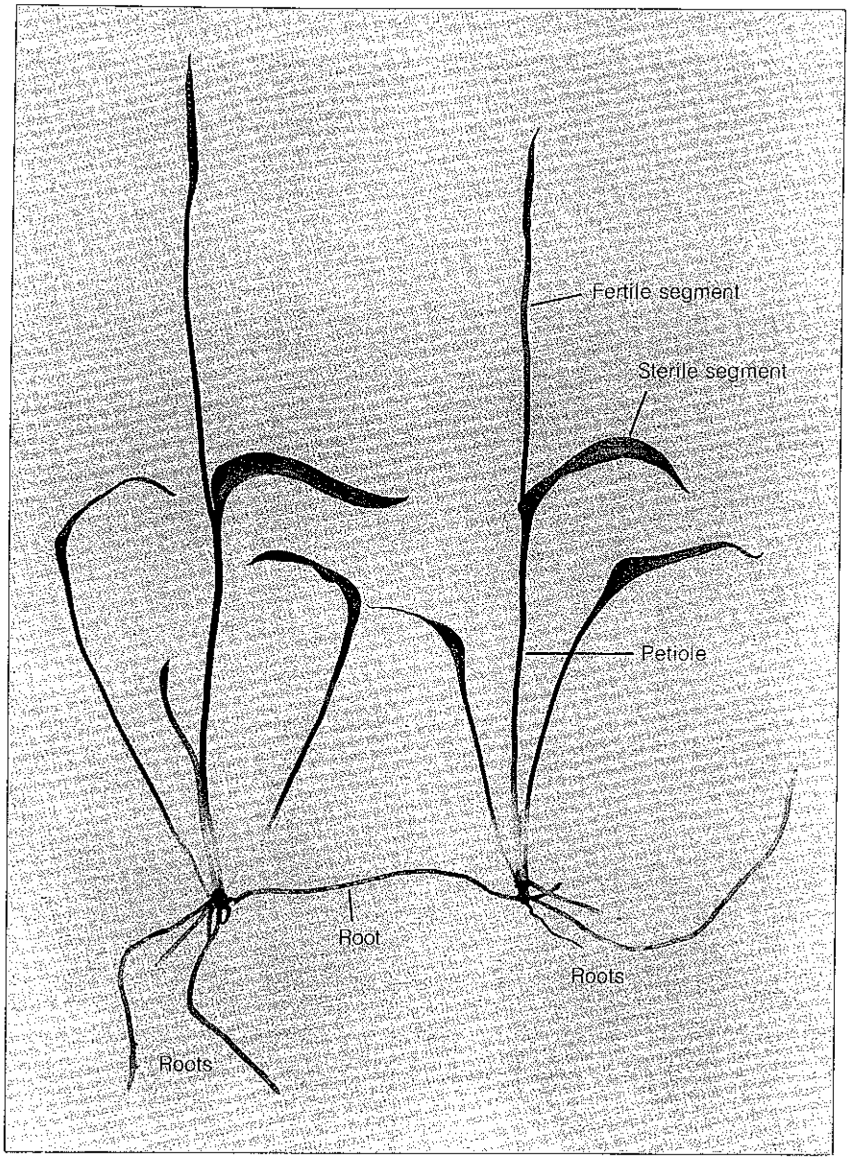

FIGURE 12-10 Entire plants of *Ophioglossum petiolatum.* Note that the short erect stems arise from roots; only one leaf is fertile on each shoot.

for consideration are: (1) the peculiar fertile segment, (2) collateral vascular bundles, (3) roots with endophytic fungus and without root hairs, (4) noncircinate vernation of leaves (although see section on *Botrychium*), (5) lack of sclerenchyma in the plant body, and (6) subterranean gametophytes with an associated fungus. Although some of these features are not confined to the Ophioglossales, no other group of vascular plants has all of these attributes. The Ophioglossales is undoubtedly an ancient group, but the meager number of fossils continues to shroud its phylogeny.

Marattiales — Marattiaceae

This group of plants more closely resembles the Filicales than the Ophioglossales. Many of them

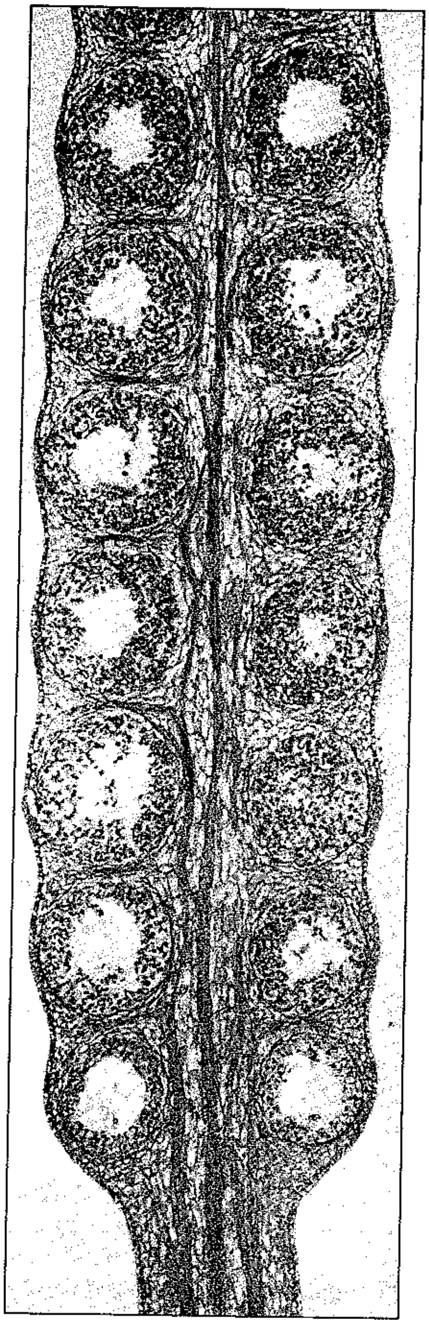

FIGURE 12-11 Longisection, fertile segment of *Ophioglossum lusitanicum* var. *californicum,* showing two rows of embedded sporangia. Branches of the main vascular system are evident between sporangia at left.

