CHAPTER 11

Filicophyta: Ferns

GENERAL MORPHOLOGY; EARLY FERNS

FOR the groups of plants discussed thus far (Chapters 7 through 10) the *microphyll,* with some exceptions (e.g., in *Sphenophyllum*), is the prevailing type of foliar appendage. Most of the primary vascular tissue of microphyllous plants is cauline; the leaf traces are small strands of vascular tissue that separate from the periphery of the stele at the nodes. Ferns, on the contrary, have *megaphylls.* A megaphyll, whether large or small, usually has a branched venation system, and its leaf-trace system in ferns is associated with a *leaf gap* in the vascular cylinder of the stem unless, of course, the stem is protostelic. (Refer to Chapter 3 for a more complete discussion of microphylls and megaphylls). In megaphyllous plants, the form of the primary vascular system of the stem is markedly affected by the development of the larger leaves and their associated leaf traces. It should be pointed out, however, that regardless of the stelar pattern of the shoot axis, the primary vascular system of the fern *root* is exarch and radial in organization as it is in all other vascular plants. This remarkable conservatism of the root seems to be correlated with the absence of foliar appendages, and thus lends further support to the idea that the vascularization of stems in most ferns and seed plants is significantly correlated with the development of megaphylls and their leaf traces.

Today approximately 11,000 species of ferns are widely distributed over the earth's surface. Some species are restricted to narrow environmental niches and are endemic to certain localities. The common bracken fern *(Pteridium aquilinum),* on the other hand, is worldwide in distribution in the tropics and temperate zones and is a troublesome weed in some regions. Ferns are quite numerous and are most diverse in the tropical rain forests, many of them becoming trees 6 to 12 meters high, or growing as epiphytes. However, even desert areas and mountains of the temperate regions may have a fern population.

What general characteristics do we associate with a common field, garden, or house fern? Naturally we think of a large fern leaf, commonly called a *frond* in everyday usage—a term also used by many fern specialists. The fern frond may be a simple expanded blade or lamina with a petiole or *stipe*—the latter term used by some students of fern morphology —or, which is more common, the frond may have incisions in the blade, resulting in a pinnatifid leaf from the Latin (*pinnatus,* meaning "featherlike," or "with parts arranged along the two sides of an axis"). The pinnate plan of organization reaches its highest degree of development in pinnately compound leaves. In the latter type of organization the petiole (stipe) is devoid of any expanded blade, and its continuation as the main axis of the frond is called the *rachis*. Attached to the rachis by petiolules, and approximately opposite each other, are pairs of leaflets, each called a *pinna* (plura, *pinnae*). Each pinna may likewise by subdivided into pairs of *pinnules*, and there may be further subdivisions. Thus, a frond may be once pinnate, bipinnate, tripinnate, and so on (Fig. 13-1). These plans of organization do not describe all of the variations of pattern in fern fronds, but do describe those of a large number of ferns.

In most ferns the stem is an underground rhizome and is not apparent except in stocky, erect species. The large trunks of tropical ferns, however, compare in size with the trunks of moderately large palms. Roots usually are apparent at the lower part of an aerial stem or arise from the lower surface of a rhizome, often characteristically related to each leaf (Fig. 3-6).

Young fern fronds expand by unrolling and are often referred to as "fiddleheads," "monkey tails," or "croziers" (Figs. 11-1, 11-2).

Sporangia

Ferns have brownish to black splotches on the lower surface (abaxial side) of the frond. Each "spot" is technically a *sorus*, i.e., a collection of sporangia that is, in some species, protected by an outgrowth from the leaf surface called an *indusium* (Fig. 13-9).

In contrast with the adaxial, solitary sporangia of the Lycophyta, the sporangia of higher ferns are either marginal or, more commonly, on the abaxial surface of the fertile pinnae (Fig. 13-7). Abaxial sporgania, frequently fused into synangia, are also typical of certain members of the Marattiaceae (Fig. 12-15, B). In the Ophioglossaceae, often regarded as the most primitive family in the ferns, the sporangia occur singly on the upper part of the fertile leaf segment *(Botrychium)* or are embedded in tissue of the fertile segment or spike of *Ophioglossum* (Figs. 12-2, B; 12-11). In some members of the coenopterid ferns (extinct) individual sporangia were terminal on frond segments (Fig. 11-4, A). In general, three sporangial positions occur in the Filicophyta: terminal, marginal, and abaxial. The abaxial position is common in the more specialized ferns (Filicales) and serves to help demarcate this group of ferns.

From the standpoint of the structure and method of development of their sporangia, the Filicophyta are either *eusporangiate* or *leptosporangiate*. Eusporangiate development is characteristic of the more primitive orders of ferns (i.e., Ophioglossales and Marattiales). The more specialized ferns (Filicales, Marsileales, Salviniales) are remarkable among all vascular plants by virtue of the presence of leptosporangia, one of the most distinctive morphological features of these plants. As pointed out in Chapter 4, the leptosporangium is evidently an extreme modification of the more archaic eusporangium.

With reference to the kinds of spores produced, the ferns are characterized by both homosporous and heterosporous types. *Homospory* is typical of most ferns; *heterospory* occurs in certain "water ferns" (Marsileales and Salviniales). There is no strict correlation between sporangial type and type of spores produced.

