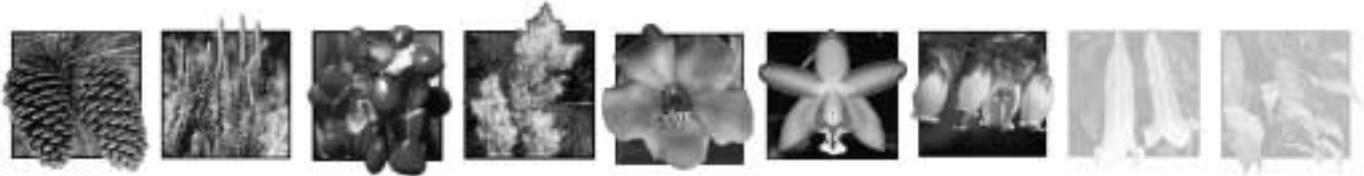


7 *An Overview of Green Plant Phylogeny*



The word *plant* is commonly used to refer to any autotrophic eukaryotic organism capable of converting light energy into chemical energy via the process of photosynthesis. More specifically, these organisms produce carbohydrates from carbon dioxide and water in the presence of chlorophyll inside of organelles called chloroplasts. Sometimes the term *plant* is extended to include autotrophic prokaryotic forms, especially the (eu)bacterial lineage known as the cyanobacteria (or blue-green algae). Many traditional botany textbooks even include the fungi, which differ dramatically in being heterotrophic eukaryotic organisms that enzymatically break down living or dead organic material and then absorb the simpler products. Fungi appear to be more closely related to animals, another lineage of heterotrophs characterized by eating other organisms and digesting them internally.

In this chapter we first briefly discuss the origin and evolution of several separately evolved plant lineages, both to acquaint you with these important branches of the tree of life and to help put the green plant lineage in broad phylogenetic perspective. We then focus attention on the evolution of green plants, emphasizing several critical transitions. Specifically, we concentrate on the origins of land plants (embryophytes), of vascular plants (tracheophytes), of

seed plants (spermatophytes), and of flowering plants (angiosperms).

Although knowledge of fossil plants is critical to a deep understanding of each of these shifts and some key fossils are mentioned, much of our discussion focuses on extant groups. In Chapter 8 you will find detailed descriptions of the major extant groups of vascular plants and of seed plants, along with much more information on the biology of these plants. Likewise, Chapter 9 focuses on the attributes of flowering plant lineages, and their phylogenetic relationships.

Our main aim is to chronicle the evolutionary events leading up to angiosperms. We therefore pay rather little attention to major branches such as the chlorophytes, the mosses, the lycophytes, and the ferns and their allies. From a phylogenetic standpoint we could just as well “tell the story” of green plant evolution as leading up to the evolution of the mosses, the horsetails, or any other group (O’Hara 1992), but we follow the path leading to angiosperms simply because they are the focus of this book.

Before we proceed, it is important comment on the taxonomic names we will use in this chapter. Our knowledge of phylogenetic relationships among the major plant lineages has long been uncertain, and this is reflected in the existence of many contrasting classification systems. Sometimes the same name has been used to refer to different groups. For example, the name Chlorophyta is sometimes applied to the entire green plant clade, and sometimes to a branch within the green plants that includes all or most of the “green algae.” In other cases different names have been used for the same group: The green plants have been called Chlorophyta by some authors and Viridiplantae by others.

To a large extent these differences reflect the attempts of different authors to assign taxonomic ranks to groups in what they believe to be an internally consistent manner. However, as we have stressed elsewhere (see Chapter 2), the assignment of taxonomic ranks is basically arbitrary, and typically it reflects only the traditions of the relevant taxonomic community. Thus, taxa assigned to a particular taxonomic rank (such as class, order, or family) are not necessarily equivalent with respect to age, species diversity, or ecological breadth.

Other problems relate to changes in our knowledge of phylogeny. Progress in discerning relationships has quite often resulted in the realization that traditionally recognized groups are not, in fact, clades. For example, the name Bryophyta has long been applied to a group that includes the liverworts, hornworts, and mosses. In recent years, however, it has become clear that these groups do not form a clade; instead, “bryophytes” refers to a grade, or paraphyletic group, at the base of the embryophytes (land plants).

As we will emphasize, the same is true of several other traditional groups, including “green algae,” “seedless vascular plants,” “gymnosperms,” and “dicotyle-

dons.” In some cases it is possible to abandon such names entirely, but in others it is tempting to retain them, either as common names for certain forms of organization (e.g., the “bryophytic” life cycle), or to refer to a clade (e.g., applying “gymnosperms” to a hypothesized clade including just the extant “naked seed plants”).

In this chapter we simply do not refer to taxonomic ranks. Elsewhere in the text, major clades within vascular plants are referred to orders and families, and we use the same names here. Likewise, standard genus and species names are used. However, whether a taxon is considered to be a class or an order by a particular author is not important in our discussion of green plant phylogeny.

Our choice of names reflects our sense of which ones are most commonly used in the literature and will therefore create the least confusion. Where possible, we have chosen names with rank-neutral endings, especially the ending *-phytes*, which means “plants.” In addition, we avoid using names that refer to non-monophyletic groups, but when we do use such names (e.g., to clarify historical usage) we put them in quotation marks.

Endosymbiotic Events

The chloroplasts found in eukaryotes are endosymbiotic organelles derived ultimately from cyanobacteria. This view of the origin of plastids is now firmly established on the basis of structural evidence (e.g., the form and number of membranes) and molecular studies establishing that the DNA in plastids is more closely related to free-living cyanobacterial DNA than it is to DNA in the nucleus of the same cell.

Endosymbiosis entailed massive reduction in the size and gene content of the plastid genome relative to free-living cyanobacteria (see Chapter 5) (Palmer and Delwiche 1998; Delwiche 1999; Palmer 2000). An average cyanobacterium has a genome size of about 3600 kilobases and some 3200 genes. By contrast, a red algal chloroplast has on the order of 190 kilobases and only about 250 genes. Green algal chloroplasts are even smaller in most cases: about 120 kilobases and 120 genes. This reduction has involved the complete loss of some genes and the transfer of others from the chloroplast to the nucleus (e.g., Baldauf and Palmer 1990). There are many more proteins active within plastids (from 500 to 5000) than there are genes, meaning that some of these are products of genes that reside outside of the chloroplast, which then need to be imported into the plastid.

How many endosymbiotic events have there been? Recent phylogenetic evidence is consistent with just a single primary endosymbiotic event. For example, a recent analysis of eukaryote phylogeny (Baldauf et al. 2000) recovered a clade containing viridophytes (green plants), rhodophytes (red algae), and glaucophytes (Figure 7.1). This result, combined with evidence on the number of membranes and other morphological charac-

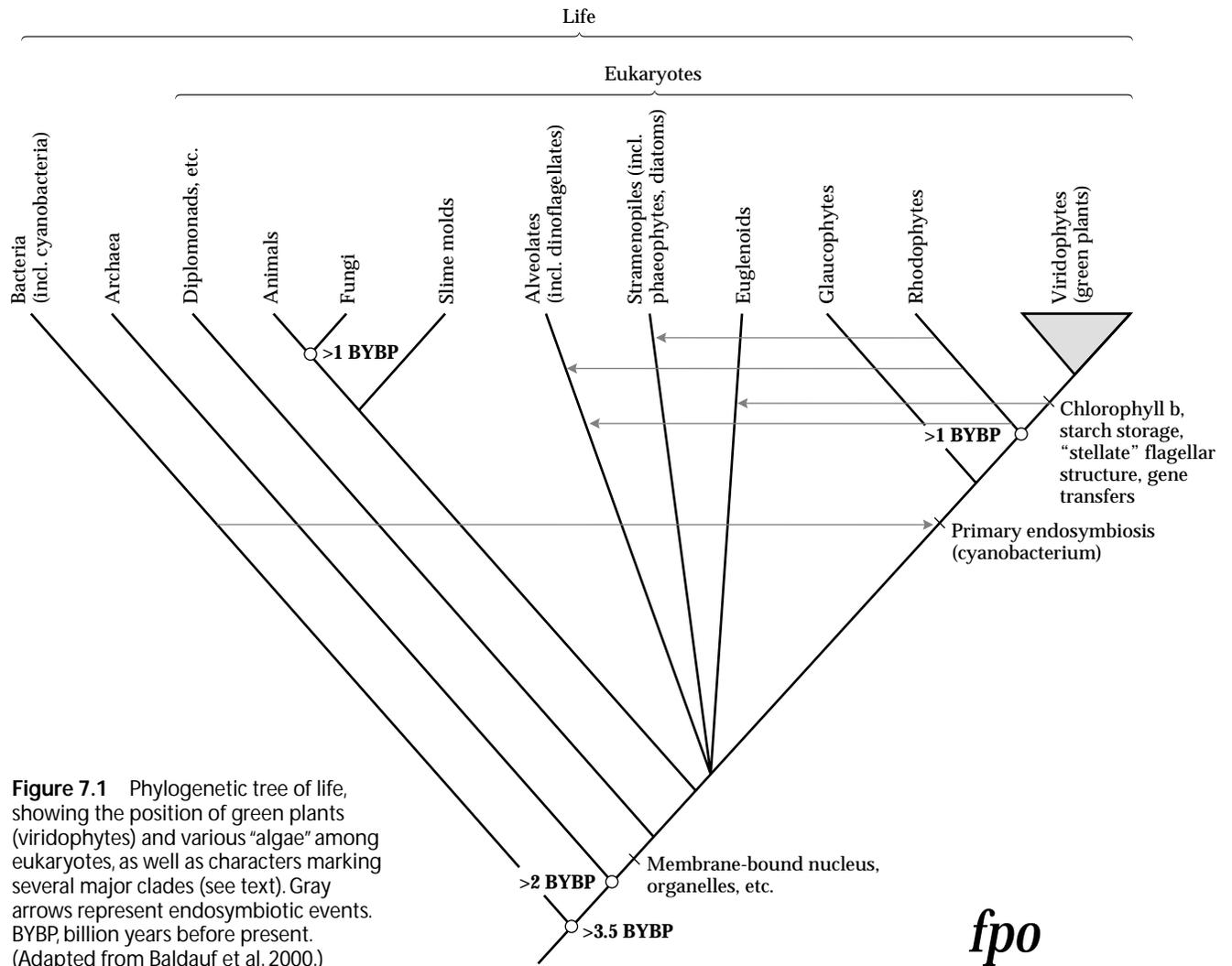


Figure 7.1 Phylogenetic tree of life, showing the position of green plants (viridophytes) and various “algae” among eukaryotes, as well as characters marking several major clades (see text). Gray arrows represent endosymbiotic events. BYBP, billion years before present. (Adapted from Baldauf et al. 2000.)

ters, suggests that a primary endosymbiotic event occurred in the common ancestor of this clade. In the glaucophytes the cyanobacterial cell wall is still present surrounding the plastid, but the wall was lost in the lineage that includes red algae and green plants.

Plastids in red algae and in green plants differ significantly from one another, which makes it possible to distinguish with considerable confidence between a red plastid lineage and a green plastid lineage (Delwiche 1999). This is important because it helps us identify situations in which plastids have been acquired by permanent incorporation of either red or green eukaryotes. It appears that red algal chloroplasts were acquired via such secondary endosymbiosis in stramenopiles (including brown algae, golden algae, and diatoms, which are discussed in the next section) and several other lineages. Endosymbiotic events involving the uptake of green algal eukaryotes appear to account for euglenas and several other groups. Dinoflagellates include a mixture of different types and may even (in one lineage) involve a tertiary symbiotic event. The origin of the remnant plastids found in apicomplexans (including *Plasmodium*, the

malaria parasite) is controversial, though recent analyses suggest a secondary endosymbiotic event involving a member of the red algal line.

Miscellaneous “Algae”

The term *algae* is applied to a wide variety of aquatic photosynthetic organisms belonging to several lineages that are not directly related to one another (see Figure 7.1). Before we provide brief descriptions of several of the major groups of “algae,” it is first important to briefly review life cycle diversity. In humans and other animals, the diploid phase of the life cycle is the **dominant phase**, and the only haploid cells are the gametes (produced by meiosis). This kind of life cycle occurs among plants but is very rare. Some plants have life cycles that are basically the opposite of ours: A multicellular haploid organism is the dominant phase and gives rise to gametes by mitosis; syngamy (fusion of gametes) yields a diploid zygote that undergoes meiosis to yield haploid spores. Most autotrophic life cycles lie somewhere in the middle of these two extremes and exhibit

what is known as **alternation of generations**—that is, alternation between a multicellular haploid phase (the gametophyte) and a multicellular diploid phase (the sporophyte).

The **red algae** (rhodophytes) include about 6000 species, most of which live in marine environments and in tropical waters (e.g., coral reefs). In addition to chlorophyll *a*, they have accessory pigments called phycobilins, which make it possible for them to live in dark waters well below the surface. A few red algae are unicellular, but most are filamentous and attach to rocks or to other algae (some are even parasites). The cells in these filaments are cytoplasmically connected to one another by distinctive pit connections. Red algae have no motile cells at any stage, and they often show exceptionally complex life cycles in which there may be two morphologically and ecologically distinct diploid phases. As noted already, red algae may be the sister group of the green plants.

The brown algae, diatoms, and some other groups of algae, along with the water molds (Oomycetes), make up the **stramenopiles** (see Figure 7.1). This clade is characterized by reproductive cells with two different kinds of flagellae—a smooth “whiplash” flagellum, and a “tinsel” flagellum with numerous fine hairs along its length.

The **brown algae** (phaeophytes) form a clade of some 2000 described species of mostly marine organisms, many of which are conspicuous in cooler regions. In addition to chlorophylls *a* and *c*, they have carotenoid pigments that account for the brown color. All brown algae are multicellular, but this condition presumably evolved within stramenopiles from a unicellular condition. Many brown algae are filamentous, but some are very large and show complex differentiation of the body into a holdfast, a stipe, a float, and one or more flat blades. Some of the larger forms show considerable anatomical differentiation, and some cells are even specialized for nutrient transport. Brown algal life cycles run the gamut from alternation between similar looking diploid and haploid phases to extreme differentiation (usually with a dominant diploid phase). In *Fucus* and some related kelp-like organisms, the multicellular haploid phase has been eliminated completely; in such cases the products of meiosis function directly as gametes, as they do in animal life cycles.

There are about 6000 living species of **diatoms** (bacillariophytes), and many more (perhaps as many as 40,000) that are known only as fossils. Diatoms are unicellular organisms (though sometimes they form loose filaments or clusters) found in both marine and freshwater environments. Like the closely related brown algae, diatoms produce chlorophylls *a* and *c* and carotenoids. Their most distinctive feature is the formation of cell walls made of two often elaborately sculptured silicon valves that together form a tiny box. Flagellae are lacking, except in some male gametes.