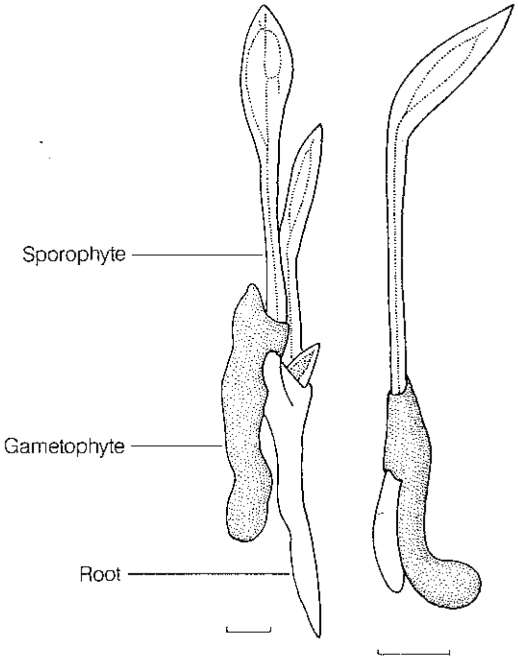

FIGURE 12-12 Gametophytes and attached young sporophytes of *Ophioglossum nudicaule;* the gametophytes stand erect in the soil. Scale bars = 1 millimeter. [Redrawn from Mesler et al., *Phytomorphology* 25:156, 1975.]

possess large pinnate fronds with sporangia located on their lower surfaces. It is an ancient group with a fossil record that extends back to the transition of Lower to Upper Carboniferous. It is a tropical order and is generally known in temperate zones only through specimens in conservatories and dried specimens in herbaria.

There are six genera and perhaps 200 living species in the order. The two better-known genera are *Angiopteris* (about 100 species) and *Marattia* (about sixty species); the former is distributed throughout the tropics of southeastern Asia, the latter is pantropical. In growth habit the two genera typically have upright, unbranched, fleshy tuberous stems or short trunks bearing large, pinnately compound leaves (circinate in vernation) and thick fleshy roots (Fig. 12-14). A pair of clasping fleshy stipules is present at the base of each leaf, covering part of the stem; they persist, along with leaf bases, even after the fronds abscise. New plantlets can arise from the stipules. On the lower surface (abaxial side) of the fronds, which may be up to 5 or 6 meters long, sporangia occur along veins; venation in the ultimate segments is of the open dichotomous type. In *Angiopteris* a sorus consists of sporangia crowded together in two rows along a vein; each sporangium dehisces by a longitudinal slit on the side facing the other row of sporangia (Figs. 12-15, A; 12-16). In *Marattia* the two rows of sporangia are united into a compact soral group surrounded by a common wall (Fig. 12-15, B). This structure is termed a *synangium*. At maturity the synangium opens, much like a clam shell, exposing the sporangia which dehisce by longitudinal slits.

In most other genera the stems are trailing, dorsiventral rhizomes. The fronds may be simple to once pinnate *(Danaea)*, or palmately compound with reticulate venation and scattered circular or ringlike synangia *(Christensenia)*.

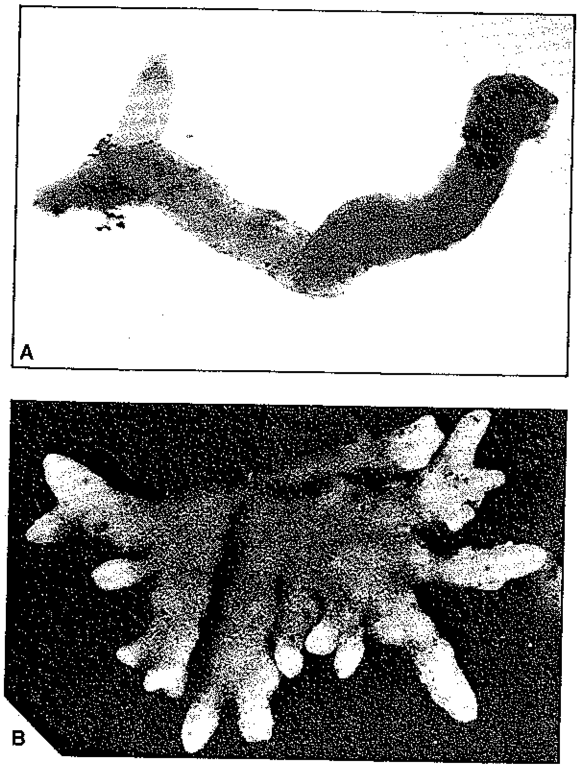

FIGURE 12-13 Gametophytes of *Ophioglossum*. **A**, *O. vulgatum;* precocious root of young attached sporophyte is seen at left (× 7). **B**, *O. palmatum;* branching confined essentially to a single plane (× 10). [Specimen for **A** supplied by Dr. D. Stevenson; **B** from Mesler, *Amer. Jour. Bot.* 62:982, 1975.]

ANATOMY OF THE SHOOT. The apical meristem of a mature adult plant is reported to have a group of apical initials or an apical cell that is not regular or precise in its divisions (Charles, 1911; Bower, 1923). As mentioned previously, the stems are fleshy and have numerous mucilage canals and tannin-filled cells throughout the plant body. The stem is protostelic at the base of the plant. Higher up, the stele is an amphiphloic siphonostele with overlapping leaf gaps. At even higher levels in older plants the stele is a complex polycyclic dictyostele consisting of two or more concentric vascular cylinders (Fig. 12-17). It should be emphasized that the inner cylinders are continuous with the outer cylinder at lower levels in the stem. In the petiole the leaf trace becomes subdivided in the formation of concentric cylinders of vascular bundles; the cylinders decrease in number higher up in the frond rachis. Root primordia have their origin in the pericycle of stem vascular bundles of the outer and inner vascular cylinders. After their initiation, the large roots "bore" their way through the stem cortex and then grow between the leaf bases, generally being evident on the surface of the stem before entering the soil.