Gametophytes and Embryos

The type and relative prominence of the gametophytes are closely correlated with the conditions of homospory and heterospory in the ferns. Thus, in the homosporous ferns the gametophyte is a freely developed, independent plant *(exosporic)* that is photosynthetic or (as in many of the eusporangiate groups) subterranean and associated with a fungus. In contrast, the male and female gametophytes of heterosporous ferns are *endosporic* and much smaller than those of homosporous ferns. All known living ferns produce multiflagellate sperm.

No single type of polarity characterizes the embryogeny of ferns. The pattern in which the first division of the zygote is longitudinal, and hence results in a *lateral orientation* of the apical and basal poles, characterizes the largest number of ferns (see Chapter 6). *Exoscopic* and *endoscopic* embryos also are found in ferns. The intermediate, called "prone," type of embryo, devoid of a suspensor, is

FIGURE 11-1 Tree ferns growing in Golden Gate Park, San Francisco, California. Young leaves, which exhibit circinate vernation, are seen in various stages of growth. The mature fronds are large and compound pinnate. [Courtesy Dr. T. E. Weier, from *Botany. An Introduction to Plant Science.* 2d edition, by W. W. Robbins, T. E. Weier, and C. R. Stocking. Wiley, New York, 1957.]

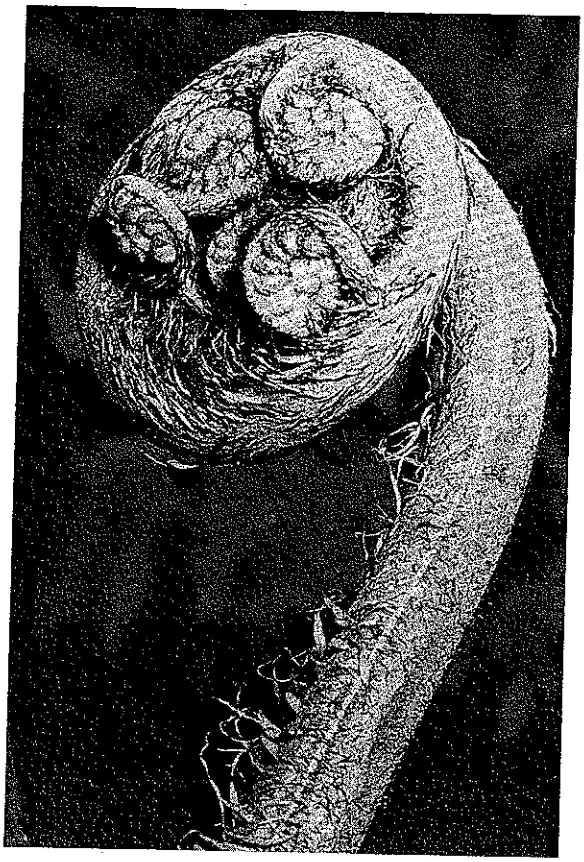

FIGURE 11-2 Greatly enlarged crozier, or fiddlehead, of a fern. Note that the pinnae and further subdivisions exhibit circinate vernation. [Courtesy Dr. T. E. Weier.]

another feature that separates the highly specialized leptosporangiate ferns (except for a few species) from other vascular plants.

Early Ferns

The ferns are well known from a fossil record extending back to the Lower Devonian. Some of these putative ferns were not too different from those of certain trimerophytes from which they probably took their origin. Ferns increased in number and diversity in the Upper Carboniferous and have persisted to the present day. However, some groups did not leave any direct descendents in today's flora. Even so, the Filicophyta, especially the Filicales, is a highly diversified and successful group at present, having overcome the rigors of existence in a changing world much better than their frequent associates, the lycopods and horsetails.

The search for earliest fern records immediately becomes a complicated study, but one not without some degree of hope. The bulk of Paleozoic fern foliage, originally thought to be exclusively that of spore-producing ferns and to which form genera (see Chapter 9) were assigned, was shown to represent actually the leaves of a great many seed-producing ferns—the Pteridospermophyta (Fig. 15-1). Identification keys that use shape, method of attachment of pinnules, and type of venation have been established for Paleozoic fern leaves. In certain instances a "natural plant" can be synthesized from the form genus for foliage and from the numerous form genera for other parts of the plant which were originally found as isolated fragments.

The problem, then, in tracing the history of the Filicophyta is to separate those fossil forms that may represent morphological steps in the evolution of the fern type of organization, but at the same time to recognize that seed ferns may have shared a common ancestry with the Filicophyta.

As a result of extensive studies on ferns, Bower (1935) proposed certain features that would, in his opinion, characterize a primitive fern. Bower's fern archetype was an upright, dichotomizing plant, if branched at all, in which the distinction between leaf and axis was either absent or ill defined. The leaf, where recognizable, was long-stalked and dichotomously branched with the shanks of the dichotomies free from one another. Sporangia were relatively large, solitary, and located at the distal ends of the subdivisions of leaves. The sporangial wall was thick, opening by a simple dehiscence mechanism, and the sporangia contained only one type of spore.