The dinoflagellates, ciliates, and apicomplexans form the **alveolates** (see Figure 7.1), a group characterized by

small membrane-bound cavities (alveoli) under their cell surfaces. **Dinoflagellates** include about 3000 described species, found in both freshwater and salt water. They have two flagellae located in characteristic grooves between cellulose plates embedded in the cell walls, which together make the cell spin as it moves. Many dinoflagellates are symbiotic with other organisms, including corals, sponges, squids, and giant clams. The symbiotic forms typically lack cellulose plates and are referred to as zooxanthellae. These organisms are of great ecological importance in maintaining coral reefs; for example, the phenomenon known as coral “bleaching” involves the death of the zooxanthellae. Dinoflagellates are also responsible for periodic “red tides” or “algal blooms” that can have dramatic negative impacts owing to the production of highly toxic substances.

Viridophytes (Green Plants)

As shown in **Figure 7.2**, the traditional “green algae” are related to the land plants, and together these constitute a clade called the **green plants** (Viridiplantae, or what we will call viridophytes). This clade includes more than 300,000 described species, or over one-sixth of all known extant species on Earth. Molecular evidence strongly supports the monophyly of green plants, including DNA sequence data (from the nucleus and the organelles) and structural features (such as the transfer of particular genes from the chloroplast to the nucleus). This clade is also supported by numerous chemical and morphological features, including probably the loss of phycobilins (found in cyanobacteria and red algae) and the production of chlorophyll *b* (in addition to chlorophyll *a*). Green plants also store carbohydrates in the form of starch granules in their cells, and their motile cells have a characteristic stellate structure at the base of each of the usually two anterior whiplash flagellae.

It now appears that several lineages of unicellular organisms with distinctive scaly cell walls (so-called micromonads, or prasinophytes) are situated around the base of the green plant phylogeny. However, the most comprehensive analyses to date (Karol et al. 2001) support a basal split of green plants into a **chlorophyte** clade, containing most of the traditional “green algae,” and a **streptophyte** clade, which includes the land plants and several other lineages formerly placed in “green algae” (see Figure 7.2). In these recent studies one of the micromonads, *Mesostigma*, appears to be the sister group of the rest of the streptophyte line.

CHLOROPHYTES

Within the chlorophytes are several well-supported clades (see Figure 7.2): Chlorophyceae, Ulvophyceae, and Trebouxiophyceae (McCourt 1995; Chapman et al. 1998).

The **Chlorophyceae** are marked by somewhat obscure ultrastructural features (such as clockwise rotation of the

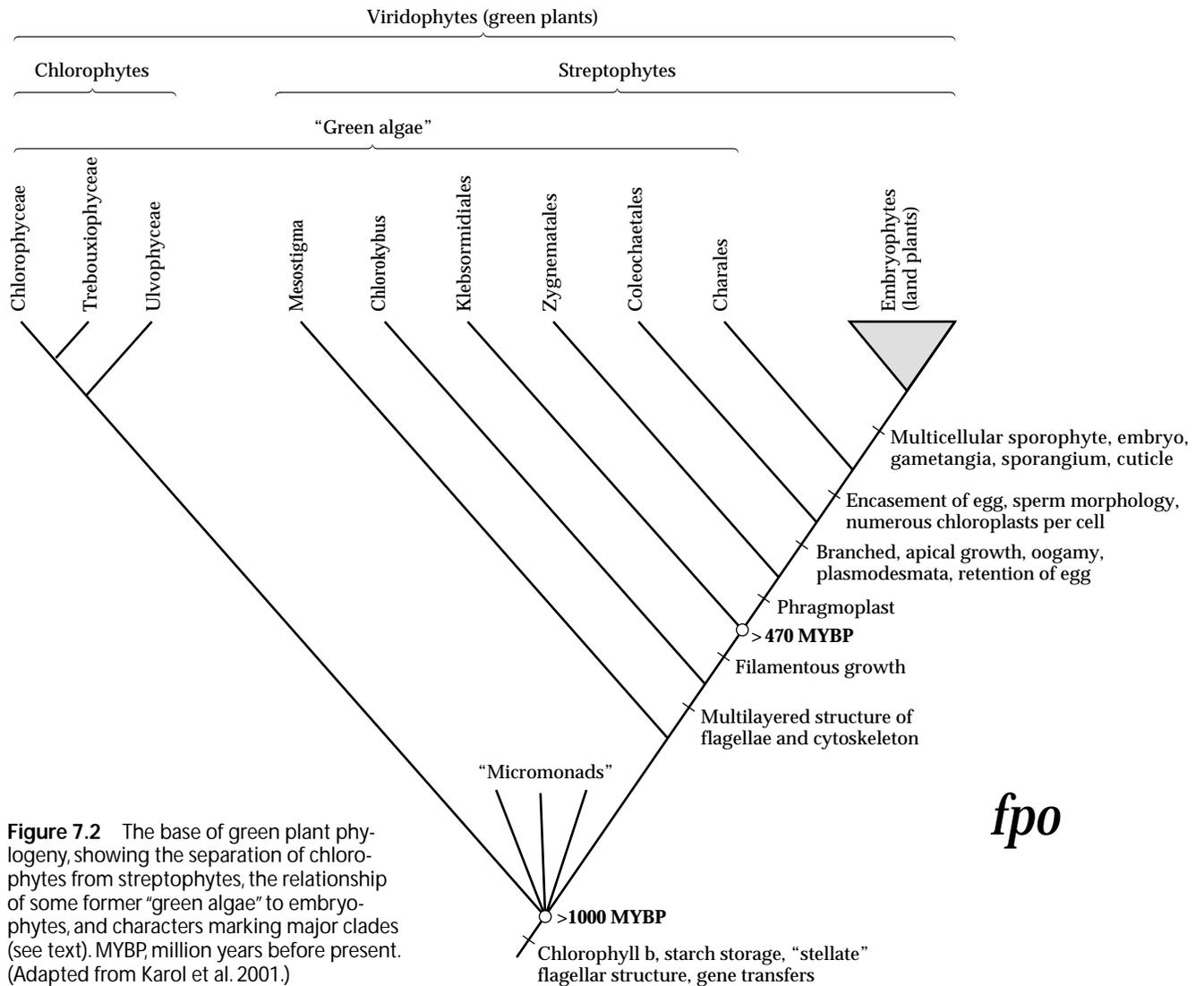


Figure 7.2 The base of green plant phylogeny, showing the separation of chlorophytes from streptophytes, the relationship of some former "green algae" to embryophytes, and characters marking major clades (see text). MYBP, million years before present. (Adapted from Karol et al. 2001.)

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basal bodies), but they have been supported as a clade in most molecular studies as well. Included within this line is the so-called volvocine lineage, within which progressively more complex colonies (from 4 cells in *Gonium* to as many as 500–50,000 cells in the hollow spherical colonies of *Volvox*) were presumed to have been derived from unicells not unlike the model organism *Chlamydomonas* (Figure 7.3A, B). Recent studies indicate that the story is more complex, with several colonial lines derived independently, perhaps from within *Chlamydomonas* itself, which has hundreds of species (Larsen et al. 1991; Buchheim et al. 1994; Chapman et al. 1998).

The **Ulvophyceae** include many marine forms and is marked by the production of multinucleate cells (Figure 7.3D–F). In some, the entire body is a coenocytic thallus, lacking walls between the nuclei except in the case of reproductive cells. Included in this group is the model organism *Acetabularia* (Figure 7.3F).

Finally, the **Trebouxiophyceae** contain forms with flagellate spores, but most are small round forms (appar-

ently derived several times independently) that completely lack motile cells at any stage. Many of the non-motile forms live in terrestrial habitats, often in association with lichen-forming fungi or invertebrate animals. Lichen associations appear to have originated and to have been lost multiple times (Lutzoni et al. 2001).

STREPTOPHYTES

The discovery of the streptophyte lineage began in the late 1960s, when detailed ultrastructural studies of cell division first revealed a major difference in the orientation of the spindle microtubules among the organisms that had traditionally been classified as "green algae" (Pickett-Heaps 1979; Mattox and Stewart 1984; McCourt 1995). Some of these were found to have the phragmoplast orientation found in all land plants, in which the spindle is oriented perpendicular to the formation of the cell wall. A thorough survey showed that the phragmoplast condition occurred in the so-called charophycean algae (Coleochaetales and Charales). These plants show

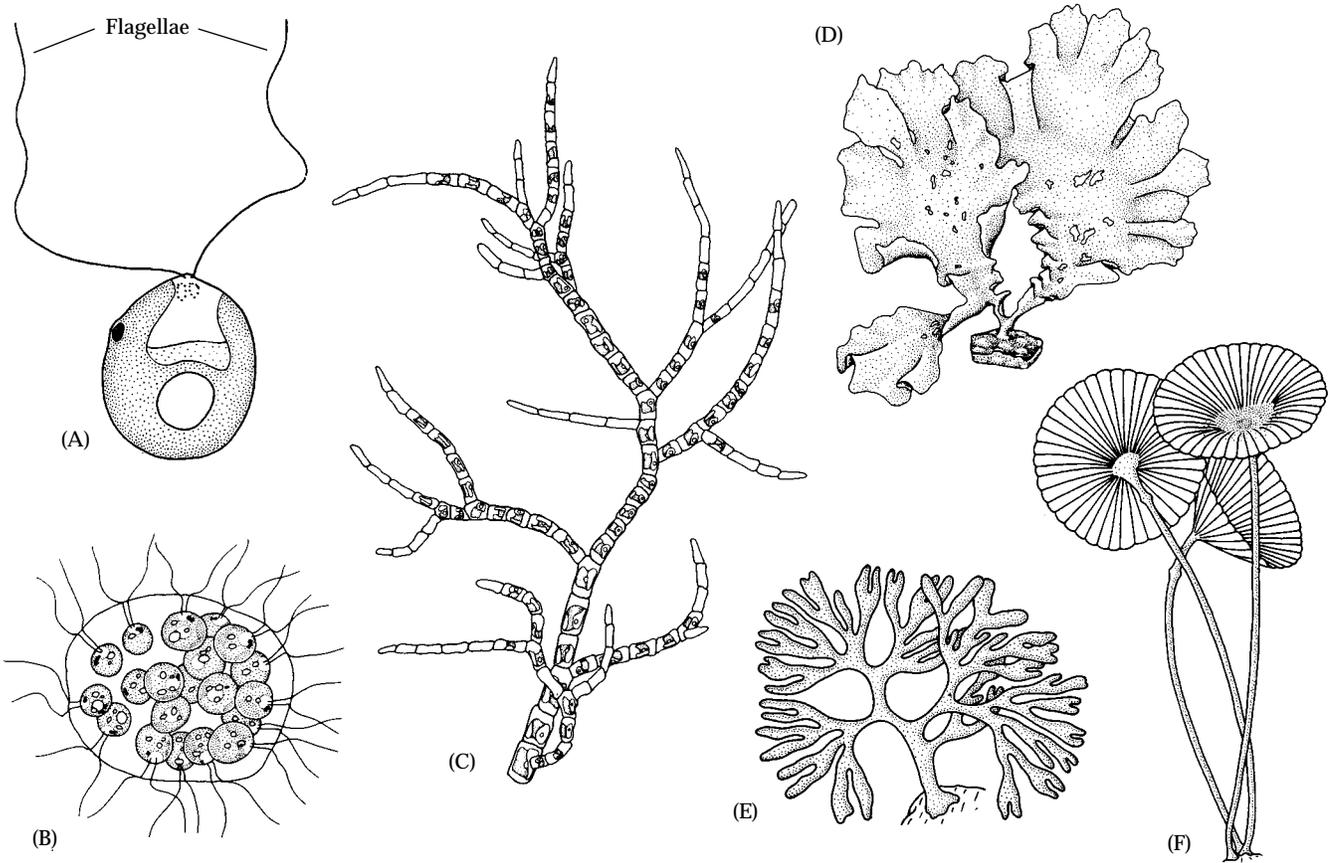


Figure 7.3 Morphology of chlorophytes. (A–C) Chlorophyceae: (A) *Chlamydomonas*, showing flagellae (f); (B) *Eudorina*, a colonial “volvocine” form; (C) *Stigeoclonium*, a branched filamentous form. (D–F) Ulvophyceae: (A) *Ulva*; (B) *Codium*, showing a coenocytic diploid thallus; (C) *Acetabularia*. (From Scagel et al. 1969.)

a range of different life forms (including upright, branching forms, as in *Chara* and *Nitella*, and flattened forms, as in *Coleochaete*) and live in near-shore, freshwater habitats (Figure 7.4A–C). As these organisms were studied in more detail, the idea emerged that they were actually more closely related to land plants than they were to other “green algae.” It has since become clear that several other former green algal lineages belong in the streptophyte clade, including Klebsormidiales and Zygnematales (McCourt 1995; Chapman et al. 1998). Of these, the Zygnematales may be familiar as the group that includes *Spirogyra* and its relatives (Figure 7.4D–E). These are the so-called conjugating “green algae,” in reference to a form of sexual reproduction that involves the formation of a tubular connection between cells of adjacent filaments, passage of the protoplast from one cell to another, and the eventual fusion of nuclei to form a zygote.

The relationships among the streptophyte groups shown in Figure 7.2 have been confirmed by molecular studies (Karol et al. 2001), including some structural

molecular data. For example, the protein elongation factor *tufA* appears to have moved from the chloroplast to the nucleus in the ancestor of the “charophyte” lineages and the land plants (Baldauf and Palmer 1990). Coleochaetales and Charales possess some functionally important traits that are found otherwise only in land plants, such as flavonoids and the chemical precursors of cuticle. Most important from the standpoint of the evolution of the land plant life cycle is the fact that they retain the egg and sometimes even the zygote (after fertilization) on the body of the haploid plant (Graham 1993).