The leaves of marattiaceous ferns are circinate in vernation during development. The ultimate frond segments in most species have a single midvein with lateral dichotomous veins. The mesophyll in most forms is differentiated into an adaxial palisade tissue and an abaxial spongy mesophyll. Stomata occur on the abaxial surface. Mucilage cavities, hypodermal sclerenchyma, or collenchyma are often present in the petiole.

THE ROOT. In the primary root and the first-formed roots on the stem there is a definite apical cell; later-formed roots are reported to have a group of about four equivalent initials (West, 1917). Roots become large and fleshy and contain mucilage cavities. Typically the vascular cylinder is polyarch—a feature not generally found in other ferns.

THE SPORANGIUM. Sporangia are of the eusporangiate type and commonly originate from mounds of tissue paralleling the veins of developing fronds. At maturity each sporangium has a broad base and a sporangial wall that consists of several layers of

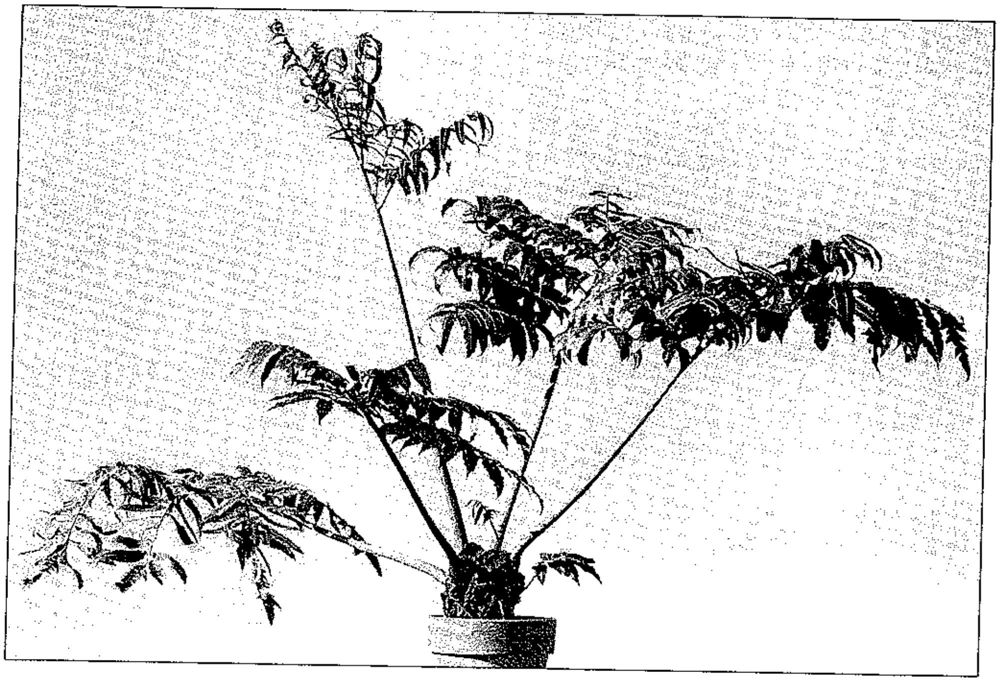

FIGURE 12-14 *Angiopteris evecta,* showing short, tuberous stem and large bipinnate leaves.

cells. When mature the sporangia may be separate from each other *(Angiopteris),* or the sporangial walls may become confluent during development so that each sporangium is actually a pocket or loculus in a compact structure, the synangium (Fig. 12-15, B). Dehiscence of individual sporangia in a synangium is brought about by the drying out of wall cells, which results in longitudinal splitting of each sporangium (after the halves of the synangium separate in *Marattia*), or by the formation of a pore at the tip of each sporangium as in *Danaea.* Spore output is large; spore numbers range from a minimum of 1,000 up to a maximum of 7,000 spores formed by each sporangium (Bower, 1935). In *Marattia* the spores are small, bilateral (monolete); those of *Angiopteris* are tetrahedral (trilete).

CHROMOSOME NUMBERS. Chromosome numbers are known for three genera. The theoretical base number for *Danaea* and *Angiopteris* is $x = 10$, with actual counts of $n = 40, 80$. For *Marattia,* $x = 13$ is the probable base number with actual counts of $n = 78, 156$ (Löve et al., 1977). As with some other ferns, polyploidy apparently has been operative in the order.

THE GAMETOPHYTE. The gametophyte is a large, green, dorsiventral ribbon-shaped or heart-shaped structure with a prominent ventral midrib or cushion and thinner, ruffled, lateral winglike extensions (Fig. 12-18). The gametophyte, which may be 2 centimeters or more in length, is slow growing, long lived, and has an endophytic fungus which, however, must play only a minor role in the nutrition of the gametophyte because of the presence of chlorophyll. There are absorbing rhizoids along the ventral midrib. Gametangia of *Angiopteris* show the following pattern of distribution: antheridia are on the ventral surface but may occur on the dorsal side (Nozu, 1956); archegonia are restricted to the projecting ventral midrib (Haupt, 1940). Both antheridia and archegonia are sunken, and the main stages in their development are shown in Fig. 12-19. Mature sperms are multiflagellate.