Cladoxylales

One assemblage of ancient fernlike plants is the order Cladoxylales (sometimes elevated to the rank of class). These Paleozoic plants [Lower Devonian (Emsion) into the Lower Carboniferous] are of interest because of their complex stelar configurations and leaf forms. Most species were relatively small plants with irregularly branched main axes and dichotomously branched smaller ones. The

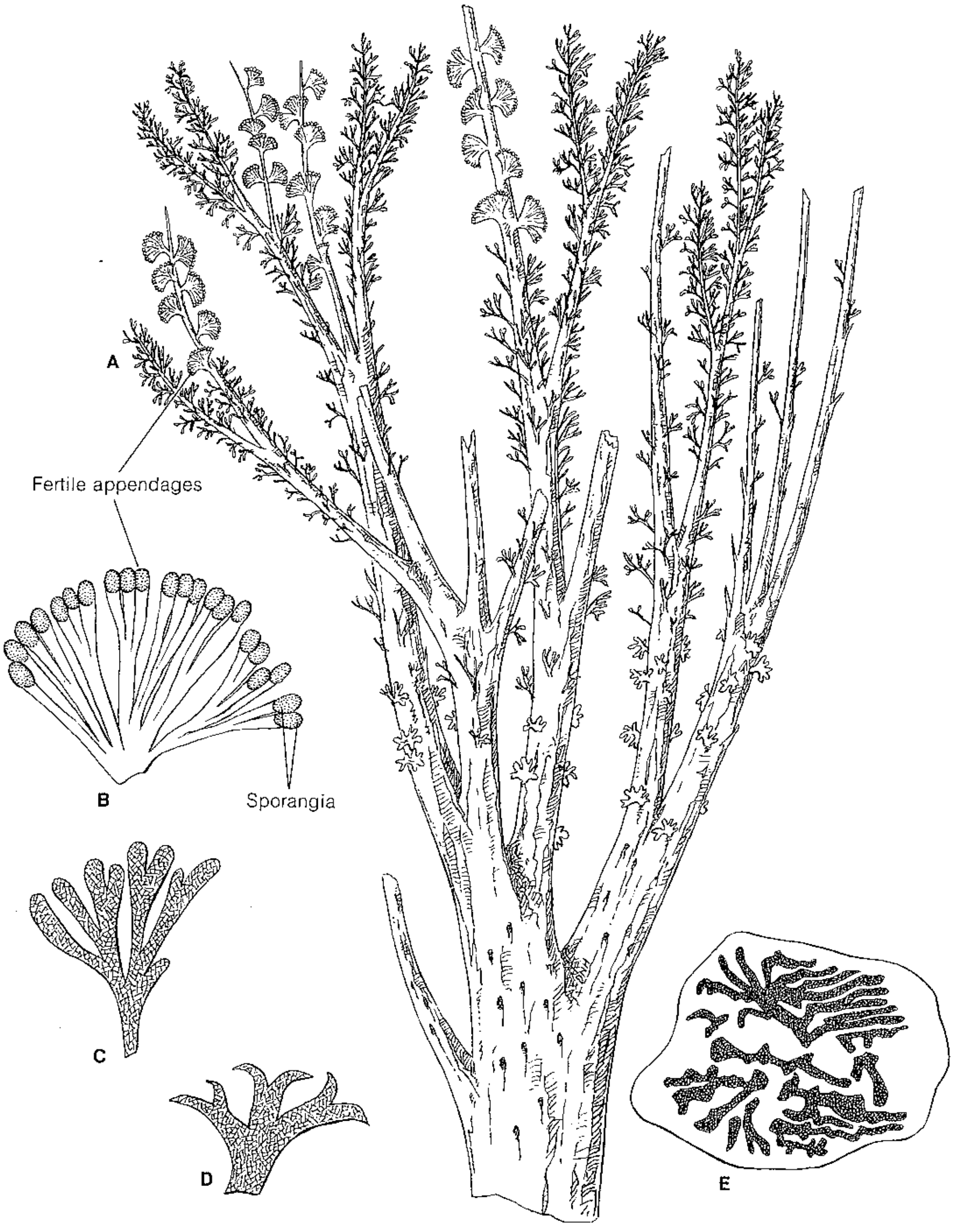

FIGURE 11-3 Cladoxylales—*Cladoxylon scoparium*. **A**, reconstruction, portion of a plant; **B**, fertile appendages: **C**, **D**, sterile appendages from upper (C) and lower (D) portions of the plant; E, xylem of stem as seen in transverse section. [Redrawn from Kräusel and Weyland, *Abh. Senckenberg. Naturforsch. Ges.* 40:115–155, 1926.]

smaller appendages were forked and the fertile leaves were flat, fan-shaped, and bore terminal sporangia on partially fused ultimate segments (Fig. 11-3). The vascular tissue in the stem was organized as a system of interconnected strands (each strand, on many specimens, being elongated radially as seen in transverse section of a stem). Some species are reported to have had secondary xylem around each primary vascular bundle, a feature uncharacteristic of ferns. However, some paleobotanists believe that the tissue consisted of regularly aligned metaxylem cells that were not derived from a vascular cambium.