These phylogenetic results have many important implications for our understanding of green plant evolution. For instance, they imply that there were several independent originations of multicellularity. As we have noted, the volvocine forms explored a lifestyle in which the cells became aggregated into colonies. The larger of these colonies also show cytoplasmic interconnections and a division of labor, with some cells specialized for reproduction. Other chlorophytes formed filaments or membranous parenchymatous bodies of much larger size (such as the sea lettuce, *Ulva*, and its relatives), which show a more complex morphological integration and differentiation of cell functions. The Ulvophyceae followed a separate path involving multinucleate cells, sometimes forming filaments, and sometimes (as in

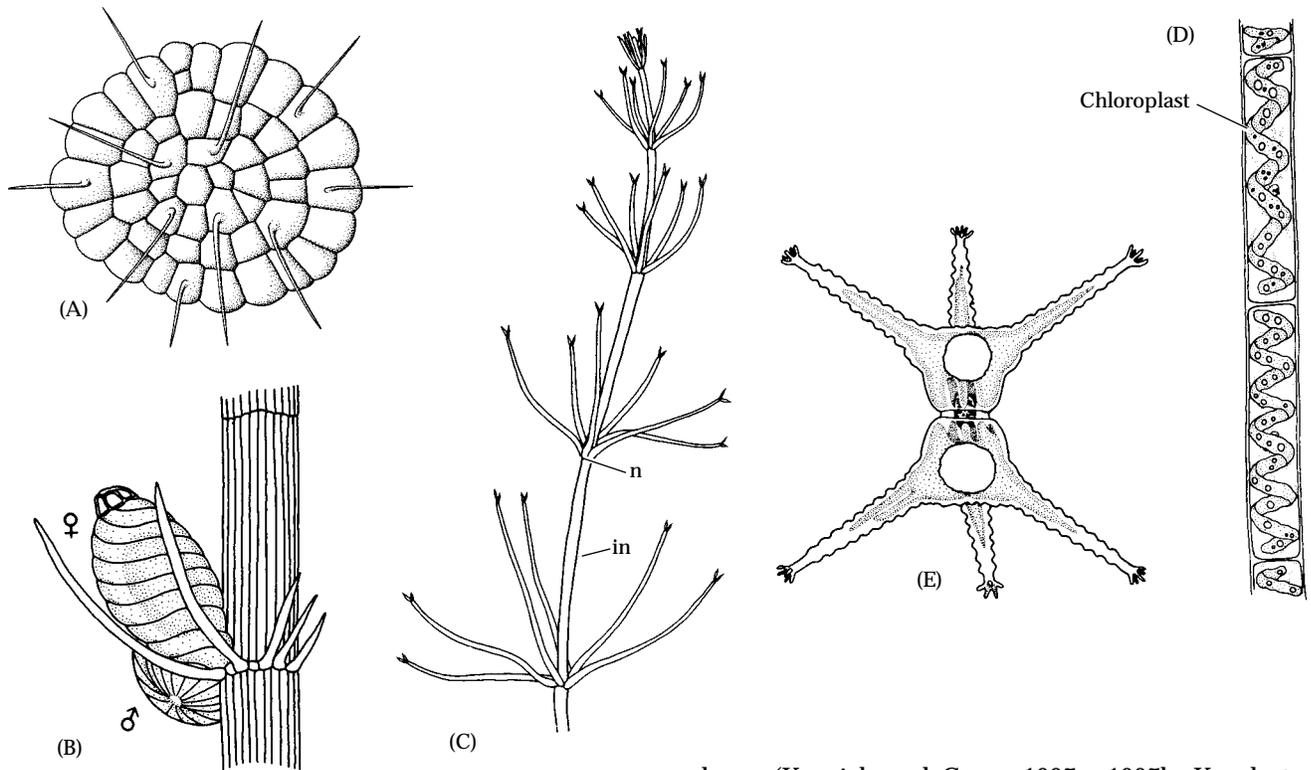


Figure 7.4 Morphology of basal streptophytes. (A) Coleochaete, showing a haploid discoidal thallus, with setae. (B, C) Charales: (B) *Chara*, showing a node with an egg-bearing structure (above) and a sperm-producing structure (below). (C) *Nitella* habit, showing node (n) and internode (in) construction. (D, E) Zygnematales: (D) *Spirogyra*, a filamentous form, showing helical chloroplasts (ch). (E) *Staurastrum*, a unicellular desmid, forming two mirror-image semicells. (A from Taylor and Taylor 1993; B–E from Scagel et al. 1969.)

Codium) forming a thallus by densely intertwining the filaments. Finally, multicellularity evolved separately in the streptophyte line. Many Zygnematales are filamentous, and parenchymatous forms (with plasmodesmata connecting adjacent cells) are found in the two charophyte lineages and the land plants.

Among the early-diverging lineages of green plants, we also encounter a wide variety of life cycles. Alternation of similar haploid gametophyte and diploid sporophyte generations (as in *Ulva*) is quite common. In contrast, *Codium* (Ulvophyceae) evolved a life cycle like that of humans, in which gametes are the only haploid cells. In stark contrast, in charophytes the plants are haploid, and the only diploid cell in the life cycle is the zygote, which results from fertilization of a large nonmotile egg by a swimming sperm (oogamy).

Embryophytes (Land Plants)

The land plants are depicted as stemming from a single common ancestor in Figure 7.2, a finding that is strongly supported by both molecular and morphological evi-

dence (Kenrick and Crane 1997a, 1997b; Karol et al. 2001). Land plants are also called embryophytes because they have a resting embryo stage early in the life of the sporophyte. *Embryophyte* is the preferable term in this case because several algal lineages have independently (though less conspicuously) also made the transition to life on land (e.g., in Trebouxiophyceae). In addition to the embryo, embryophytes are characterized by production of a multicellular sporophyte, multicellular reproductive structures (antheridia, archegonia, and sporangia), cuticle, and thick-walled spores with characteristic trilete marks (see Figure 7.7C).

Traditionally, embryophytes have been classified as either bryophytes or vascular plants. There are three major lineages of bryophytes—mosses, hornworts, and liverworts—which we will characterize briefly in the next few paragraphs (see also Shaw and Goffinet 2000). As we shall discuss, however, it has become increasingly clear that “bryophytes” are paraphyletic with respect to vascular plants (see Figure 7.6).

MOSSES

Mosses are probably the most familiar bryophytic plants and, with some 15,000 species, they are also the most diverse. The upright and leafy gametophyte is the dominant phase in the moss life cycle (Figure 7.5A–C). The sporophyte forms a single unbranched stalk terminated by a sporangium (or capsule). Haploid spores, produced via meiosis, are released from the sporangium; typically, dehiscence of the sporangium occurs by the detachment of a lid or operculum.

When a spore germinates, it forms a protonemal stage, which resembles a green algal filament. The pro-

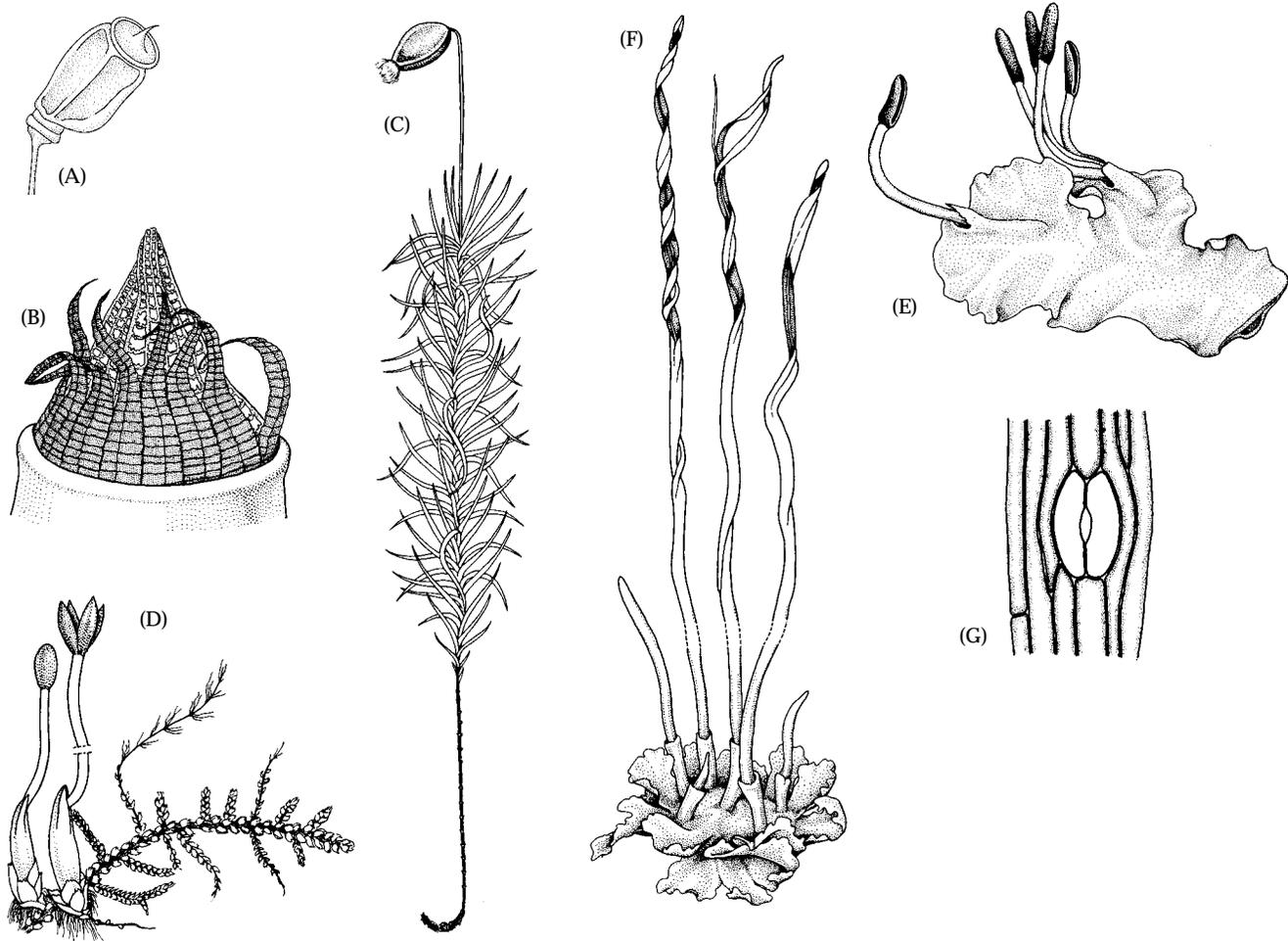


Figure 7.5 Morphology of “bryophytes.” (A–C) Mosses: (A) *Dawsonia superba* habit, showing leafy gametophyte and unbranched sporophyte with terminal sporangium; (B) sporangium (capsule) of a moss prior to dehiscence; (C) apex of the dehiscing sporangium of a moss, *Fontinalis antipyretica*, showing the peristome teeth. (D, E) Liverworts: (D) A leafy liverwort, *Lepidozia reptans*, showing dehiscence of the sporangium by four valves; (E) portion of a thalloid liverwort, *Monoclea forsteri*, showing sporangia with longitudinal dehiscence. (F, G) Hornworts: (F) *Phaeoceros laevis* habit, showing the thalloid gametophyte and dehiscing sporangia of the sporophyte; (G) stomate, with guard cells, from the sporangium wall of *Anthoceros*. (A from Barnes 1998; B–G from Scagel et al. 1969.)

tonema produces one or more upright leafy gametophytes, which ultimately produce sperm and eggs in antheridia and archegonia, respectively. Fusion of the gametes yields the zygote, which develops through a series of mitotic divisions into the embryo and eventually into the mature sporophyte.

Analyses of relationships within mosses have generally supported the idea that *Sphagnum* (peat moss) is situated near the base of the tree and that *Andreaea* and a few close relatives also form an early branch (see Kenrick and Crane 1997a). The enigmatic *Takakia*, which was considered to be a liverwort until the recent discovery of the sporophyte phase, is also probably situated near the

base of the moss tree. The sporangium in *Andreaea* opens by four vertical slits, and in *Takakia* by a single helical slit, as opposed to the lid-like operculum found in the vast majority of mosses. The operculum of most mosses is also characterized by a distinctive row of tooth-like structures, which together make up the peristome.

LIVERWORTS

There are about 9000 species of **liverworts**, which come in a thalloid form or, more commonly, a leafy form (Figure 7.5D,E). Unlike mosses and hornworts, liverworts lack stomates, although some have epidermal pores without true guard cells. They also lack a characteristic columnar mass of sterile tissue (the columella) in the sporangium, which is present in mosses, hornworts, and early vascular plant lineages.

These liverwort features have sometimes been interpreted as ancestral within land plants, but this is no longer clear. Sex in liverworts involves the production of sperm-producing antheridia and egg-containing archegonia. The sporophyte phase, with its terminal sporangium, is rather small and inconspicuous. The capsule typically opens through four valves, and sterile hygroscopic cells (elaters) among the spores may aid in dispersal.

HORNWORTS

There are only about 100 species of **hornworts** (Figure 7.5A,B), which are encountered much more rarely than either mosses or liverworts. One presumably derived feature of this entirely thalloid group is the presence of an intercalary meristem in the sporophyte located at the base of the capsule. The activity of this meristem accounts for the continued upward growth of the capsule, which is quite extensive in some groups (e.g., *Anthoceros*).