THE EMBRYO. Just as in the Ophioglossales, the first division of the zygote is transverse, resulting in a two-celled embryo. Details of embryogeny in the Marattiales are not too well known, but in contrast to the Ophioglossales, the Marattiales exhibit only endoscopic polarity (Chapter 6, Fig. 6-1). The fu-

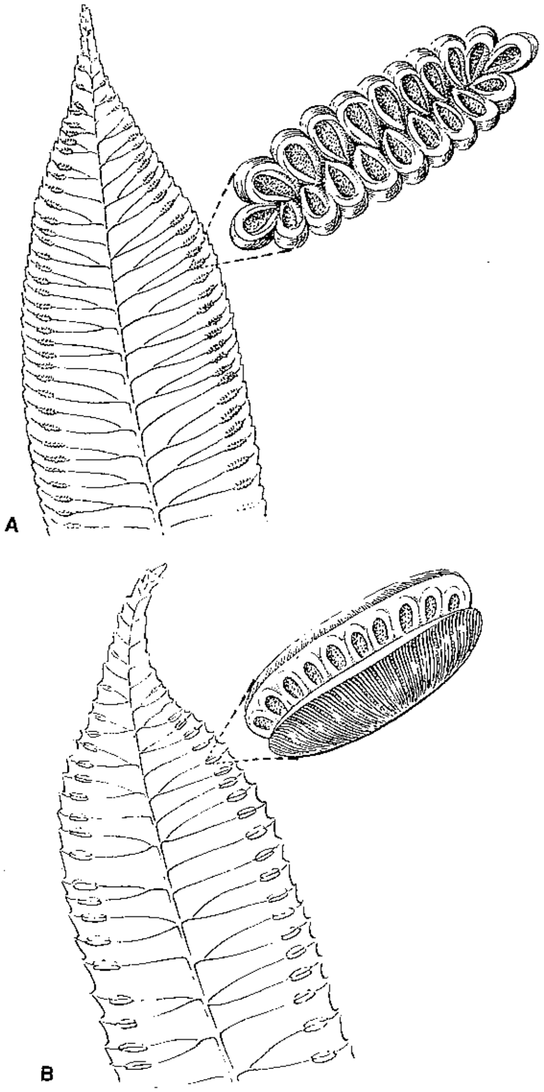

FIGURE 12-15 Abaxial views of fertile pinnae. **A,** *Angiopteris;* **B,** *Marattia.* One sorus of each is enlarged. The sporangia in *Marattia* form a definite synangium. [Pinnae redrawn from *The Ferns,* Vol. II, by F. O. Bower. Cambridge University Press, London. 1926.]

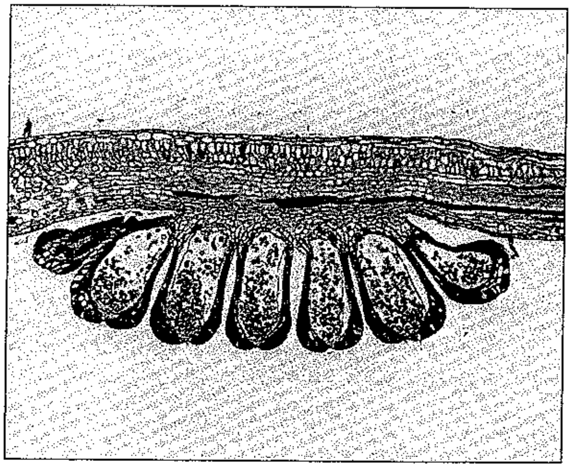

FIGURE 12-16 Section, lamina and sorus of *Angiopteris* sp. Note the presence of numerous spores within each thick-walled sporangium.

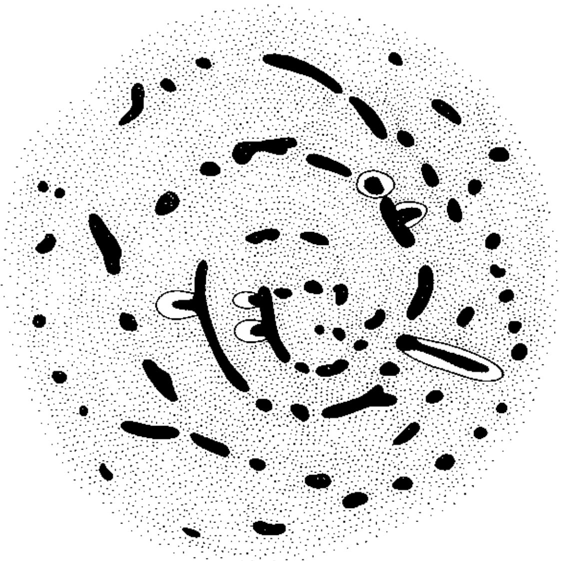

FIGURE 12-17 *Angiopteris evecta.* Transverse section of stem, showing polycyclic dictyostele. Root traces enclosed in clear areas. [Redrawn from *The Ferns,* Vol. II, by F. O. Bower. Cambridge University Press, London. 1926.]

ture shoot apex and first leaf have their origin from the cell (epibasal cell) directed away from the neck of the archegonium. The cell (hypobasal cell) toward the archegonial neck gives rise to a multicellular foot. The root meristem, appearing late in embryogeny, is endogenous in origin, and in one study it was reported to be derived from the epibasal portion of the embryo. With subsequent growth

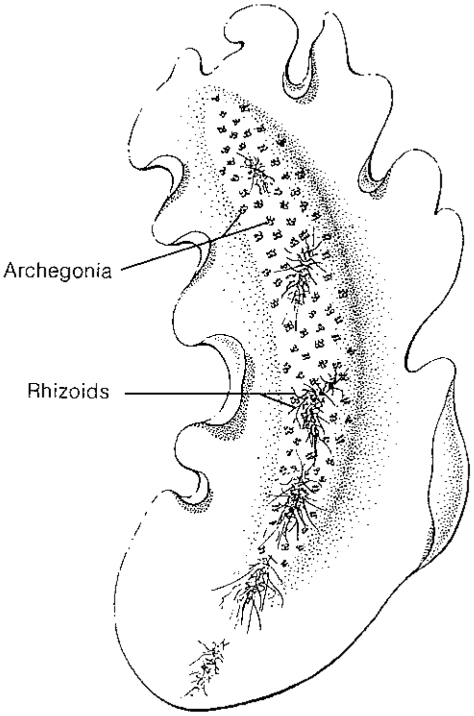

FIGURE 12-18 Ventral surface of ribbon-shaped gametophyte of *Marattia douglasii.* Most of the antheridia (not shown in drawing) are on the ventral surface (× 5). [Drawn from specimen supplied by Dr. W. H. Wagner, Jr.]

of the embryo the young shoot grows up through the gametophyte, emerging from the upper surface. The presence of a suspensor has been reported in some species of *Angiopteris* (Land, 1923) and other genera (Campbell, 1940). The first vascular bundle of the embryo is continuous between the root and first leaf. The vascular bundle of the next leaf is joined to the first vascular strand.

