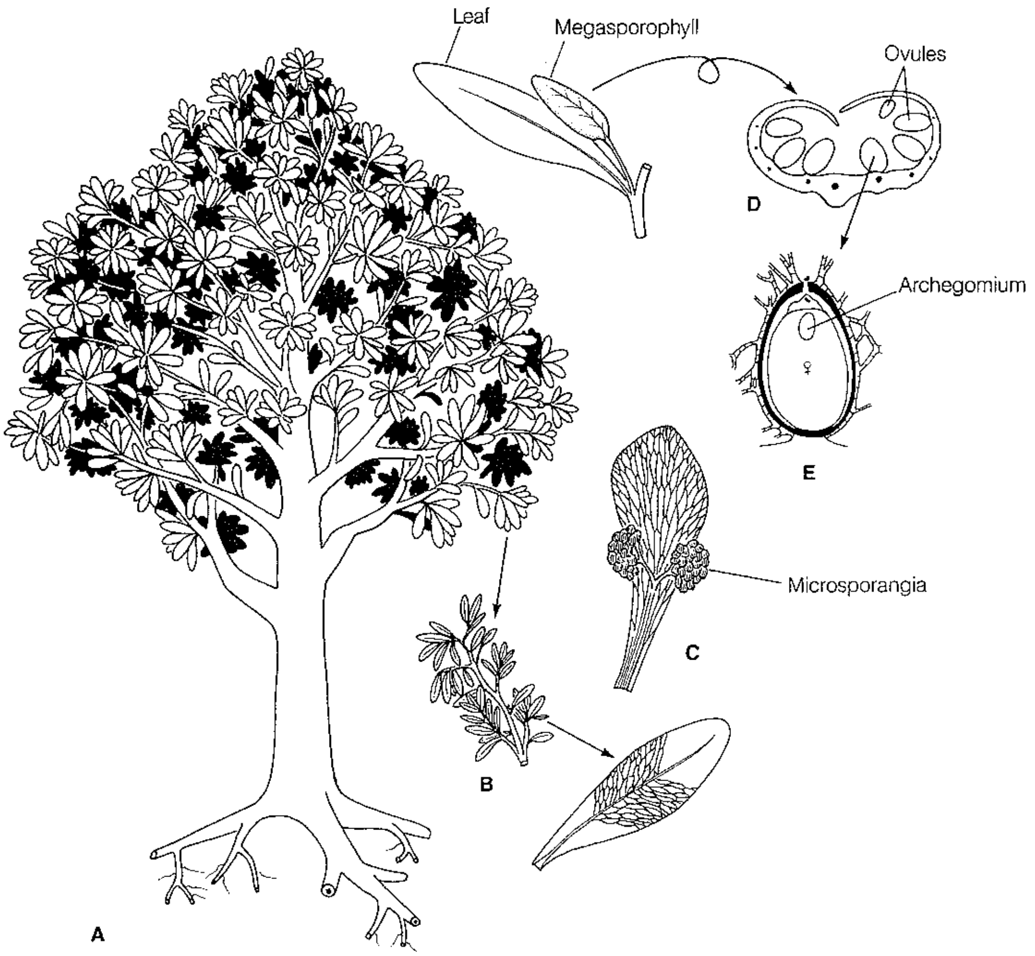


FIGURE 15-9 Stylized reconstruction of a *Glossopteris* tree. **A**, growth habit; **B**, leafy shoot and leaf; **C**, microsporophyll with two clusters of microsporangia (pollen sacs); **D**, inverted megasporophyll, or seed-bearing structure; **E**, longitudinal section of ovule showing position of female gametophyte (♀) and one archegonium. [Redrawn from Gould and Delevoryas, *Alcheringa* 1:387–399, 1977.]

FIGURE 15-8 Reproductive structures of Caytoniales. **A**, megasporophyll of *Caytonia nathorsti* showing two rows of cupules. **B**, *Caytonia thomasi*, longitudinal section of a cupule showing position of ovules. **C, D**, *Caytonanthus kochi*, portion of microsporophyll (**C**) and sectioned synangia showing microsporangia (**D**). [**A** redrawn from Thomas, *Phil. Trans. Roy. Soc.*, London, 213(B):299–363, 1925; **B** redrawn from Harris, *New Phytol.* 32:97–114, 1933; **C, D** redrawn from *Studies in Paleobotany* by H. N. Andrews, Jr. Wiley and Sons, New York. 1961.]