PHYLOGENETIC RELATIONSHIPS OF EMBRYOPHYTES

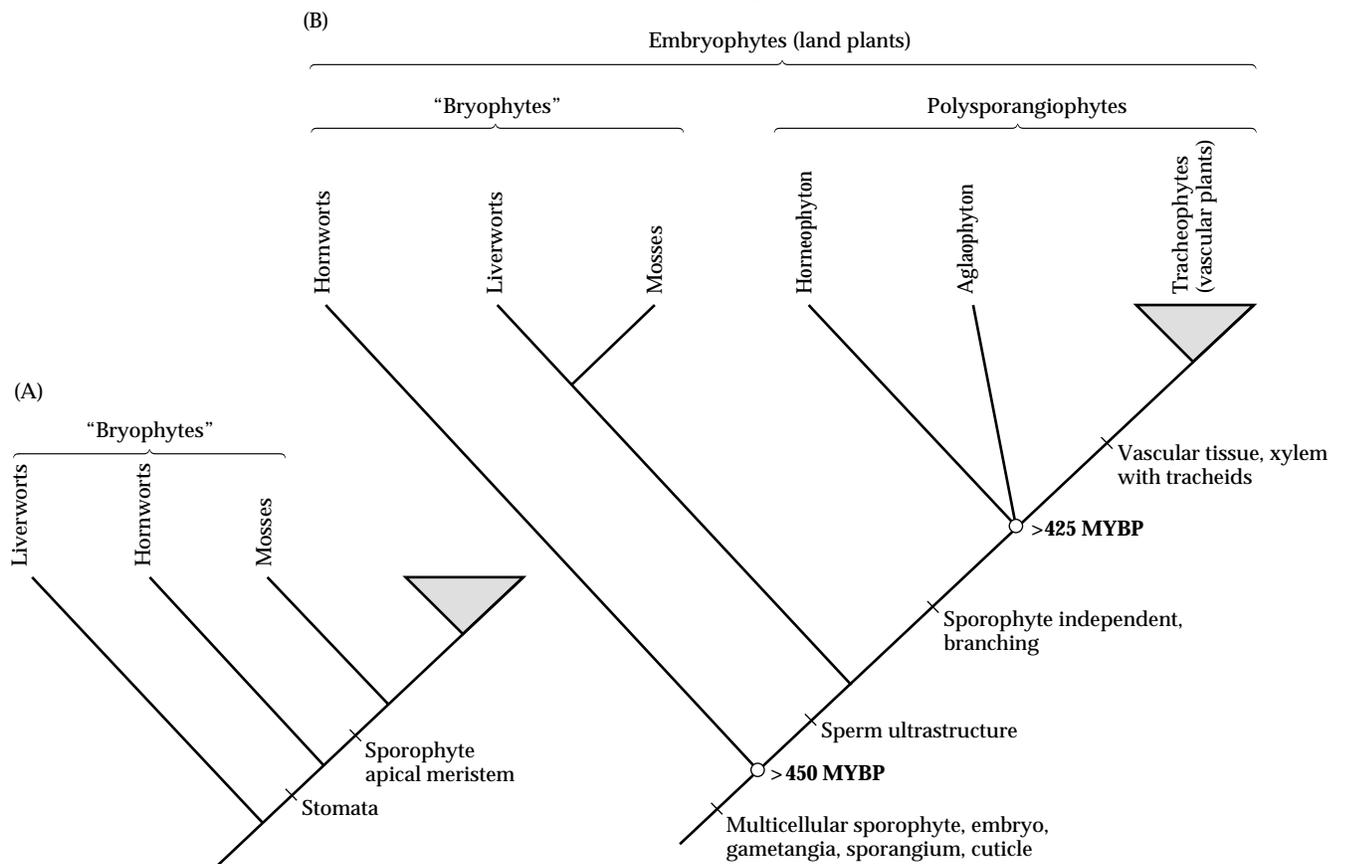
All recent phylogenetic analyses of land plants have concluded that “bryophytes” are paraphyletic. However, the exact relationships are still controversial (Figure 7.6). Initially, morphological analyses supported a basal split between the liverwort lineage and everything else, and placed the mosses as the sister group to the vascular plants (Mishler and Churchill 1984, 1985). Under this view, stomates are considered to be an innovation linking hornworts, mosses, and vascular plants, to the exclusion of liverworts. Likewise, specialized cells in the stems of mosses (in both the gametophyte and sporophyte of some species), called hydroids and leptoids, have been interpreted as precursors of the water- and nutrient-conducting cells found in vascular plants. Mosses and vascular plants have sporophytes that

increase in height through cell divisions in an apical meristem, and the first vascular plants also had upright gametophytes, as do mosses. These interpretations have been upheld by some molecular studies, including an analysis showing the gain of three mitochondrial introns in all land plants except liverworts (Qiu et al. 1998).

Several recent studies of molecular data, however—alone and in combination with a variety of morphological and ultrastructural characters (especially sperm ultrastructure)—support an alternative hypothesis (Figure 7.6B). In these trees, hornworts are the sister group of all other extant land plants, and a clade containing mosses and liverworts is the sister group of the vascular plants (Nickrent et al. 2000; Renzaglia et al. 2000).

This hypothesis is consistent with detailed studies indicating that the hydroids and leptoids in mosses probably are not homologous with tracheids in the xylem and sieve cells in the phloem of vascular plants (Ligrone et al. 2000). However, such relationships would imply either the loss or the independent evolution of stomates and apical meristems. Although this issue remains

Figure 7.6 Phylogenetic relationships at the base of the embryophytes (land plants), showing characters that mark major clades under two hypotheses of how the “bryophyte” groups (hornworts, liverworts, and mosses) are related to vascular plants (see text). MYBP, million years before present. (A adapted from Mishler and Churchill 1984; B adapted from Nickrent et al. 2000 and Renzaglia et al. 2000.)



unsettled, note that all recent analyses support the view that “bryophytes” are paraphyletic with respect to vascular plants.

TRANSITION TO LAND

This phylogenetic knowledge illuminates the origin of several key adaptations to life on land (Graham 1993). Cuticle and sporopollenin (present in the thick spore wall) appear to be responses to desiccation. Gas exchange is facilitated by small pores in the epidermis or by genuine stomates with guard cells that can open or close the stomate depending on environmental conditions, thereby regulating water loss. Flavonoids help absorb damaging long-wavelength UV radiation. A glycolate oxidase system helps ameliorate the fact that carbon dioxide fixation is inhibited in the presence of oxygen, which is in much higher concentrations in the air than in water. The first land plants probably depended on symbiotic relationships with fungi to obtain nutrients from the soil, and such relationships have been documented in the major bryophytic lineages, as well as in vascular plants (where they are ubiquitous). The precursors of many of these adaptations can be found among the closely related *Coleochaetales* and *Charales*, and these plants therefore appear to have been preadapted to make the transition to land (Delwiche et al. 1989; Graham et al. 1991; Graham 1993).

Appreciation that both the traditional “green algae” and the “bryophytes” are paraphyletic has also helped us understand the origin of the characteristic land plant life cycle, involving an alternation of multicellular gametophyte and sporophyte phases (Mishler and Churchill 1985; Graham 1993). As noted earlier, in *Coleochaete* and *Chara* the egg is retained on the haploid parent plant. In *Coleochaete* the zygote (the only diploid stage) also remains on the parent plant until it undergoes meiosis to give rise to haploid spores. A key innovation in the line that includes the charophyte lineages and the embryophytes was the establishment of nutrient transport between haploid and diploid phases through a placental transfer tissue (Graham and Wilcox 2000). The land plant life cycle was probably derived from a charophyte-like ancestral condition by simple delay of meiosis and interpolation of a multicellular diploid phase via a series of mitotic divisions of the zygote.

In the embryophytes, the egg—and after fertilization, the embryo—is protected by a multicellular structure called an **archegonium** (plural *archegonia*). Sperm are produced and protected by a multicellular structure called an **antheridium** (plural *antheridia*). Initially, the gametophyte phase was dominant, as it is today in hornworts, liverworts, and mosses, and the sporophyte remained attached to, and was nutritionally dependent on, the gametophyte. In vascular plants, the sporophyte became dominant and nutritionally independent, and there was progressive reduction in gametophyte size (Kenrick and Crane 1997a, 1997b).

These findings also help us interpret the absolute timing of events (see Figures 7.1, 7.2, and 7.6). Green plants may be a billion or more years old, and it is possible that some major green plant lineages existed in the Precambrian (Heckman et al. 2001). From the Cambrian (about 550 million years ago), a variety of chlorophyte fossils have been found, including well-preserved lime-secreting *Ulvophyceae*, such as relatives of *Acetabularia*. Charophytes (in the form of calcified *Charales*) do not appear in the fossil record until the mid-Silurian, but the wholesale occupation of land by green plants probably took place beginning in the mid-Ordovician, about 450 million years ago. Starting at that time (and possibly even earlier, in the Cambrian), dispersed spores are found, sometimes in envelope-enclosed tetrads or diads (sets of four or two, respectively) resembling those seen today in some liverworts. Tiny bits of cuticle and tubular structures of plant origin also appear in the Ordovician, and individual spores with the characteristic trilete marks of land plants (see Figure 7.7C) have been recovered from the early Silurian.

It is probable, therefore, that hornworts, liverworts, mosses, and vascular plants were all in existence by the late Ordovician. Somewhat later, beginning in the mid-Silurian, there are well-preserved macrofossils representing the vascular plant lineage. The occupation of land was certainly in full swing by then.

Tracheophytes (Vascular Plants)

All indications are that the first land plants were small and very simple in structure. In the case of the vascular plant lineage, the sporophyte was basically a dichotomously branching stem, about the height of a matchstick at first, with the sporangia (the site of meiosis yielding haploid spores) produced at the tips of the branches (Figure 7.7A). These plants had no leaves or roots. In some cases (e.g., *Rhynia*, from the Rhynie chert in Scotland), the preservation of these plants is spectacular, and it is possible to discern many anatomical details, including stomates, spores, and the vascular tissue inside the stem.

On the basis of such fossils, it was recently discovered that the first **polysporangiophytes**—plants with branching sporophytes—did not actually produce bona fide water-conducting cells (**tracheids**) in the xylem tissue and must therefore have depended on turgor pressure to remain upright. True water-conducting cells evolved somewhat later and characterize a clade known as the true vascular plants, or the **tracheophytes** (Kenrick and Crane 1997a, 1997b).

Tracheids are elongate cells with thickened walls that are dead at maturity. Where one tracheid connects to the next, there are characteristic openings or pits, but a pit membrane (primary cell wall) remains intact, and water must pass through it as it moves from one cell to the next. In the first tracheophytes (represented by *Rhynia*),

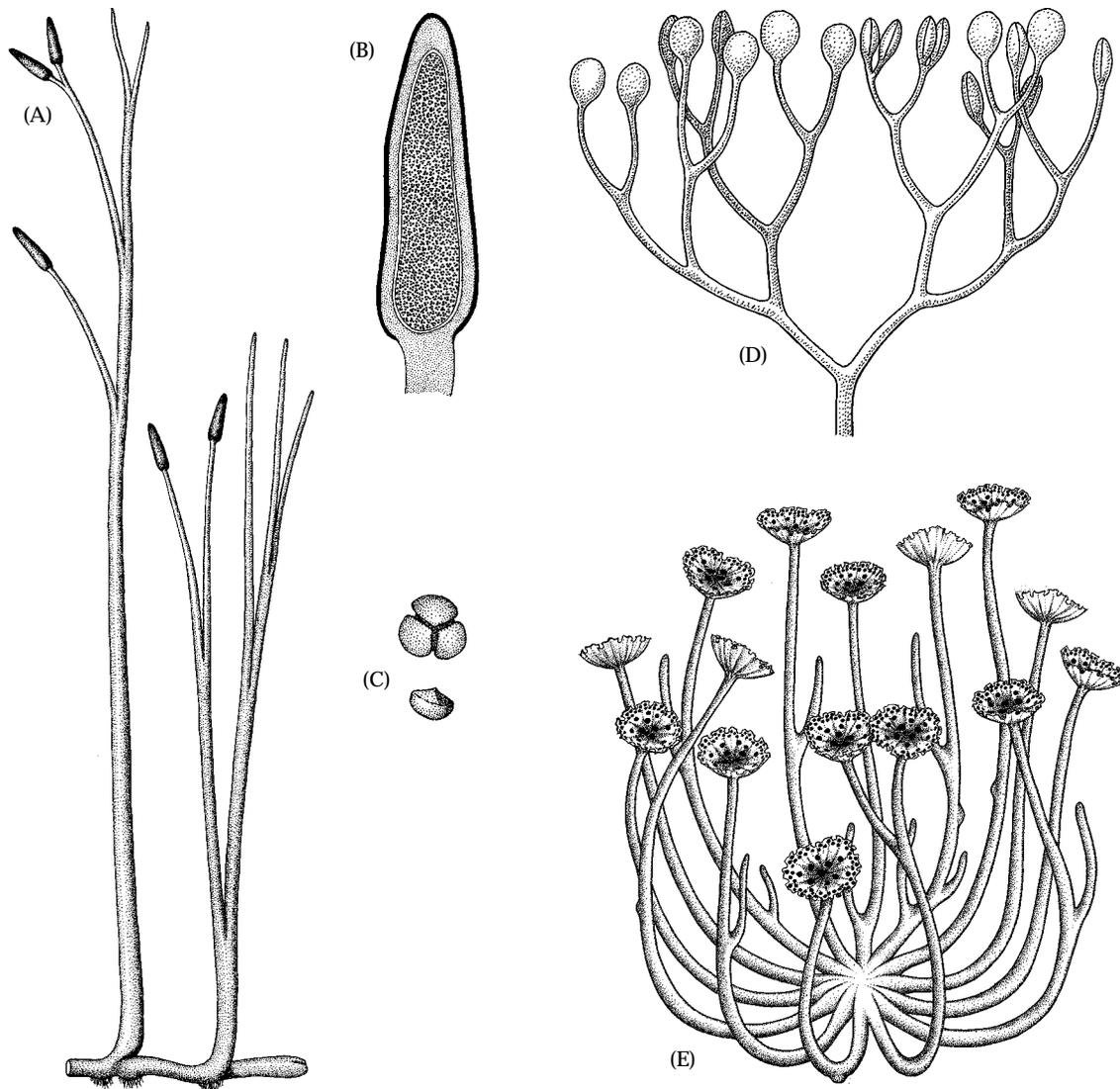


Figure 7.7 Fossils of early tracheophytes (vascular plants). (A) Reconstruction of *Rhynia major*, showing the dichotomously branching stem (without leaves or roots) and terminal sporangia. (B) Enlarged terminal sporangium of *R. major*, with spores inside. (C) *R. major* spores in tetrad, and a single thick-walled spore with the trilete mark characteristic of land plants. (D) Reconstruction of *Uskiella spargens*, showing the dichotomously branched stem and terminal sporangia with distal dehiscence. (E) Reconstruction of a Devonian gametophyte, *Sciadophyton* sp.; gametangia are present on the terminal disk-shaped structures. (A–C from Stewart 1983; D and E from Kenrick and Crane 1997a.)

In recent years, careful paleobotanical studies have revealed that some early land plant fossils are actually haploid gametophytes, bearing antheridia and archegonia (Remy 1982; Remy et al. 1993). These fossils are remarkable because they are rather large, upright, and branched, and in general they resemble the sporophyte phase of the life cycle (see Figure 7.7E). This finding has led to the view that the first members of the vascular plant lineage exhibited alternation of more or less similar generations. Thus, in relation to the bryophytic groups, it seems that both the gametophyte and the sporophyte phases were elaborated.

This knowledge allows us to piece together a sequence of events leading to the life cycle that we see in vascular plants today. This life cycle includes a dramatic reduction in the gametophyte phase and an equally impressive elaboration of the sporophyte phase. In the first vascular plants, the gametophyte was nutritionally independent of the sporophyte, and this condition is retained today in the “free-spore” lineages such as ferns

the tracheids were of a distinctive type, in which decay resistance (conferred by lignification of cellulose fibers) was present only as a very thin layer. Cell walls that are much more decay-resistant characterize a eutracheophyte clade, which includes all extant vascular plants (Kenrick and Crane 1997a). In these species, the strongly lignified tracheids allow more efficient water conduction and provide internal support, allowing the plants to grow much taller.

ence of multiflagellate sperm in the euphyllophytes, as opposed to biflagellate sperm in the bryophytic lineages and in lycophytes (except in *Isoetes* and *Phylloglossum*, where multiflagellate sperm evolved independently). One compelling bit of molecular evidence is the presence in the euphyllophytes of a 30-kilobase inversion in the chloroplast DNA (Raubeson and Jansen 1992); lycophytes and the bryophytic plants lack this inversion.