FOSSIL MEMBERS OF THE MARATTIALES. Considerable information is now available on the extinct Carboniferous swamp relatives of the living members of the Marattiales. They were trees, large at the base, tapering toward the top and ending in a collection of large pinnately compound fronds which were probably very graceful in appearance (Fig. 12-20). There are form genera for these plants, but the generic name *Psaronius* is generally used in descriptions of these trees that may have reached 10 meters or more in height. The stems were relatively small in diameter and probably could not have supported the plant except for the presence of large masses of roots that formed a mantle on the stem. These roots, originating high on the stem, grew downward and produced lateral roots, forming a compact inner zone and a peripheral zone of more loosely arranged roots (Fig. 12-21). Roots of the inner zone were bound together by proliferative tissue derived in part from the stem and from the cortex of the closely appressed roots (Ehret and Phillips, 1977). Some roots are known to have been 2 centimeters in diameter—the largest for any known fern. The mantle of roots at the base of a large tree trunk could be up to 0.5 to 1 meter in diameter in some specimens. Present-day tree ferns resemble *Psaronius* in general growth habit (Fig. 11-1). The anatomy of a mature root was similar to that of *Marattia* and *Angiopteris.* Well-preserved root tips were discovered that show an apical organization remarkably similar to present-day marattialean species (Ehret and Phillips, 1977). Phyllotaxy was variable: it was helical at all levels of the stem (Rothwell and Blickle, 1982) or it was helical in the basal part of the stem, becoming whorled higher up (Morgan, 1959). Some species were distichous—two longitudinal rows of leaves, one on each side of the stem (DiMichele and Phillips, 1977). Phyllotaxy can be deduced by examining the arrangement of leaf scars from compression-impression fossils of stems (Fig. 12-22); different types are placed in form genera when internal anatomy of the stem is not known.

The stems of *Psaronius* were obconical in growth habit—that is, the stem was small in diameter at the base, increasing in width at higher levels, although the mantle of roots gives the impression that the stem was larger at the base of the plant (Fig. 12-21). Correlated with this change was a modification of the stele. It is assumed that a young plant was protostelic (this would be the stelar type at the base of an older plant). As the plant continued to grow, there was a transition to the siphonostelic condition, more specifically to a monocyclic and then to a dicyclic dictyostele (Stidd, 1974). At higher levels more cylinders of vascular tissue were formed in the production of a complex, concentric polycyclic dictyostele (Fig. 12-23, A). Each new vascular cylinder was attached to the inner face of the previously formed cylinder. What has just been de-