Coenopterid Ferns

The extinct coenopterids is a fascinating and enigmatic group of ferns. Some specimens have been identified as being of Upper Devonian, but the group was more common in the Carboniferous, and finally disappeared in the Permian. It has long been known that these ferns represent a rather artificial assemblage of plants. Originally, the ordinal name Coenopteridales was established for the entire group, but now three orders are commonly recognized. On the basis of frond morphology and sporangial characteristics, some paleobotanists

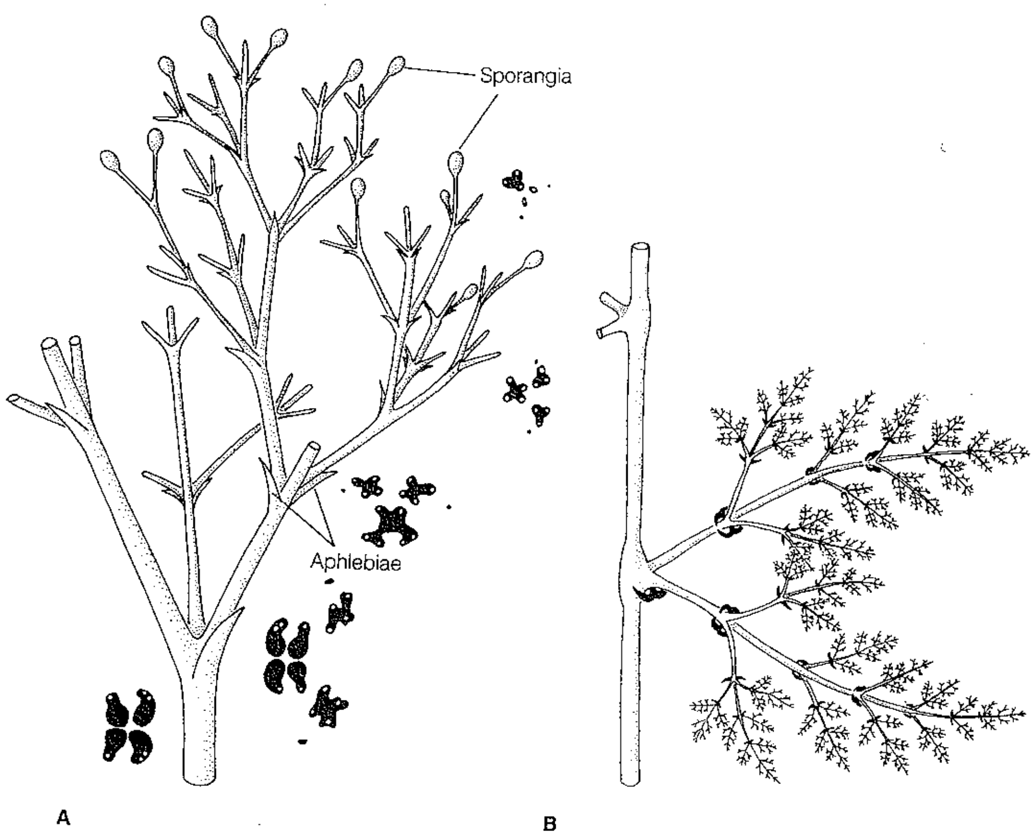

FIGURE 11-4 A, *Stauropteris oldhamia*. Idealized reconstruction, portion of the aerial system. Transverse sectional configurations of the xylem at successively higher levels in the branching system shown at left and right. Protoxylem indicated in white; the small vascular strands belong to aphlebiae. B, *Stauropteris burntislandica*. Diagrammatic reconstruction of part of a frond; aphlebiae shown in black. [A from Eggert, *Mem. Torrey Bot. Club* 21:38, 1964; B from Surange, *Philos. Trans. Roy. Soc.* (London), 237(B):73, 1952.]

(Taylor, 1981) have transferred certain families to the Filicales (leptosporangiate ferns).

In some coenopterids, there was a general lack of distinction between stem axis and the frond petiole (stipe) at the level of frond attachment. Stem and petiole, however, generally had quite different vascular anatomy. Certain coenopterid ferns exhibited primitiveness by the fact that the stem was commonly protostelic, by the three-dimensional branching of the frond, and by the terminal position of sporangia on ultimate frond segments. Specialization led to (1) the development of siphonostelic stems in certain genera, (2) the formation of elaborate vascular cylinders in the frond, and (3) planate megaphylls with sporangia located near the margins on the abaxial side of ultimate