LYCOPHYTES

The **lycophyte** lineage (see Figures 7.8 and 7.9; see also Figures 8.2 and 8.3) appeared in the fossil record very soon after the first appearance of vascular plants and is marked by the lateral position, reniform shape, and transverse dehiscence of the sporangia. Small, microphyllous leaves with a single vascular strand evolved within this lineage (possibly through modification of lateral sporangia), as did distinctive dichotomously branching roots. During the Carboniferous period lycophytes were especially diverse and abundant, and the remains of these plants account for our major coal deposits. In particular, they dominated coastal swamps of tropical lowlands (DiMichele and Skog 1992; Bateman et al. 1998).

Some lycophytes became large trees, with secondary growth allowing an increase in girth (Figure 7.9). The stems of these plants were covered by leaves, which left the distinctive leaf bases seen in fossils. These plants also evolved so-called stigmarian root systems; these are presumed to have been derived from rhizomes, in which case the spirally arranged rootlets may be modified leaves. Patterns of growth in these large plants are still poorly understood (Bateman 1994; Bateman et al. 1998), but they may have grown very slowly in height at first (while the root system became established) and later elongated rapidly. They may have died after simultaneously producing strobili at the tips of all the branches.

Today there are over 1200 species of lycophytes, belonging to several major lines (see Figures 7.8 and 7.9). Of these, rhizomatous species of *Huperzia*, *Lycopodiella*, and *Lycopodium* (club mosses) are commonly encountered in forests of the Northern Hemisphere. These plants and their tropical relatives are homosporous, meaning that they produce just a single kind of spore, which gives rise to a bisexual gametophyte, producing both sperm and eggs.

The other living lycophytes (*Selaginella*, *Isoetes*) are heterosporous, producing microspores, which give rise to male gametophytes, and megaspores, which give rise to female gametophytes. The heterosporous taxa form a clade, which is also united by the association of a leaf-like flap of tissue, the ligule, with the adaxial side of the leaf base.

Selaginella (spike mosses) (see Figure 7.9F–I), with over 700 species, is most diverse in the tropics, where many species grow as epiphytes. *Isoetes* (quillworts, with perhaps 150 species) is the only living remnant of the

clade that included the giant lycopods of the Carboniferous, though it may have been derived from plants in this lineage that never attained the size of *Lepidodendron* (see Figure 7.9D) and the other very large lycophte trees. *Isoetes* has retained the cambium and some secondary growth, and it has rootlets that resemble those of the extinct trees (see Figure 7.9J).

EUPHYLLOPHYTES

An advance of the **euphyllophytes** (see Figure 7.8) was differentiation between a main axis and side branches (pseudomonopodial growth), an arrangement found in a variety of Devonian fossils known as trimerophytes (Figure 7.10A). According to the “telome theory” (Zimmermann 1952, 1965), large megaphyllous leaves characteristic of the euphyllophytes were derived from flattened lateral branch systems. This derivation involved planation of the branch system and then webbing to form the leaf blade. It seems clear that leaves evolved independently, and by very different pathways, in the lycophyte line versus the euphyllophyte line.

Living euphyllophytes appear to belong to two major clades (see Figure 7.8): the seed plants (spermatophytes) and a clade that includes several “fern” lineages, the horsetails (equisetophytes), and the whisk ferns (the monilophytes; Moniliformopses of Kenrick and Crane 1997a). This new view of relationships is well supported in combined analyses of morphological characters and both chloroplast and nuclear genes (Pryer et al. 2001). Within the **monilophytes** (ferns and their allies), there are five major lineages, each discussed briefly here: (1) leptosporangiate ferns (Polypodiales), (2) Ophioglossaceae, (3) Psilotaceae, (4) Marattiales, and (5) equisetophytes (see also Chapter 8).

The common name *fern* is applied to the members of three of these major lineages: Polypodiales, Marattiales, and Ophioglossaceae. These plants are superficially similar in usually having large (often highly dissected) frond-like leaves that unfold from a “fiddlehead” (so-called circinate vernation). These three lineages are usually divided into two groups on the basis of the structure and development of the sporangia. The Marattiales and the Ophioglossaceae are so-called eusporangiate ferns (see Figure 7.10). These appear to have retained the ancestral condition, in which the sporangium develops from several initial cells and the mature wall of the sporangium is more than one cell layer thick. Eusporangia also tend to contain large numbers of haploid spores at maturity.

In contrast, the Polypodiales are characterized by a derived development in which the sporangium arises from a single cell and the mature wall is only one cell thick. These leptosporangia are borne on a distinct stalk and have a characteristic annulus consisting of a row of cells with thickened inner walls and thin outer walls (see Figure 8.12). The leptosporangia of most species contain a relatively small and definite number of haploid spores

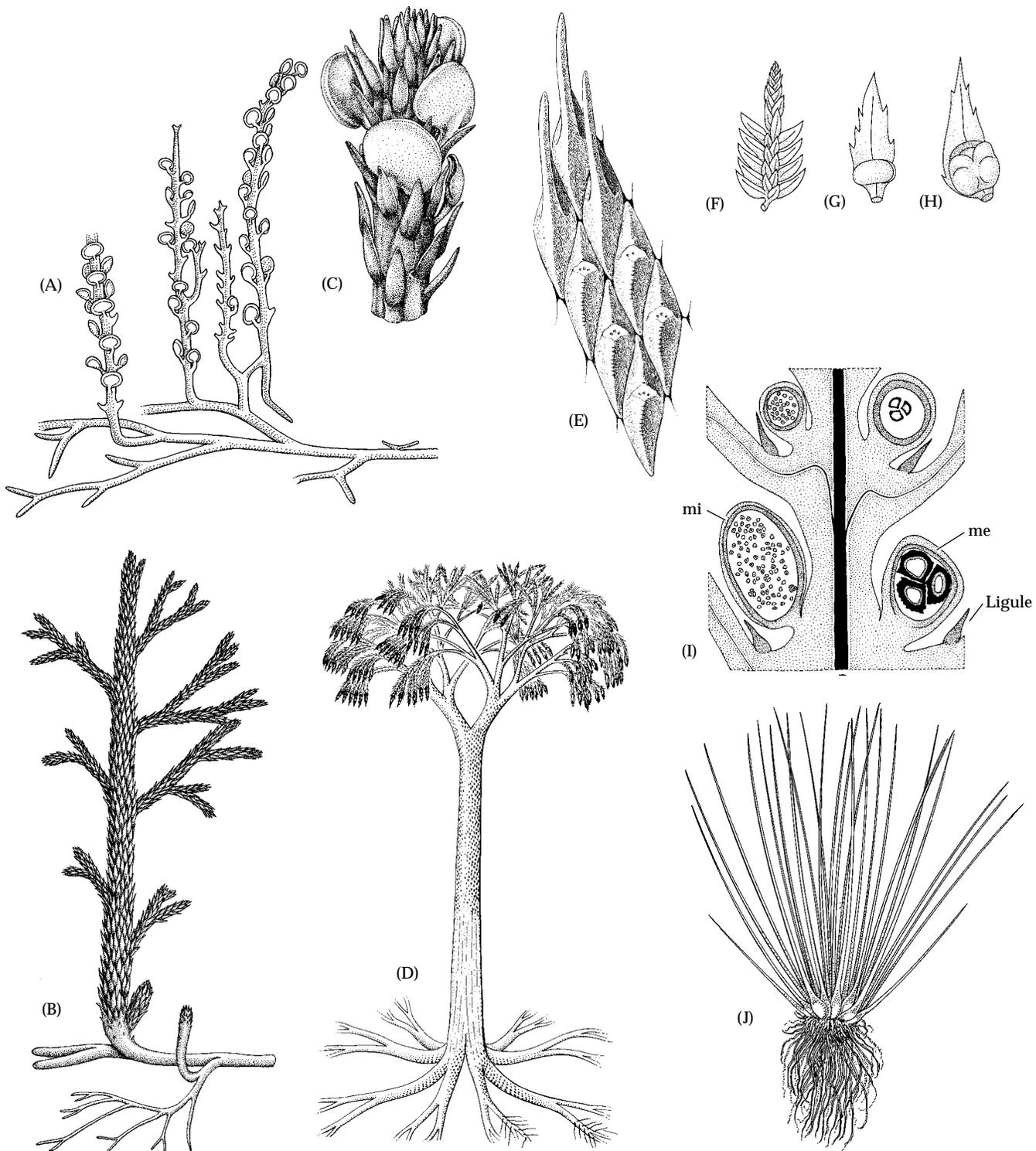


Figure 7.9 Morphology of lycophytes. (A) Reconstruction of the extinct *Zosterophyllum deciduum*, showing prostrate rhizome bearing leafless upright axes with lateral reniform sporangia. (B) Reconstruction of the extinct *Asteroxylon mackiei*, showing upright dichotomizing stems covered by microphyllous leaves, and rootlike axes. (C) *A. mackiei*, showing part of a fertile axis with reniform sporangia and transverse dehiscence. (D) Reconstruction of an extinct *Lepidodendron* sp., showing the dichotomously branching root system, the massive trunk with dichotomous branching above, and terminal strobili. (E) Portion of the surface of a stem of a *Lepidodendron* sp., showing three

attached leaves and the scars left by the abscission of five others. (F) Tip of a branch of *Selaginella*, showing microphyllous leaves and a terminal strobilus. (G) Microsporangium of *Selaginella* in the axil of a microsporophyll. (H) Megasporangium of *Selaginella* in the axil of a megasporophyll. (I) Longitudinal section through a strobilus of *Selaginella harrisiana*, showing megasporangia (me) with four large megaspores, microsporangia (mi) with many tiny microspores, and ligules. (J) *Isoetes bolanderi* habit, showing leaves and roots. (A and J from Kenrick and Crane 1997a; B, C, and I from Stewart 1983; D and E from Gifford and Foster 1989; F–H from Barnes 1998.)

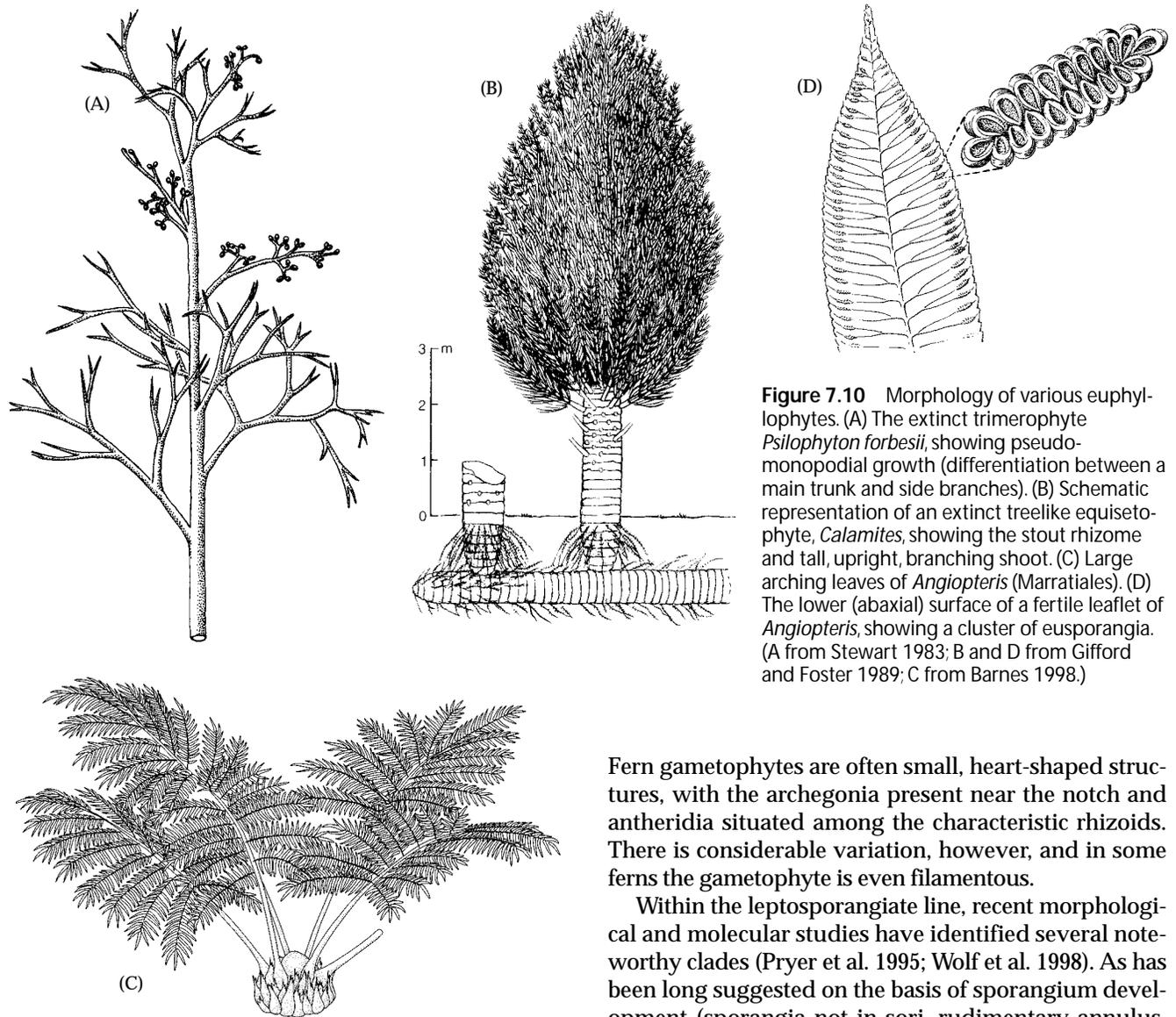


Figure 7.10 Morphology of various euphyllophytes. (A) The extinct trimerophyte *Psilophyton forbesii*, showing pseudo-monopodial growth (differentiation between a main trunk and side branches). (B) Schematic representation of an extinct treelike equisetophyte, *Calamites*, showing the stout rhizome and tall, upright, branching shoot. (C) Large arching leaves of *Angiopteris* (Marrattiales). (D) The lower (abaxial) surface of a fertile leaflet of *Angiopteris*, showing a cluster of eusporangia. (A from Stewart 1983; B and D from Gifford and Foster 1989; C from Barnes 1998.)

(e.g., 16, 32, 64), which are ejected from the sporangia by a mechanism driven by changes in moisture content in the annulus cells.