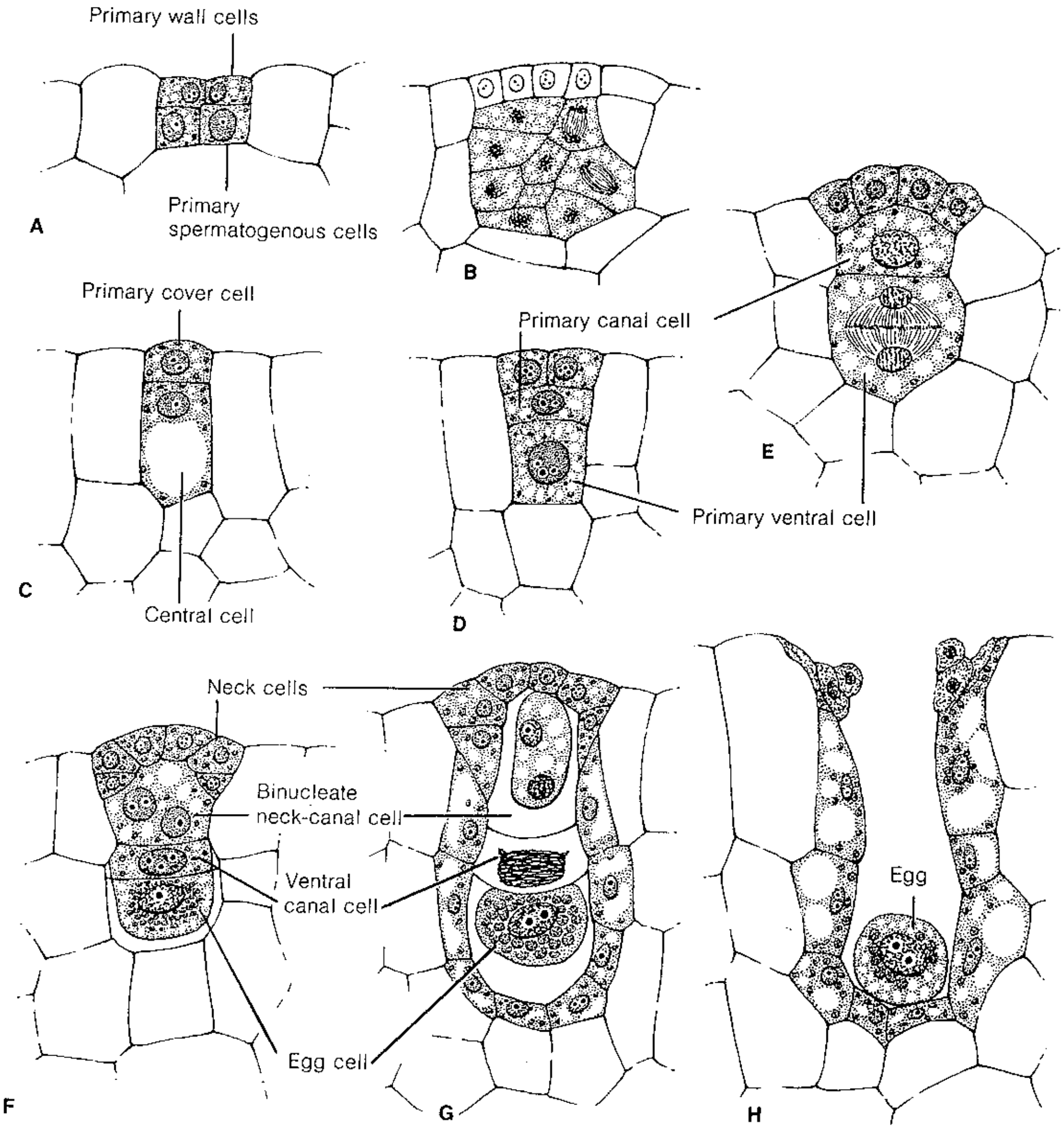

FIGURE 12-19 Stages in the development of an antheridium (**A, B**) and of an archegonium (**C–H**) of *Angiopteris evecta*. [Redrawn from Haupt, *Bull. Torrey Bot. Club* 67:125, 1940.]

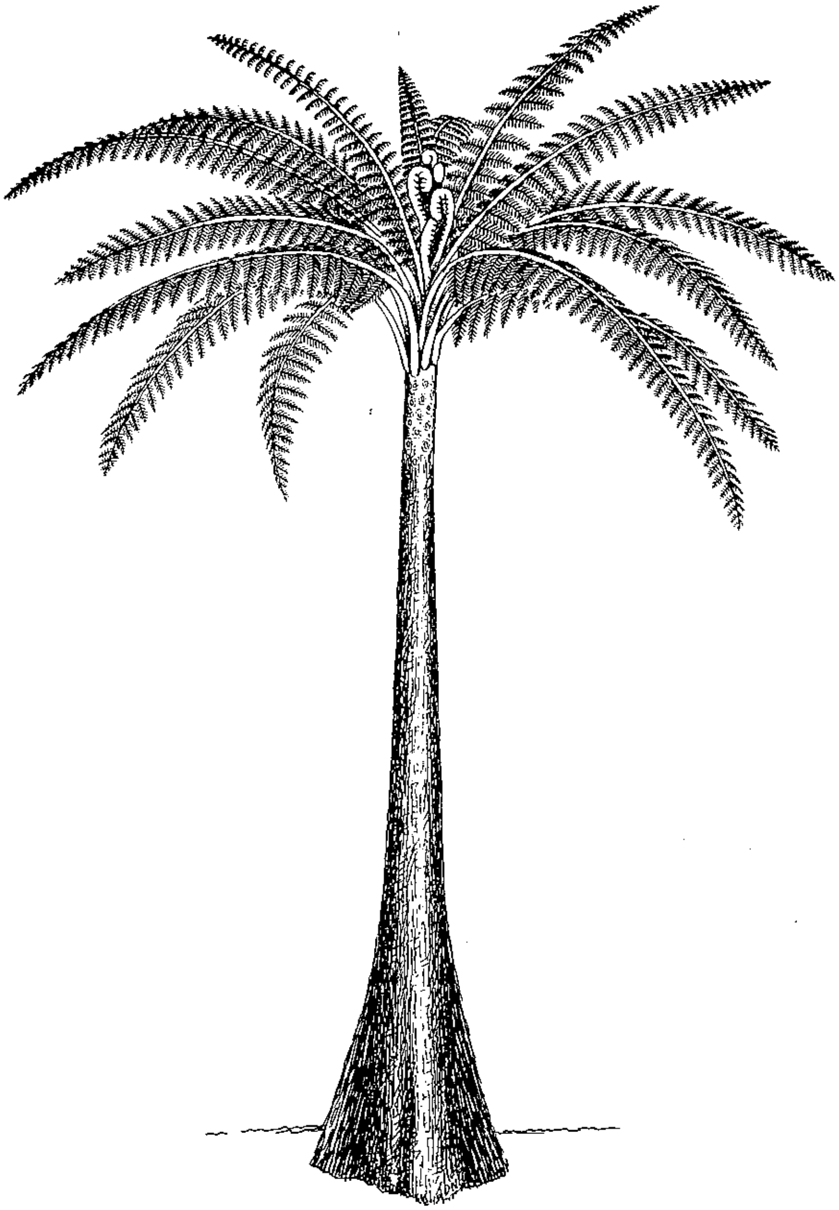

Figure 12-20 Reconstruction of the tree fern *Psaronius*, considered to have been approximately 6 to 8 meters tall. [Redrawn from Morgan, *Illinois Biol. Monogr.* 27:1–108, 1959.]

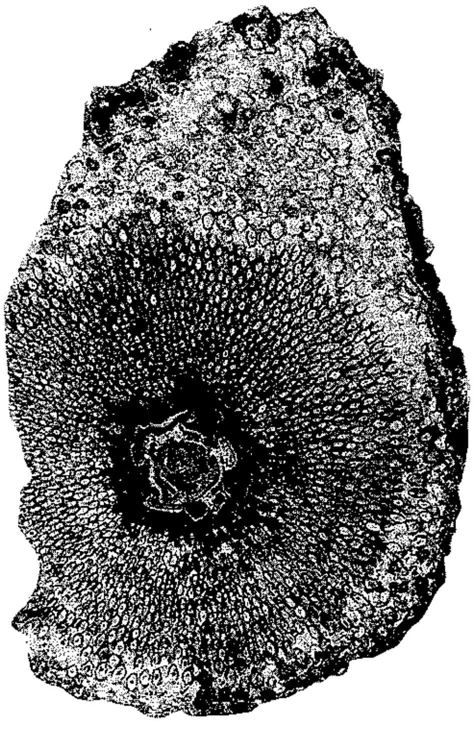

FIGURE 12-21 *Psaronius magnificus.* Transverse section of trunk showing the small central stem, prominent inner zone of compact roots, and peripheral free roots (× 0.3). [From Rothwell and Blickle, *Jour. of Paleontology* 56:459, 1982.]

scribed is an overview of a possible sequence. The stem of *P. simplicicaulis* was probably smaller than most Upper Carboniferous forms; it had distichous leaf arrangement, and the stele remained as a monocyclic dictyostele (DiMichele and Phillips, 1977). *Psaronius magnificus* had helically arranged leaves at all levels and the stem had three to six stelar cycles (Rothwell and Blickle, 1982). The dictyosteles of other species were amazingly complex, consisting of several concentric cycles (Morgan, 1959) as shown in Fig. 12-23, B.