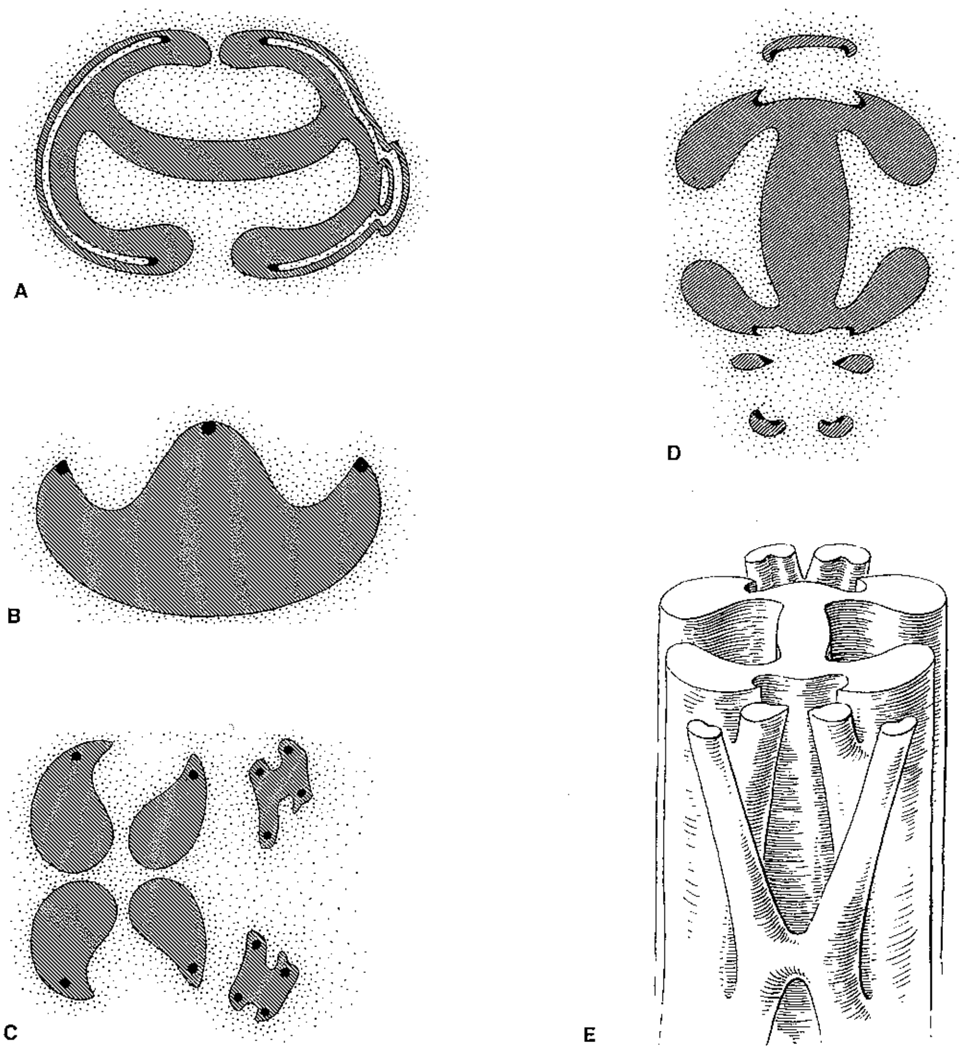

FIGURE 11-5 Petioles (stipes, phyllophores) of the coenopterid ferns. A–D, xylem cylinders only, as seen in transection (solid black areas represent positions of protoxylem). A, *Ankyropteris;* B, *Botryopteris;* C, *Stauropteris;* D, *Etapteris;* E, stereogram of xylem cylinder in *Etapteris.* Smaller, peripheral strands in all diagrams are traces departing to subdivisions of the frond. [A, D, E redrawn from *Handbuch der Paläobotanik* by M. Hirmer. R. Oldenbourg, Munich, 1927; B, C redrawn from Anatomie der Vegetationsorgane der Pteridophyten by Y. Ogura. In *Handbuch der Pflanzenanatomie.* Gebrüder Borntraeger, Berlin, 1938.]

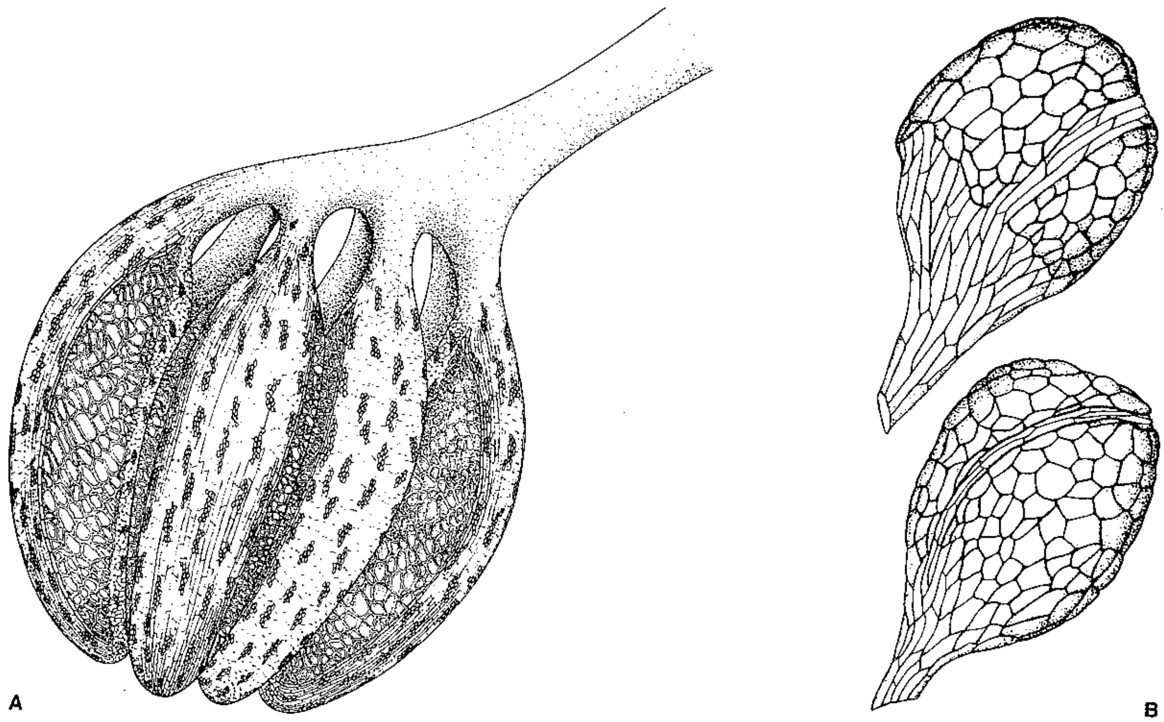

FIGURE 11-6 A, cluster of banana-shaped sporangia of *Biscalitheca musata;* annuli are lateral in position with thick cell walls; B, sporangia of *Botryopteris globosa;* note that the line of dehiscence runs over the top of the sporangia. [A from Phillips and Andrews, *Paleontology* 11:104–115, 1968; B from Murdy and Andrews, *Bull. Torrey Bot. Club* 84:252–267, 1957.]

laminate segments. Tracheids were scalariformly pitted in some (considered to be the primitive condition); others had elliptical to circular bordered pits. (See Eggert, 1964, and Phillips, 1974, for more detailed discussions).