Probably the most familiar monilophytes are the **Polypodiales**, of which there are more than 12,000 living species (see Figures 8.1, and 8.8 through 8.14). Many of these plants have highly dissected pinnate leaves, of the type we commonly associate with ferns, but leaf form is actually extremely variable, and some even have simple, undissected leaves. The sporangia are typically produced in small clusters (each cluster is called a sorus, collectively the *sori*) on the undersides of the leaves. The sori are often covered by a flap of tissue called an indusium, though some are “naked.” The structure and position of the sori and the indusium vary enormously from one fern group to another, and this variation has been emphasized in taxonomic treatments (see Chapter 8).

Fern gametophytes are often small, heart-shaped structures, with the archegonia present near the notch and antheridia situated among the characteristic rhizoids. There is considerable variation, however, and in some ferns the gametophyte is even filamentous.

Within the leptosporangiate line, recent morphological and molecular studies have identified several noteworthy clades (Pryer et al. 1995; Wolf et al. 1998). As has been long suggested on the basis of sporangium development (sporangia not in sori, rudimentary annulus, large number of spores), Osmundaceae (cinnamon ferns) are seen to be the sister group of the rest. One distinctive leptosporangiate clade includes the large tree ferns (Cyatheaceae), and another contains all of the heterosporous aquatic fern groups (placed in Marsileaceae and Salviniaceae). Although the aquatic ferns are morphologically quite different from one another (e.g., *Salvinia* and *Azolla* with small floating leaves, versus *Marsilea* with leaves resembling those of a four-leaf clover; see Figure 8.11), the existence of fossil intermediates also supports the monophyly of the group (Rothwell 1999; Lupia et al. 2000). Another interesting result concerns the Polypodiaceae. Despite earlier views that this diverse group was polyphyletic, recent studies indicate that its members form a clade.

The **Marattiales** are mainly plants of the wet tropics that tend to have very large pinnate fronds with thick-walled eusporangia in distinctive clusters (sometimes fused) on the lower surfaces (see Figure 7.10D). There are perhaps 300 living species in this clade, most of

which belong to *Angiopteris* (over 100 species) or *Marrattia* (about 60 species), but they have a long fossil record, and extinct relatives (especially *Psaronius*) were important components of Carboniferous swamps. Consistent with their relative morphological stasis, these plants may have a decelerated rate of molecular evolution (Soltis et al. 2002).

The **Ophioglossaceae** (with perhaps a total of 80 species) are characterized by fronds that are divided into a flattened vegetative portion (or sterile segment) and a sporangium-bearing fertile segment (see Figure 8.6). This peculiar arrangement may have been derived from a dichotomous branch system. The gametophytes are subterranean, achlorophyllous, tuber-like structures that are associated with an endophytic fungus.

The **Psilotaceae** includes about 15 species placed in *Psilotum* (the widespread whisk ferns) and *Tmesipteris* (from Australia and the South Pacific) (see Figure 8.5). Because the plant body consists of dichotomously branching stems, psilophytes have often been viewed as the last remnants of the first vascular plants. An alternative theory, based mainly on their subterranean gametophytes, which are associated with fungi, has been that they are reduced leptosporangiate ferns (possibly related to Gleicheniaceae) (Bierhorst 1977). Recent molecular phylogenetic studies have established with considerable certainty that neither of these ideas is correct (Pryer et al. 2001). Instead, it appears that Psilotaceae are most closely related to the Ophioglossaceae, with which they share some similarities in gametophytes and in the development and position of the sporangia. Under this view, the tiny leaves and the absence of true roots in the Psilotaceae are considered to be derived conditions.

Today there are only about 15 species of **equisetophytes**, or horsetails, all placed in *Equisetum* (Equisetaceae; see Figure 8.7). Equisetophytes have jointed, hollow stems, with distinct ridges where the epidermal cells deposit silica on their surfaces. The leaves are generally reduced to small scales and are borne in a whorl at each node. The haploid spores are produced in sporangia that are attached on the undersides of unusual peltate sporangiophores and clustered in strobili at the tips of the stems. Although the modern equisetophytes are homosporous, there is controversy over whether the gametophytes have separate sexes. Some gametophytes start out producing just antheridia and some only archegonia, but at least the female forms later become bisexual.

Equisetophytes are well known as fossils, which can easily be identified by the characteristic stem architecture. Like the lycophytes, these plants were present in the Devonian but became much more abundant and diverse in the Carboniferous, when some of them also had much larger leaves, evolved heterospory, and became impressive trees. The position of equisetophytes within monilophytes is uncertain (see Figure 7.8), but there is some indication of a connection to Marattiales (Pryer et al. 2001).

Spermatophytes (Seed Plants)

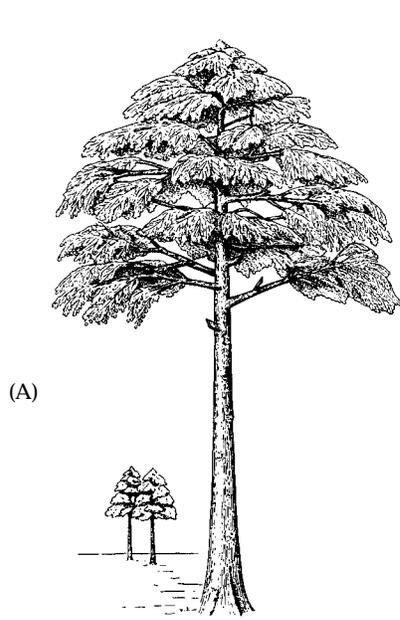
Spermatophytes, or seed plants, are by far the most diverse lineage within the vascular plants, with about 270,000 living species. Most of this diversity is accounted for by just one subclade: the flowering plants, or angiosperms. Morphological evidence for the monophyly of seed plants includes the seed habit itself, but also the fact that the major extant seed plant lineages all share (at least ancestrally) the production of wood (secondary xylem) through the activity of a secondary meristem called the cambium. Another noteworthy vegetative characteristic is axillary branching, as compared with the unequal dichotomous branching that preceded it within euphyllophytes.

MAJOR CHARACTERISTICS OF SEED PLANTS

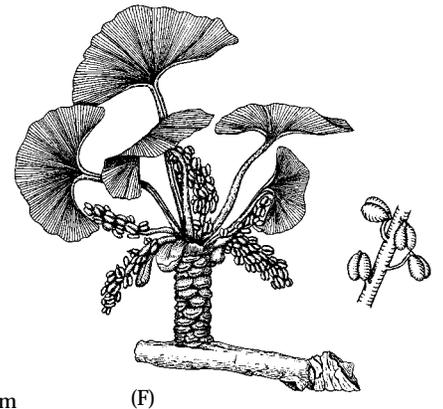
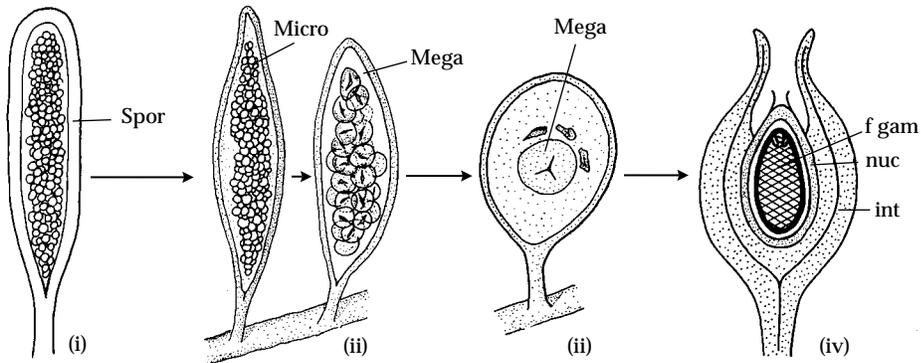
To understand the seed, it helps to think about how it evolved (Figure 7.11). Seed plants are nested well within a lineage characterized by **homospory** (one kind of spore, bisexual gametophytes). A critical step in the evolution of the seed was the evolution of **heterospory**—the production of two kinds of spores (microspores and megaspores), which produce two kinds of gametophytes (male or microgametophytes, which ultimately produce sperm; and female or megagametophytes, which produce one or more eggs).

Heterospory evolved several times within separate vascular plant lineages, including the lycophytes, the

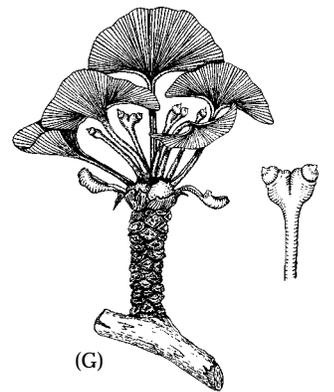
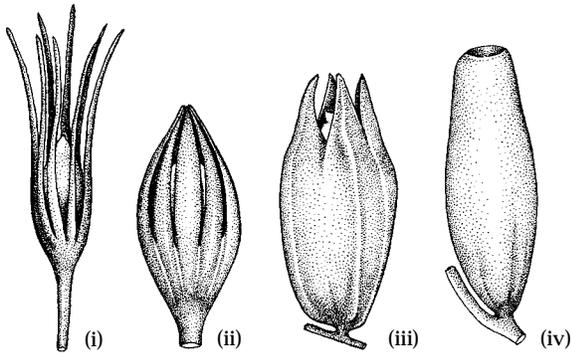
Figure 7.11 *Archaeopteris* and early seed plants. (A) Reconstruction of the habit of *Archaeopteris*, an extinct “progymnosperm” with a large trunk and flattened lateral branch systems. (B) Reconstruction of an extinct “seed fern,” *Medullosa noei* (3.5–4.5 m high), showing the large compound leaves. (C) Probable steps in the evolution of the seed: (i) homospory in a distant ancestor; (ii) heterospory, with differentiation between sporangia that produce microspores and megaspores; (iii) reduction of the number of functional megaspores to one, and its development inside of the sporangium (endospory); (iv) envelopment of the megasporangium by integument tissue, leaving a micropyle at the apex (f gam, female gametophyte; int, integument; mega, megaspores; micro, microspores; nuc, nucellus or megasporangium wall; spor, sporangium). (D) Stages in the evolution of the integument in early seeds (all extinct): (i) *Genomosperma kidstoni*, (ii) *G. latens*, (iii) *Eurystoma angulare*, (iv) *Stannostoma huttonense*. (E) Pollen-receiving structures at the apex of the ovule in early seeds (all extinct): (i) *Physostoma elegans*; (ii) *P. elegans*, longitudinal section showing pollen chamber within; (iii) *Eurystoma angulare*, showing cup-shaped opening. (F) Portion of long shoot and spur shoot of the extant ginkgophyte, *Ginkgo biloba*, showing axillary microsporangiote strobili; detail of axis and four microsporangium-bearing structures at right. (G) Portion similar to that in F of an ovule-bearing plant of *G. biloba*, showing axillary stalks, each bearing a pair of ovules; detail of the tip of a stalk at right. (H) Longitudinal section of the seed of *G. biloba* with young embryo (emb, embryo; ii, inner layer of integument; mi, middle layer of integument; oi, outer layer of integument). (A, F, and G from Bold et al. 1967; B and D from Gifford and Foster 1989; C and H from Scagel et al. 1969; E from Stewart 1983.)



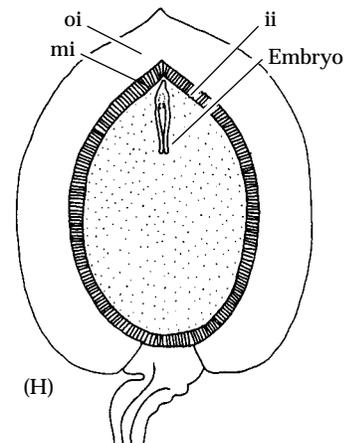
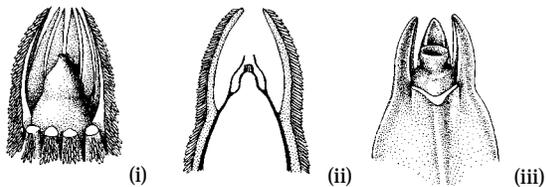
(C) Probable steps of seed evolution



(D) Evolution of the integument



(E) Pollen-receiving structures



leptosporangiate ferns, the equisetophytes, and the line including the seed plants (Bateman and DiMichele 1994). In several of these cases, the evolution of heterospory was followed by a reduction in the number of functional megaspores. In the line leading to seed plants the number was reduced to just one by abortion of all but one of the four haploid products of a single meiotic division. The single remaining megaspore was retained within the megasporangium and went on to produce a female gametophyte within the spore (endosporic development). Finally, the megasporangium became enveloped by sterile sporophyte tissue known as integument (Figure 7.11D), but leaving open a little hole at the apex called the micropyle. In seed plants except angiosperms, the micropyle serves as the entrance for one or more pollen grains, which are microspores within which the male gametophyte has developed.

It is helpful to look at the developmental events leading to a mature seed in a plant like a cycad or a pine tree. A single meiotic division occurs within the ovule (young seed), three of the resulting haploid products disintegrate, and within the remaining spore the female gametophyte develops. Eventually the female gametophyte may contain thousands of cells, with one or more egg cells differentiated near the micropylar end of the seed. Microspores are produced in microsporangia, which are borne elsewhere on the same plant (monoecy) or on separate plants (dioecy).

One or more pollen grains are transported to the vicinity of the micropyle—presumably by wind in the first seed plants. In many cases a drop of liquid (a pollen droplet) is exuded from the micropyle, which pulls adhering pollen grains inside when it retracts. A pollen grain germinates and sends out a tubular male gametophyte, which eventually delivers sperm to the vicinity of the egg. In modern cycads and ginkgos (discussed later in this section), the pollen tube is haustorial, ramifying slowly through the megasporangium wall, and two very large multiflagellate sperm are eventually produced. In contrast, in the remaining modern seed plant lineages a pair of nonmotile sperm are delivered directly to the female gametophyte by the pollen tube. Following fertilization, the diploid zygote develops into a new sporophyte embryo, and the female gametophyte serves as the nutritive tissue.

The second major characteristic of seed plants is the production of wood, or secondary xylem, which (along with the evolution of a mechanism to regenerate the outer covering of the stem—the periderm) allows the development of a substantial trunk. Understanding how wood is produced requires some basic knowledge of how vascular plants develop. They grow in length through the activity of primary apical meristems at the tip of each shoot and of each root. These apical meristems are populated by undifferentiated cells that undergo mitotic cell divisions, leaving behind derivative cells that go on to differentiate into all of the different cell

types and tissues in the plant body. Shoot apical meristems are also the site of initiation of new buds and leaves.

Some of the cells produced by the apical meristem differentiate within the stem into distinct strands of tissue that ultimately will function as vascular tissue. Within these strands, or vascular bundles, one sees the differentiation of the first (primary) xylem, situated toward the inside of the plant axis, and of phloem, situated toward the outside. Between the xylem and the phloem there remains an undifferentiated layer of cells called the cambium. The cambium acts as a secondary meristem, giving rise to new cells both toward the inside and the outside of the stem, which then go on to differentiate into new xylem cells (such as tracheids) and new phloem cells (such as sieve cells).