The xylem in each vascular bundle (meristele) was endarch in development; phloem surrounded the xylem, but an endodermis with casparian strips has not been identified (Smoot and Taylor, 1981). No secondary vascular tissues were formed. This type of anatomy, except for the occasional appearance of a typical endodermis, also characterizes the living members of the Marattiales as well as the occurrence of polycyclic dictyosteles in most of them. Additional information on anatomy can be found in the treatise by Ogura (1972).

There is a wealth of information concerning sporangial structures of the Upper Carboniferous marattialean ferns. Pinnae have been found with

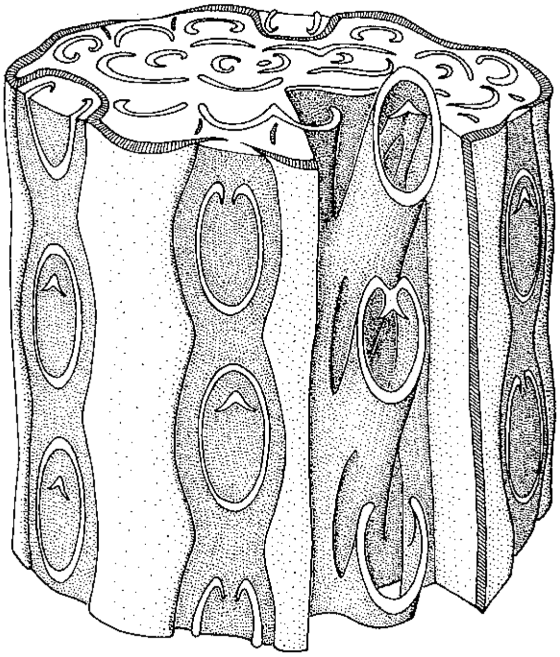

FIGURE 12-22 Reconstruction of a *Psaronius* stem showing origin of leaf traces (in cut-away portion) in a helical phyllotaxy. The vascular system of the stem is a polycyclic dictyostele. [Redrawn from Stidd, *Ann. Missouri Bot. Gard.* 61:388, 1974.]

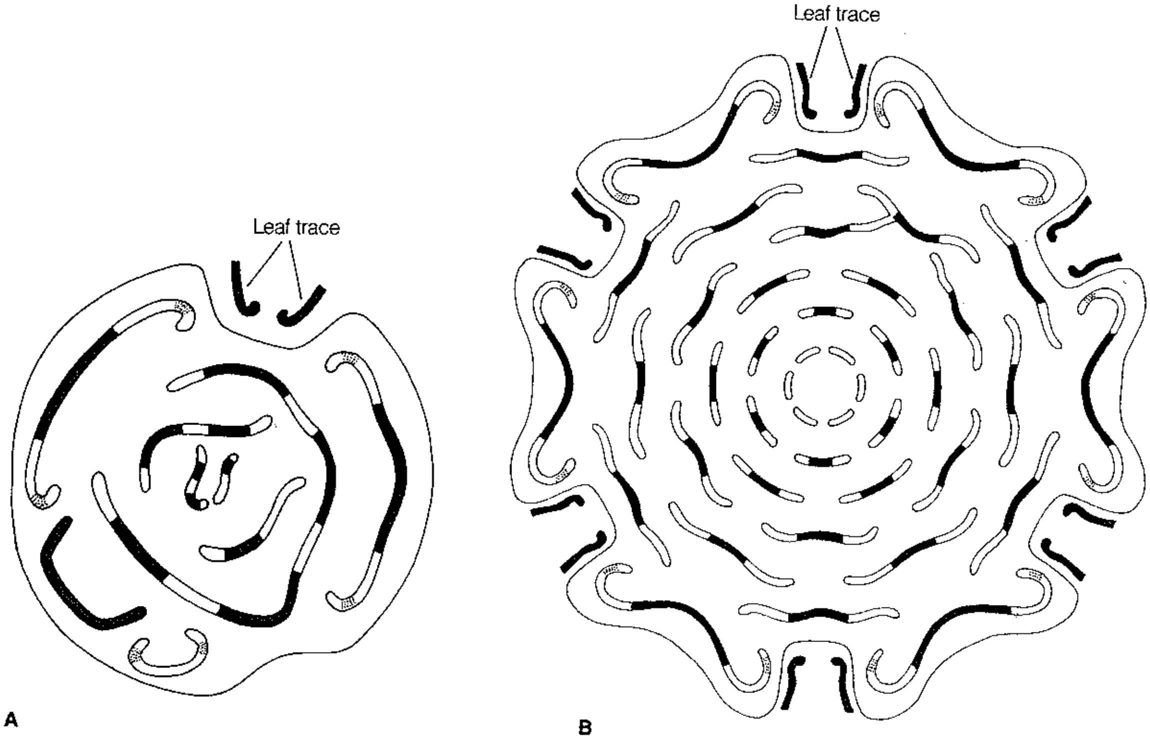

FIGURE 12-23 *Psaronius blicklei.* Diagrammatic reconstructions of stem transverse sections showing polycyclic dictyosteles. **A**, stem with helical phyllotaxy. **B**, large stem with whorled phyllotaxy. Leaf traces and potential leaf-trace tissue shown in solid black; cauline vascular tissue unshaded; stippling represents cauline vascular tissue that will contribute to departing leaf traces at higher levels. Compare with Fig. 12-22. [From Morgan, *Illinois Biol. Monogr.* 27:1–108, 1959.]