Space does not permit a complete discussion of these ferns; only representative genera will be described with notations as to which order and family each belongs.

STAUROPTERIS (Stauropteridales—Stauropteridaceae). The two species assigned to this genus were apparently small, bushy plants that exhibited three-dimensional branching (Figs. 11-4, A, B). No laminar tissue was formed and sporangia were terminal on ultimate branches. At each level of branching the pairs of branches were associated with a pair of scalelike appendages termed aphlebiae (Figs. 11-4, A, B). The vascular cylinder was four-lobed, or the lobes were separated by parenchyma (Fig. 11-4, A). There were no distinctive fronds in *S. oldhamia* which suggests that the entire plant may have consisted of a three-dimensional branch system. The frond of *S. burntislandica* consisted of alternate pairs of branches on opposite sides of all axes (Fig. 11-4, B). *Stauropteris oldhamia* was homosporous, but heterospory has been documented for *S. burntislandica* (Surange, 1952) which is rather unique for a fern from the Carboniferous.

ZYGOPTERIS (Zygopteridales-Zygopteridaceae). Representatives of this order existed in the Upper Devonian, but were more common in the Carboniferous. Some species of *Zygopteris* were rhizomatous, branched dichotomously, and bore fronds in two lateral ranks. The vascular tissue of the frond axis or *phyllophore* was in the form of the letter H as seen in transverse section. The form genus *Etapteris* is applied to fronds (Fig. 11-5, D, E). The term phyllophore (leaf-bearing structure) traditionally has been used to designate the petiole and rachis of a frond, coined at a time when paleobotanists were

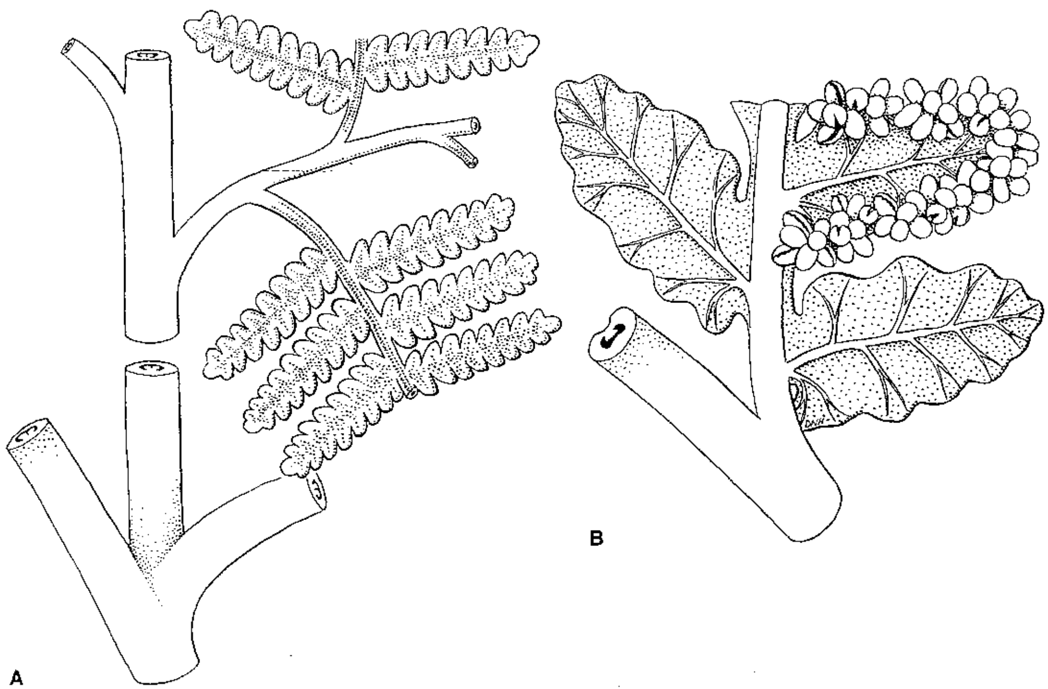

FIGURE 11-7 Reconstructions of portions of fronds of two coenopterid genera. **A**, *Botryopteris forensis*, distal part of a frond; **B**, *Ankyropteris*, portion of fertile frond (form genus *Tedelea*) showing sporangia on abaxial side of one leaf segment. [**A** redrawn from Delevoryas and Morgan, *Amer. Midland Natur.* 52:374–387, 1954; **B** redrawn from Eggert and Taylor, *Palaeontographica* 118(B):52–73, 1966.]

uncertain as to what constituted a frond in coenopterid ferns. The ultimate segments (pinnules) of the frond were planated in some; clusters of elongate, banana-shaped sporangia on segments of fertile fronds have been described and given the name *Biscalitheca musata* (Fig. 11-6, A).