The tissues that are produced through this process are referred to as secondary xylem and secondary phloem, respectively. Secondary xylem builds up over the years, forming wood, which is made up of dead, thick-walled cells that are quite sturdy and resistant to decay. Secondary phloem does not build up because phloem cells are not so thick-walled and they have to be alive to carry out their function of transporting carbohydrates and nutrients up and down in the plant body.

It is interesting to note that in contrast to the bifacial cambium of seed plants, the giant lycophytes and equisetophytes of the Carboniferous seem to have had unifacial cambia, producing secondary xylem internally but not phloem. They also lacked the ability to substantially increase the size of the cambial ring, so wood production in these plants was actually quite limited (Cichan and Taylor 1990; Bateman et al. 1998).

EARLY EVOLUTION

With this background on the seed and on wood, let us briefly consider the origin and early evolution of seed plants (see Figures 7.8, 7.11, and 7.12). Our knowledge of the relevant events relies heavily on well-preserved fossils from the late Devonian and early Carboniferous, which have been called “progymnosperms” and “seed ferns” (see Figure 7.11).

Recall that the differentiation of a main trunk and side branches had already evolved in the euphyllophyte lineage. One first sees the appearance of very large trunks, with wood rather similar in structural detail to that of modern conifers, in the late Devonian. These trunks were connected to large frond-like branch systems bearing many small leaves (see Figure 7.11A). *Archaeopteris*, as this plant is now called, was found to be heterosporous, yet without seeds.

The accurate reconstruction and phylogenetic placement of *Archaeopteris* and other “progymnosperms,” such as *Aneurophyton* (Beck 1981, 1988; Beck and Wight 1988), was fundamental in establishing that both heterospory and the production of wood pre-dated the evolution of the seed. The clade containing the seed plants

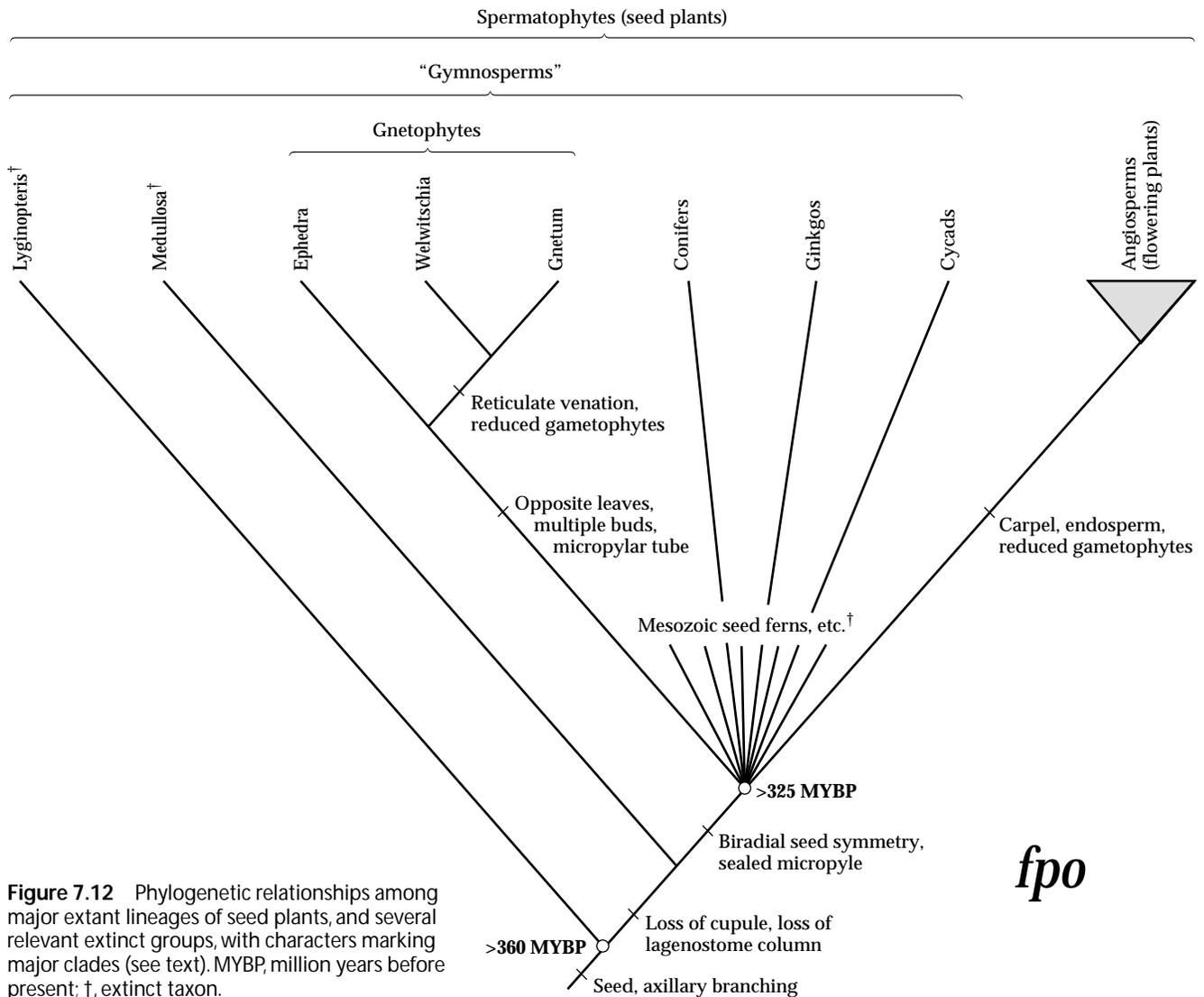


Figure 7.12 Phylogenetic relationships among major extant lineages of seed plants, and several relevant extinct groups, with characters marking major clades (see text). MYBP, million years before present; †, extinct taxon.

plus “progymnosperms” has been called the lignophytes (Doyle and Donoghue 1986), in reference to the production of wood (see Figure 7.8).

The term *seed fern* is applied to a wide variety of early seed plants with large, frond-like leaves, resembling those seen in ferns today but bearing bona fide seeds (Stewart and Rothwell 1993; Taylor and Taylor 1993). It is clear that these are not all most closely related to one another and that a series of Paleozoic seed fern groups form a paraphyletic grade at the base of the seed plant radiation.

Careful analyses (e.g., Serbet and Rothwell 1992) have revealed that the first seeds were situated in “cupules” and that each seed had an elaborate outgrowth of the sporangium wall that formed a specialized pollen chamber. This structure presumably functioned in pollen grain capture through secretion of a pollination droplet. Integument tissue may have been derived from a series of sterilized sporangia, which initially formed lobes at the apex as opposed to a distinct micropyle (see Figure 7.11D).

Through much of the last century, extant and extinct seed plant lineages were commonly divided into two major groups: the cycadophytes and the coniferophytes. The **cycadophytes**, including modern cycads, were distinguished by rather limited production of wood with wide rays (manoxylic wood) and by large frond-like leaves and radially symmetrical seeds. In contrast, in **coniferophytes**, including the ginkgos and the conifers, the wood is well developed and dense (pycnoxylic), the leaves are simple and often needle-like, and the seeds are biradially symmetrical (platyspermic, or flattened). Here this distinction suggested to some workers that seed plants actually originated twice. Under this view, the cycadophyte line was derived from a progymnospermous ancestor by the modification of flattened lateral branch systems into large, frond-like leaves. In coniferophytes, on the other hand, the individual leaves of a precursor like *Archaeopteris* might have been modified into needle-like leaves. This scenario implies that the seed itself evolved twice, corresponding to the two different symmetries.

However, phylogenetic analyses that have included the extant lineages along with representative fossils have generally supported the relationships shown in Figures 7.8 and 7.12 (e.g., Crane 1985; Doyle and Donoghue 1986; Nixon et al. 1994; Rothwell and Serbet 1994). These studies imply that the seed evolved just once, and that the first seed plants were more cycadophytic, at least in having large dissected leaves and radially symmetrical seeds. Specifically, it appears that a series of Devonian-Carboniferous “seed ferns” (*Lyginopteris* and medullosans) are situated at the base of the seed plant phylogeny and that coniferophytes are variously nested well within the tree, in a platyspermic clade. This arrangement implies a later shift to small, needle-like leaves and to smaller flattened seeds—both perhaps as adaptations to arid environments.

EXTANT LINEAGES OF SPERMATOPHYTES

Today there are five major lineages of seed plants: cycads (Cycadales), ginkgos (Ginkgoales), conifers (Coniferales), gnetophytes (Gnetales), and flowering plants (angiosperms). The first four groups are often called gymnosperms, in reference to having naked seeds, as opposed to angiosperms, in which the seeds are enclosed inside of a carpel. Despite many efforts to resolve the phylogenetic relationships among these lines using morphological and molecular data, they remain quite uncertain (see Figure 7.12).

Some recent molecular analyses have indicated that the extant groups of “naked seed plants” form a clade, which is sister to the angiosperms (see the next section). However, note that even if this were true, the “gymnosperms” as a whole would not be monophyletic. They are paraphyletic when one takes into account the early-diverging fossil lineages already mentioned (see Figure 7.12), as well as several other “seed fern” lineages from the later Permian and Mesozoic, at least some of which are probably on the line leading to modern angiosperms. We will return to a discussion of these relationships following a brief introduction to each of the major groups (see also Chapter 8).

Cycads

Cycads (Cycadales) were most abundant and diverse during the Mesozoic. Today there are perhaps 130 species left. Cycads generally produce squat trunks, with limited secondary xylem, and large compound leaves resembling those of ferns or palms (see Figure 8.15). They are dioecious, meaning that some plants bear strobili producing only seeds, whereas others bear only pollen strobili. Both types of strobili are typically very large, and in some cases brightly colored. Likewise the seeds are generally large and usually have a fleshy and colorful seed coat, presumably to attract vertebrate dispersal agents.

Several cycad features may be ancestral within seed plants, such as haustorial pollen and gigantic multifa-

gellate sperm. However, cycads are united by several apparently derived morphological characters, including the loss of axillary branching, the presence of “girdling” leaf traces, and the production of coralloid roots that house nitrogen-fixing cyanobacteria.

Within cycads, phylogenetic analyses indicate that the first split divides *Cycas* from the remaining groups. *Cycas* has retained the presumed ancestral condition (seen in some fossil relatives, such as *Taeniopteris*) of having several ovules borne on the rather leaf-like megasporophylls, which are not clustered into strobili. The derived condition, seen in the other line, is a reduction to two ovules borne on a peltate megasporophyll, with the ovules pointing in toward the axis of the strobilus.

Ginkgos

There is just one surviving species of **ginkgo** (Ginkgoales): *Ginkgo biloba* (see Figure 7.11F–H). This species is hardly known in the wild, but it has been maintained for centuries around temples in China, and in modern times it has been spread by humans as a street tree. Perhaps the most characteristic feature of the modern ginkgo is the production of deciduous, fan-shaped leaves with dichotomous venation. Ginkgos are well known in the fossil record, where a greater diversity of leaf shapes is seen.

Like cycads, ginkgos are dioecious (see Figure 7.11F, G). The ovules are borne in pairs on axillary stalks, thought to be reduced strobili. The integument tissue differentiates into a fleshy (and smelly) outer layer and a hard inner layer that encloses the female gametophyte (Figure 7.11H). Again like cycads, ginkgos retain several ancestral characteristics, including haustorial pollen and swimming sperm.

Conifers

There are approximately 600 living species of **conifers** (Coniferales) (see Figures 8.17–8.20). These are shrubs or small trees with well-developed wood and often needle-like leaves. Normally the leaves are borne singly along the stem, but in pines (*Pinus*) they are clustered in short shoots. The needles often display additional adaptations to drought, such as sunken stomates. In some of the Southern Hemisphere conifers (e.g., *Podocarpus*, *Agathis*), however, the leaves are rather broad and flat, and in *Phyllocladus* the flattened branches resemble leaves.

Many conifers are monoecious, with both pollen-producing and seed-producing strobili borne on the same plant. Dioecy is found in other groups, such as in the junipers (*Juniperus*), yews (*Taxus*), and podocarps (*Podocarpus*). In the pollen cones, microsporophylls bear microsporangia on the abaxial surface. The pollen grains often have a pair of sac-like appendages, but these seem to have been lost in several lineages.

Receptive ovules are situated on the upper side of each cone scale. Meiosis occurs inside each ovule, and the one remaining haploid cell gives rise to the female

gametophyte, which eventually produces one or more eggs at the micropylar end. A pollen tube grows down through the wall of the megasporangium to deliver two sperm. The phenomenon of “polyembryony” is fairly common in conifers, with multiple embryos produced either through separate fertilization events (depending on the number of eggs and pollen tubes) or, more commonly, by a characteristic subdivision of a single embryo into several genetically identical embryos early in development.

In modern conifers the pollen strobili are said to be simple, whereas the seed cones are compound. The pollen strobilus is interpreted as a modified branch, and the microsporophylls as modified leaves. The seed cone, in contrast, was derived through modification of a branch that bore lateral branches in the axils of a series of leaves. This view is supported by fossils showing a series of steps in the reduction of a lateral branch bearing a number of seeds to the highly modified cone scale that we see in the modern groups (Figure 7.13A–E) (Florin 1951, 1954). It also follows from the observation that each cone scale is subtended by a bract, which represents the modified leaf. In a few conifers the subtending bract is noticeable, sticking out from between the cone scales. This is the case, for example, in the Douglas fir (*Pseudotsuga mensiezii*), where the cone scale is produced in the axil of a prominent three-pronged bract (Figure 7.14C). In many conifers, however, the bract is quite reduced. In Cupressaceae, such as *Taxodium* or *Cryptomeria*, the bract is fused to the cone scale, which still shows evidence of “leaves” (visible as small teeth or bumps).

Phylogenetic studies have yielded some important insights into the evolution of conifers (e.g., Stefanovic et al. 1998). Molecular data imply a basal split between the Pinaceae and a clade including all of the other conifers. The Pinaceae are distinguished by several features, including inversion of the ovules (micropyle facing the axis of the cone) and the wing of the seed being derived during development from the cone scale.

Within the other clade of conifers, the two major Southern Hemisphere groups—Podocarpaceae and Araucariaceae—form a clade, perhaps united by a shift to one ovule per cone scale. The Cupressaceae are marked by several potential apomorphies, such as fusion of the cone scale and the subtending bract. In turn, this group may be linked with the Taxaceae (the yews), which have highly reduced cones bearing just one terminal seed surrounded by a colorful fleshy aril.