sori on the abaxial side of pinnules (Fig. 12-24) which can be compared favorably with extant genera. In some, the sporangia are fused to varying degrees, forming synangia. The sorus of the form genus *Acaulangium* consisted of a group of four to six sporangia. The sporangial bases extended into a common basal pad of tissue and the sporangia were laterally attached prior to dehiscence (Millay, 1977). *Scolecopteris* was essentially the same (Fig. 12-25, A) except for a well-defined pedicel supporting the synangium (Mamay, 1950). In other forms the sporangia occurred in two rows along a vein much like the present-day *Angiopteris.* In *Eoangiopteris goodii* there were up to nineteen sporangia in a sorus. The sporangia were embedded in an elongate parenchymatous pad and the sporangia were attached for a short distance distal to the base (Millay, 1978). *Eoangiopteris andrewsii* was similar except that there were fewer sporangia in a sorus (Fig. 12-25, B).

The marattialean flora declined after the Upper Carboniferous, but fossils have been described from the Mesozoic (Triassic and Jurassic) and Cenozoic (Eocene) that were essentially similar to certain modern-day genera. There is very little doubt about the naturalness of the order. Marattialean types appeared in the transition from Lower to Upper Carboniferous, reached a high point in the world flora during the Upper Carboniferous, but derivative forms persisted to the present time. For additional information consult recent textbooks on paleobotany (Taylor, 1981; Stewart, 1983).

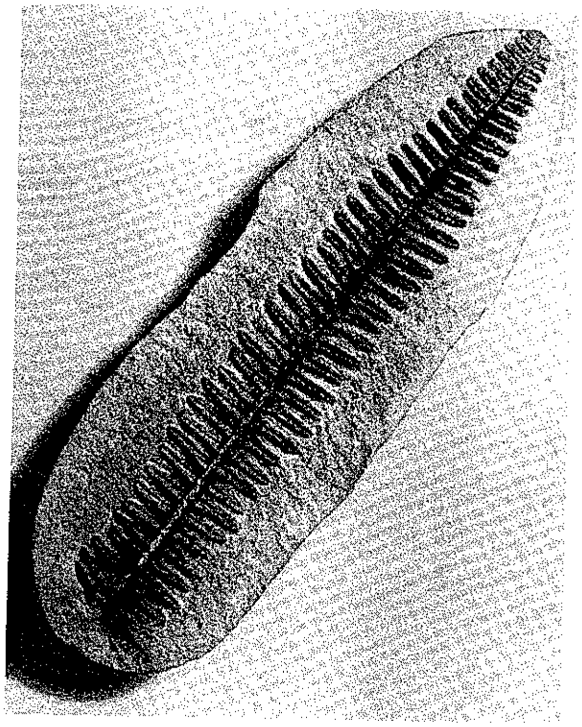

FIGURE 12-24 *Pecopteris.* Form genus for pinnules of the Carboniferous marattialean fern *Psaronius.* [From *Leaves and Stems from Fossil Plants* by R. E. Janssen. Illinois State Museum, Springfield, Ill.]

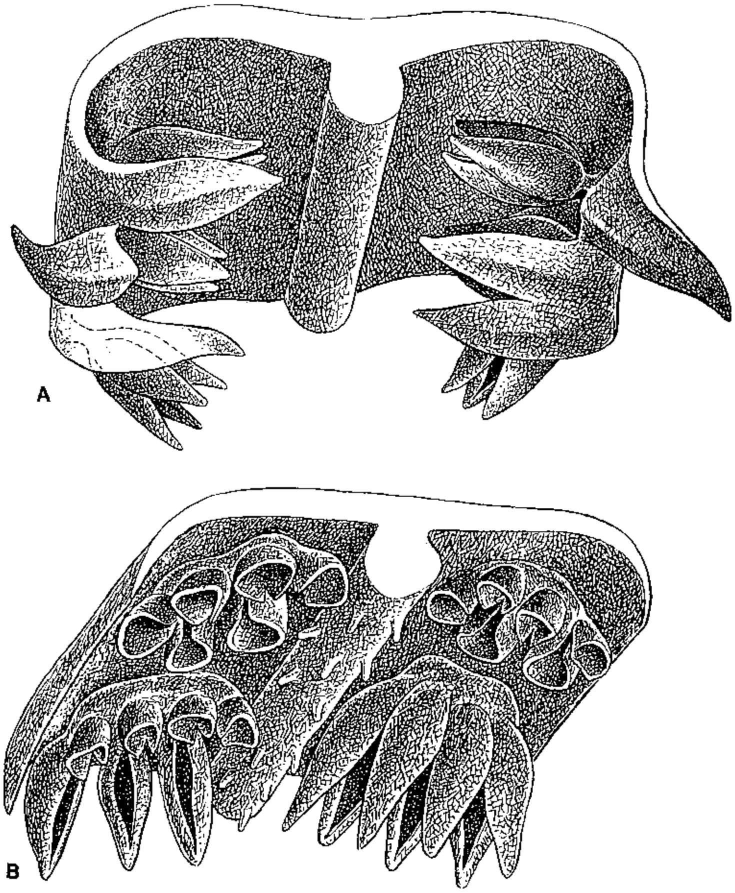

FIGURE 12-25 **A**, *Scolecopteris incisifolia:* reconstruction of lower surface of a fertile pinnule showing groups of sporangia, each group attached by a common pedicel. **B**, *Eoangiopteris andrewsii:* lower surface of a portion of a pinnule with four groups of sporangia; upper two groups sectioned transversely. [Redrawn from Mamay, *Ann. Missouri Bot. Gard.* 37:409–476, 1950.]