Glossopteridales

Fossils of the Glossopteridales have been found principally in India, South America, South Africa, Australia, and Antarctica and were the main component of the flora of the southern continent of Gondwanaland of the Permian. The glossopterids were seed-bearing plants and have been classified by various authors as seed ferns, cycads, cordaites, and angiosperms. Lacking definitive evidence that the glossopterids represent the precursor-group of the angiosperms, many paleobotanists retain the glossopterids as a specialized group of seed ferns; however, the method of enclosure of ovules suggests how a carpel may have evolved.

Numerous species of *Glossopteris* have been described, some of which may be only variants of a single species or represent ontogenetic stages in the growth of a single species. Gould and Delevoryas (1977) have described *Glossopteris* as a tree with pycnoxylic wood, unlike other seed ferns (Fig. 15-9). Leaves were arranged in tight spirals (helical phyllotaxy). In form, leaves were often lanceolate or spatulate with a prominent midrib and reticulate venation. Microsporangiate structures have been discovered; in one example it was leaflike with two stalked clusters of microsporangia (Fig. 15-9, C). Over the years there has been disagreement, often heated, on the correct interpretation of ovulate structures. In general, one or more of the ovulate structures were stalked and attached near the base of a leaf or in its axil. An entire structure has been termed a megasporophyll, capitulum, or cupule. Several to many ovules were attached to the capitulum and the margins enclosed the ovules to varying degrees (Figs. 15-9, D, E; 15-10, B). When well preserved the ovules are gymnospermous, showing the enclosed female gametophyte with one archegonium (Fig. 15-9, E; Gould and Delevoryas, 1977). In one form there were several stalked, cupulelike structures, each containing one ovule (Fig. 15-10, A). It should be mentioned that some of the "glossopterids" have been aligned with the Pteridospermales rather than with the Glossopteridales (Surange and Chandra, 1975).

Origin of Seed Integument

In Chapter 14 we pointed out that the nature and origin of the integument of the seed in gymno-

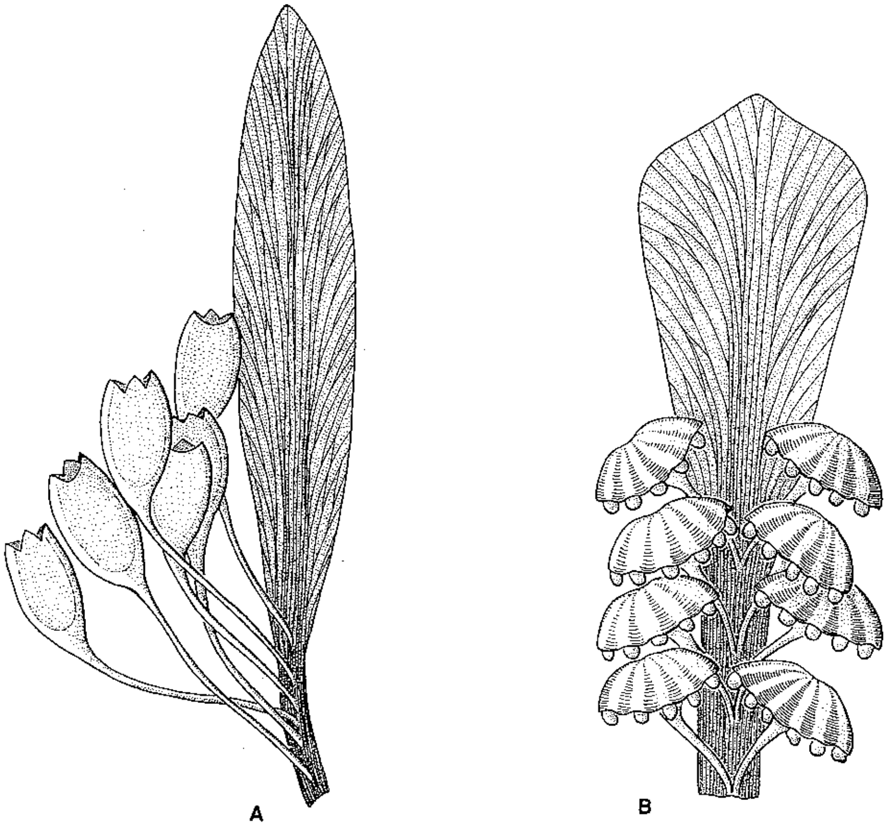


FIGURE 15-10 Reconstruction of ovulate structures of glossopterids. A, *Denkania indica;* six cupulelike structures attached to petiole of a leaf. B, *Lidettonia mucronata;* seeds attached on the lower surfaces of capitular disks. [A, B redrawn from Surange and Chandra, *Palaeontographica* 149(B):153–180, 1975.]