ANKYROPTERIS (Zygopteridales—Tedeleaceae). In *Ankyropteris* the fronds were helically arranged on the stem. The fronds were pinnately compound, with planated pinnae and small laminate pinnules, remarkably similar to modern-day ferns (Fig. 11-7, B). Unlike other coenopterids and the majority of ferns, branching was axillary—new shoots developing in the axils of fronds (Phillips, 1974). Xylem in the phyllophore was in the form of the letter H or resembled two anchors joined by a bar as seen in transverse section (Fig. 11-5, A). Fertile fronds were discovered and given the name *Tedelea* (Eggert and Taylor, 1966). Sporangia occurred in clusters near the margins on the lower surface of pinnules at the termination of lateral veins (Fig. 11-7, B). Sporangial structure was similar to certain extant ferns. On the basis of leaf morphology and sporangial characteristics, *Ankyropteris* has been transferred to the Filicales by some paleobotanists (Mickle, 1980; Taylor, 1981). *Ankyropteris brongniartii* is now recognized as the only species, with all other species of *Ankyropteris* and *Tedelea* being placed in synonomy (Mickle, 1980).

BOTRYOPTERIS (Coenopteridales—Botryopteridaceae). Ten or more species have been described that had helically arranged fronds on the stems; there was considerable variation in frond morphology. In certain species the lower (proximal) portion of the frond was branched three-dimensionally while the upper (distal) portion was planate and the ultimate segments were laminate (Fig. 11-7, A). The xylem cylinder in the petiole and rachis typically was in the form of the Greek letter omega (ω), as seen in transverse section (Fig. 11-5, B). The sporangia were borne terminally on ultimate segments of a much branched fertile portion of a frond, resulting in the formation of large masses of sporangia. The sporangia (Fig. 11-6, B) resemble those of the extant fern family Osmundaceae, and thus *Botryopteris* is considered to be a taxon more closely aligned with the Filicales (Mickle, 1980; Taylor, 1981). However, as Stewart (1983) has pointed out, all coenopterid ferns differ to varying degrees from the Filicales in their vegetative morphology, and all are extinct.

In summary, while some of the coenopterid ferns may have been ancestral to some modern-day ferns, certain ones most probably represent end points in evolutionary experimentation. The Trimerophytophyta (Chapter 7) remains as the group most likely to have been ancestral to the coenopterid ferns through the elaboration of lateral branched axes with terminal sporangia, and finally by the shifting of sporangia to the abaxial side of laminate pinnules in some taxa.

Classification

The following outline of classification will serve as a guide for discussions of fern orders found in Chapters 12 and 13. The extinct Cladoxylales and coenopterid ferns are omitted.

FILICOPHYTA: Living and extinct ferns; plants showing a conspicuous alternation of generations (in modern representatives at least); sporophyte most conspicuous and often elaborately developed; megaphylls present; stems protostelic or siphonostelic, often with complex vascular cylinders; sporangia terminal on ultimate axes, terminal on veins, marginal, or on abaxial surface of fronds; eusporangiate, or more commonly leptosporangiate in living species; homosporous, a few heterosporous; gametophytes: (1) majority exosporic and green, (2) others exosporic, nonchlorophyllous, and subterranean, and (3) endosporic (restricted to heterosporous types); multiflagellate free-swimming sperm; embryo exoscopic, endoscopic, or intermediate.

OPHIOGLOSSALES (Chapter 12): Living ferns, meager fossil record; sporophyte axis usually short and fleshy; stem siphonostelic; fronds simple or pinnately compound; vernation noncircinate to weakly circinate *(Botrychium);* each fertile frond consists of a fertile segment or spike, bearing sporangia, and a sterile or vegetative segment; eusporangiate, producing great quantities of spores per sporangium; homosporous; gametophytes subterranean, bisexual, nonchlorophyllous, tuberous or wormlike with endophytic fungus; embryo exoscopic or endoscopic.

OPHIOGLOSSACEAE: Characteristics as in Ophioglossales.

Ophioglossum, Botrychium, Helminthostachys.

MARATTIALES (Chapter 12): Living and extinct ferns; sporophyte stem in most erect and short, or may be dorsiventral; stem with complex dictyostelic vascular cylinder; fronds commonly large, simple pinnate to tripinnate, and circinate in vernation; paired, clasping stipules at base of each leaf; eusporangia free and grouped into elongate sori or united into synangia on abaxial surface of fronds; many spores formed per sporangium; homosporous; gametophyte terrestrial, green, cordate to ribbon shaped, bisexual, and with endophytic fungus; endoscopic embryo.

MARATTIACEAE: Characteristics as in Marattiales.

Representative genera: *Angiopteris, Marattia. Psaronius* (extinct), *Eoangiopteris, Scolecopteris* (form genera for sori).

FILICALES (Chapter 13): Living and extinct plants, of diverse growth habits and habitats; stems vary from protostelic to intricately dictyostelic; fronds simple to compound pinnate; sporangia scattered or grouped into sori; sori marginal or on abaxial side of fronds; sori with or without a protective structure, the indusium; leptosporangiate, most with a definite dehiscence mechanism, the annulus; spores numerous to few per sporangium, tetrahedral or bilateral; homosporous; gametophytes primarily green, exosporic, commonly thalloid, some filamentous; embryo "prone."

MARSILEALES (Chapter 13): Living and extinct ferns; grow on damp soil or submerged in water; solenostelic; lamina consisting of four pinnae, bipinnate, or without pinnae; circinate vernation; sori enclosed in sporocarps; leptosporangiate; heterosporous; microsporangia and megasporangia in same sporocarp; endosporic gametophytes.