sperms represent difficult morphological problems. Perhaps a partial answer is provided by studies on the seeds of certain pteridosperms of the Carboniferous. The nucellus of the seed, *Genomosperma kidstonii,* in place of being enclosed by and partially joined with an integument, is surrounded basally by a whorl of eight free filamentous processes (Fig. 15-11, A). A more advanced condition toward the formation of an integument is represented by the seed of *Genomosperma latens,* in which the eight integumentary "lobes" are apically appressed—forming what Andrews (1963) regards as a "rudimentary micropyle"—and joined with each other for about a third of their length (Fig. 15-11, B). Fusion of the integumentary lobes is almost complete in the seed of *Eurystoma,* and complete union is shown by the integument of the seed of *Stamnostoma* (Fig. 15-11, C–D). Much remains to be learned about Paleozoic seeds, including the nature and origin of cupulate types. The oldest record of the seed-bearing gymnosperms in the Devonian was reported by Pettitt and Beck (1968) from the Upper Devonian; the seed was named *Archaeosperma arnoldii.* More recently a cupulate form was discovered from the Upper Devonian of West Virginia that is somewhat older than *Archaeosperma* (Gillespie et al., 1981).

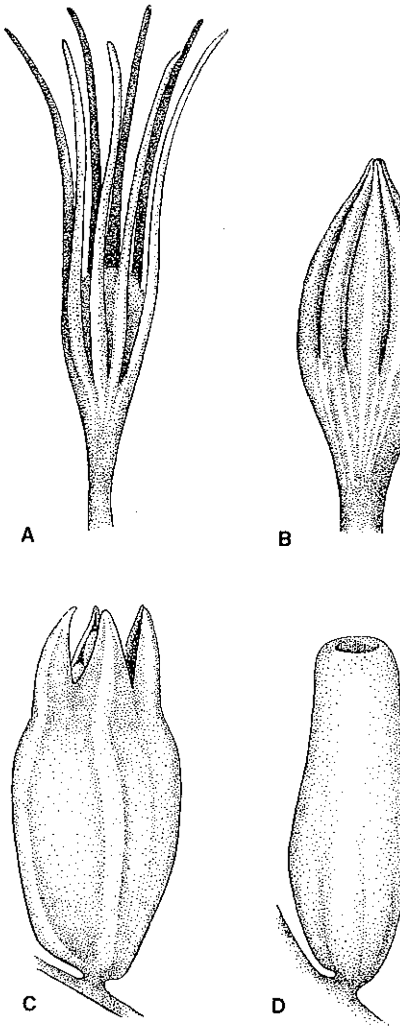


Figure 15-11 Types of pteridosperm seeds, illustrating the theoretical origin and phylogenetic development of the integument. A, *Genomosperma kidstoni:* B, *Genomosperma latens:* C, *Eurystoma angulare:* D, *Stamnostoma huttonense.* [Redrawn from Andrews, *Science* 142:925, 1963. Copyright © 1963 by the American Association for the Advancement of Science.]

Cycadeoidophyta

The extinct group Cycadeoidophyta was coexistent with extinct cycads in the Jurassic and Cretaceous. The variation in leaf morphology was quite similar in the two groups, but they can be separated from those of the Cycadophyta because the stomata were *syndetocheilic* (subsidiary cells and guard cells originate from the same initial cell). In growth habit some of the cycadeoids are depicted as having columnar trunks; in others the stem is squat and globose. This is the same variation present in the Cycadophyta. The pith was large in diameter. When preserved, the primary xylem was endarch and surrounded by a cylinder of secondary xylem, but the stems lacked the girdling leaf traces characteristic of cycads. Two families are recognized—the Williamsoniaceae and Cycadeoidaceae. Genera in the Williamsoniaceae had slender branched stems, although *Williamsonia sewardiana* has been depicted as assuming the form of a columnar cycad (Fig. 15-12, A). Leaves were simple or pinnate. Strobili were either monosporangiate or bisporangiate (both microsporophylls and ovulate structures in the same strobilus). The cone of *Williamsoniella* consisted of a central axis (receptacle) covered with long-stalked ovules with projecting micropyles. Interspersed among the ovules were sterile (interseminal) scales; surrounding the ovule-bearing portion were wedge-shaped microsporophylls, each