MARSILEACEAE: Characteristics as in Marsileales.

Marsilea, Regnellidium, Pilularia

SALVINIALES (Chapter 13): Living and extinct ferns; small plants that float on surface of water; sori enclosed in specialized indusia ("sporocarps"); leptosporangiate; heterosporous; microsporangia and megasporangia in separate sporocarps; endosporic gametophytes.

SALVINIACEAE: Characteristics as in Salviniales.

Azolla, Salvinia.

Before proceeding with a detailed account of the living orders of ferns, it is important for the reader to have a clear idea of the morphological features that are used for comparative purposes. It was the celebrated British morphologist F. O. Bower who realized the importance of exploring and exploiting the totality of morphological features before a reasonable phylogeny of ferns could be achieved. Bower (1923, 1935) concluded that there are at least twelve major morphological and anatomical criteria that should be utilized. These are listed here because discussions of these points are unavoidable in ferns, and because most of them are of great importance in later discussions.

1 External morphology and habit of plant
2 Apical meristem organization
3 Architecture and venation of the leaf
4 Vascular system of the shoot
5 Morphology of hairs and scales
6 Position and structure of the sorus
7 Protection of the sorus by an indusium
8 Development and mature structure of the sporangium including form of and markings on spores
9 Number of spores produced
10 Morphology of the gametophyte
11 Position and structure of sex organs
12 Embryology of the sporophyte

Additional information that has a bearing on the systematics and phylogeny of ferns can be found in the following list of selected publications: anatomy (White, 1963, 1979; Ogura, 1972), cytology and cytogenetics (Manton, 1950, 1959; Abraham et al., 1962; Fabbri, 1963; Löve et al., 1977; Walker, 1979), experimental physiology and morphogenesis (Wardlaw, 1952, 1968a, b; Wetmore and Wardlaw, 1951), and gametophytes (Nayar and Kaur, 1971).

REFERENCES

Abraham, A., C. A. Ninan, and P. M. Mathew
1962. Studies on the cytology and phylogeny of the pteridophytes. VII. Observations on one hundred species of South Indian ferns. *Jour. Indian Bot. Soc.* 41:339–421.

Bower, F. O.
1923. *The Ferns.* Vol. I. Cambridge University Press, London.
1935. *Primitive Land Plants.* Macmillan, London.

Eggert, D. A.
1964. The question of the phylogenetic position of the Coenopteridales. *Mem. Torrey Bot. Club* 21:38–57.

Eggert, D. A., and T. N. Taylor
1966. Studies of Paleozoic ferns: on the genus *Tedelea* gen. nov. *Palaeontographica* 118(B):52–73.

Fabbri, F.
1963. Primo supplemento alle tavole cromosomiche delle Pteridophyta di Alberto Chiarugi. *Caryologia* 16:237–335.

Löve, A., D. Löve, and R. E. G. Pichi-Sermolli
1977. *Cytotaxonomical Atlas of the Pteridophyta.* Cramer, Vaduz.

Manton, I.
1950. *Problems of Cytology and Evolution in the Pteridophyta.* Cambridge University Press, London.
1959. Chromosomes and fern phylogeny with special reference to "Pteridaceae". *Jour. Linn. Soc. London Bot.* 56:73–91.

Mickle, J. E.
1980. *Ankyropteris* from the Pennsylvanian of eastern Kentucky. *Bot. Gaz.* 141:230–243.

Nayar, B. K., and S. Kaur
1971. Gametophytes of homosporous ferns. *Bot. Rev.* 37:295–396.

Ogura, Y.
1972. Comparative Anatomy of Vegetative Organs of the Pteriodphytes, 2d edition, *Encyclopedia of Plant Anatomy,* Vol. 7, part 3. Gebrüder Borntraeger, Berlin.

Phillips, T. L.
1974. Evolution of vegetative morphology in coenopterid ferns. *Ann. Missouri Bot. Garden* 61:427–461.

Stewart, W. N.
1983. *Paleobotany and the Evolution of Plants.* Cambridge University Press, Cambridge.

Surange, K. R.
1952. The morphology of *Stauropteris burntislandica* P. Bertrand and its megasporangium *Bensonites fusiformis* R. Scott. *Phil. Trans. Roy. Soc. London* 237(B):73–91.

Taylor, T. N.
1981. *Paleobotany: An Introduction to Fossil Plant Biology:* McGraw-Hill, New York.

Walker, T. G.
1979. The cytogenetics of ferns. In A. F. Dyer (ed.), *The Experimental Biology of Ferns,* pp. 87–132. Academic, London.

Wardlaw, C. W.
1952. *Phylogeny and Morphogenesis.* Macmillan, London.
1968a. *Essays on Form in Plants.* University Press, Manchester, England.
1968b. *Morphogenesis in Plants: A Contemporary Study.* Methuen, London.

Wetmore, R. H., and C. W. Wardlaw
1951. Experimental morphogenesis in vascular plants. *Ann. Rev. Plant Physiol.* 2:269–292.

White, R. A.
1963. Tracheary elements of the ferns. II. Morphology of tracheary elements; Conclusions. *Amer. Jour. Bot.* 50:514–522.
1979. Experimental investigations of fern sporophyte development. In A. F. Dyer (ed.), *The Experimental Biology of Ferns,* pp. 505–549. Academic, London.