Gnetophytes

The fourth major extant lineage of seed plants is the **gnetophytes** (Gnetales) (Figure 7.13F–I; see also Figure 8.21). This group contains only about 80 living species, which belong to three quite distinct lineages (see Doyle 1996; Friedman 1996; Price 1996). *Ephedra* (with about 40 species in deserts around the world) has very reduced scale-like leaves (see Figure 8.21). *Gnetum* (with about 35

species in tropical forests of the Old and New Worlds) has broad leaves (Figure 7.13G–I), like those seen in most flowering plants. Finally, *Welwitschia* (with only one species, *W. mirabilis*, in southwestern Africa) produces just two (rarely four) functional leaves during its lifetime, which grow from the base and gradually fray out at the tips (Figure 7.13F).

Although these plants look very different from one another, they share some unusual features, such as opposite leaves, multiple axillary buds, vessels with circular openings between adjoining cells, compound pollen and seed strobili, and ancestrally ellipsoid pollen with characteristic striations running from tip to tip. The seeds also have two integumentary layers—the inner one forming a micropylar tube that exudes the pollen droplet, and the outer one derived from a fused pair of bracts. Molecular studies also strongly support the monophyly of this group.

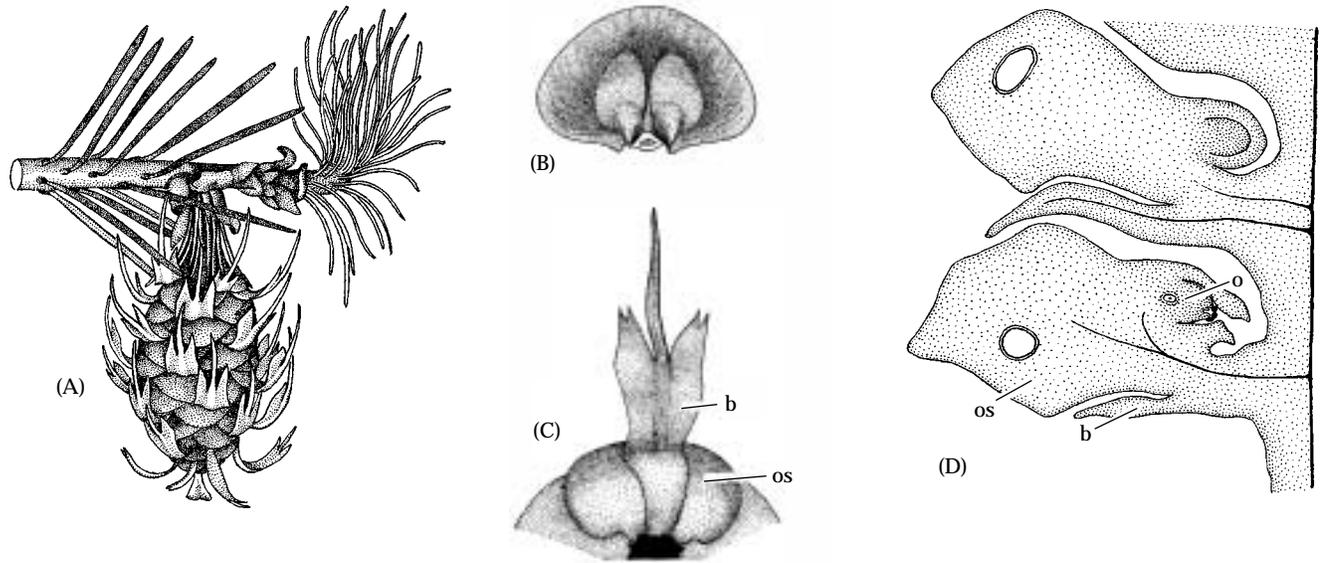
Within the gnetophytes, *Gnetum* and *Welwitschia* form a well-supported clade. Morphological synapomorphies include reticulate leaf venation, further reduction of the male gametophyte, and aspects of female gametophyte structure (tetrasporic development, loss of archegonia, free nuclei functioning as eggs). The characteristic striate pollen found in *Ephedra* and *Welwitschia* was apparently lost along the line leading to *Gnetum* (which has spiny grains with no apertures).

Aside from fossil pollen, the fossil record of this clade is rather poor; only a few macrofossils have been described (Crane 1996). Although gnetophyte pollen grains are found as far back as the Triassic, it appears that the clade containing the modern groups diversified most significantly during the mid-Cretaceous, along with the angiosperms (see the next section).

Like the angiosperms, the gnetophytes shortened the life cycle (and probably became herbaceous) and evolved insect pollination (found in some living species). In marked contrast to flowering plants, however, gnetophytes never became significant components of the vegetation at mid and high paleolatitudes, and they underwent a dramatic decline during the Late Cretaceous (Crane et al. 1995; Crane 1996).

Angiosperms (Flowering Plants)

With over 257,000 extant species, flowering plants account for most of green plant, land plant, and seed plant diversity. Strong evidence for the monophyly of angiosperms comes from molecular studies and from many shared derived morphological characters. Of these, some of the more obvious and important reproductive features are (1) seeds produced within a carpel with a stigmatic surface for pollen germination; (2) a very reduced female gametophyte, consisting in most cases of just eight nuclei in seven cells; and (3) double fertilization, leading to the formation of a typically triploid nutritive tissue called endosperm.



(E) Steps in ovuliferous cone scale evolution



Figure 7.13 Morphology of conifers and gnetophytes. (A) *Pseudotsuga taxifolia*, showing a branch with a first-year seed cone. (B) Single ovuliferous cone scale of *Pseudotsuga*, showing two ovules on the upper surface. (C) A single bract-scale complex of *Pseudotsuga*, showing the excreted three-pronged bract (b) subtending the ovuliferous scale (os). (D) Longitudinal section through two bract-scale complexes in an ovulate cone of *Pinus strobus*, showing an ovule (o) with micropyle directed toward the cone axis, the ovuliferous scale (os), and the subtending bract (b). (E) Probable evolutionary steps in the origin of the ovuliferous cone scale of conifers: (i) the extinct *Cordaites*, with several ovules (o) and sterile scales (ss) attached to a dwarf shoot (ds) in the axil of a bract (br); (ii) the extinct plant *Lebachia*, in which the number of ovules is reduced; (iii) extant *Pinus*, with two ovules attached to the upper surface of the ovuliferous scale. (F) General habit of the gnetophyte *Welwitschia mirabilis*, showing the short woody stem with two large leaves, axillary position of the multiple strobili, and taproot. (G) Leaves and compound microsporangiate strobili of *Gnetum*. (H) *Gnetum* with mature seeds. (I) Longitudinal section through a young seed of *Gnetum*, showing the inner integument (int) extended into a micropylar tube (mt), surrounded by inner and outer bracteoles (ib, ob). (A–D from Stewart 1983; E, G, and I from Sagenel et al. 1969; F from Barnes 1998.)

Several derived vegetative characteristics are also noteworthy. Almost all angiosperms produce vessels in the xylem tissue, though this feature may have evolved within the group. Vessels differ from tracheids in that water can flow from one vessel element (an individual cell, evolutionarily derived from a tracheid) to the next without traversing a pit membrane (see Figure 4.31). Vessels are extremely efficient with respect to water transport but may be more prone to damage (especially through air embolisms) when subjected to drought stress. Angiosperm phloem differs from that of all other plants in that the sieve tube elements (living but enucleate cells functioning in the transport of carbohydrates) are accompanied by one or more “companion cells” that are derived from the same mother cell.

FLOWERS AND THE ANGIOSPERM LIFE CYCLE

The production of flowers is commonly considered the diagnostic feature of angiosperms, but the term *flower* is actually a bit nebulous. If flowers are short reproductive axes with closely aggregated sporophylls, then gnetophytes and Bennettitales might be said to have flowers. It is the particular construction and arrangement of the flower parts that sets the angiosperms apart from all other seed plants (see Figure 4.16). Most angiosperm stamens have a stalk (filament) and a tip portion (anther) bearing usually two pairs of microsporangia (pollen sacs). The angiosperm carpel is typically differentiated into a lower portion (ovary) that encloses the ovules and an elongate portion (style) that elevates a surface receptive to pollen (stigma). The angiosperm ovule is unusual in several ways (see Figures 4.39 and 4.40). It generally becomes curved over (anatropous) during development, so that the micropyle lies near the stalk of the ovule (in

contrast to the orthotropous condition in other seed plants, where the micropyle faces away from the stalk). In addition, whereas non-angiosperm seeds have one layer of integument tissue (sometimes differentiated into fleshy and hard layers), angiosperms typically have two distinct integuments (bitegmic ovules).

The angiosperm life cycle is also remarkably derived (see Figure 4.17). The male gametophyte has just three nuclei, or sometimes just two at the time the pollen is shed. A pollen grain that lands on the right stigma sends out a pollen tube that delivers the sperm directly to the female gametophyte inside the ovule. In the development of a typical angiosperm female gametophyte, meiosis is followed by the abortion of three products, and the remaining haploid nucleus undergoes a very small series of mitotic divisions (see Figure 4.40).

Ultimately the egg is situated toward the micropylar end, along with two other cells (synergids), which appear to play a critical role in orienting the pollen tube and delivering the sperm nuclei. There are usually three cells (antipodals) at the opposite end of the female gametophyte, and two nuclei (polar nuclei) situated in a large cell in the middle. One of the two sperm nuclei fuses with the egg to give rise to the diploid zygote, and the other fuses with the two polar nuclei. This process is called double fertilization. The resulting triploid product undergoes a series of mitotic divisions to produce endosperm, which serves as the nutritive tissue in the seed (as opposed to the female gametophyte).

TIME OF ORIGIN

When did the flowering plants originate and radiate? It appears from the fossil record (pollen, leaves, flowers, and fruits) that angiosperms underwent a major radiation starting in the Early Cretaceous (Doyle and Hickey 1976; Friis et al. 1987; Doyle and Donoghue 1993; Crane et al. 1995). The oldest unequivocal angiosperm fossils are pollen grains from about 130 million years ago. Extraordinarily complete fossils from China were first described as being from the Late Jurassic (Sun et al. 1998, 2002), but now they are interpreted as Early Cretaceous in age. Many major lineages can be recognized by the mid-Cretaceous (water lilies, Chloranthaceae, Winteraceae, and eudicots are present by 120 million years ago), and by the end of the Cretaceous they had diversified extensively and were the dominant plants in many terrestrial environments (see Magallon and Sanderson 2001).

In discussing the age of the angiosperms (or any other group), it is important to distinguish clearly between the origin of the line leading to the modern group (i.e., when this lineage split from its sister lineage) and the origin of the least inclusive clade that contains all of the extant members (the crown clade). The clade that includes the “stem” lineage has been referred to as the “angio-phytes,” to help distinguish it from crown-clade angiosperms (Doyle and Donoghue 1993).

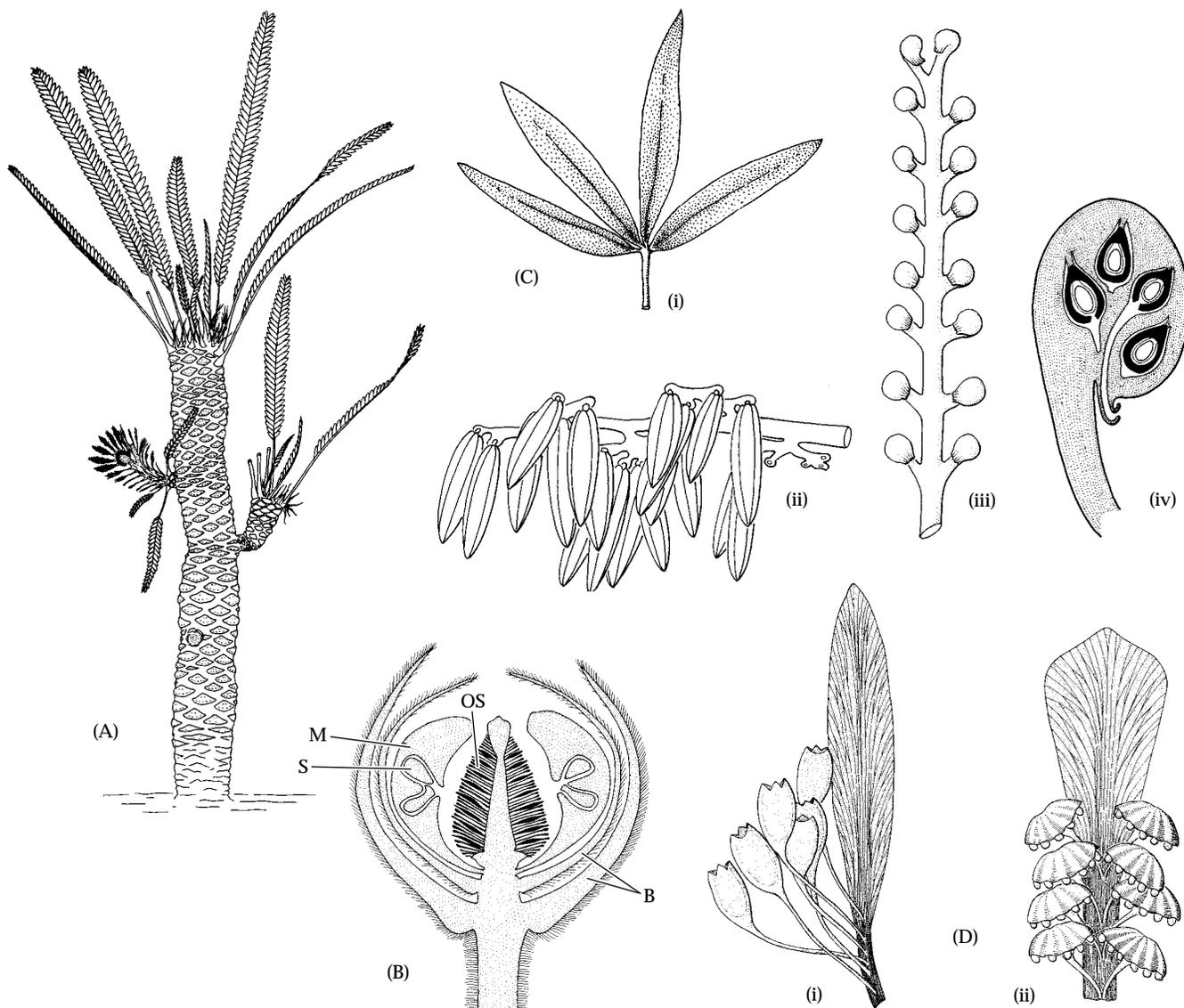


Figure 7.14 Reconstructions of Mesozoic fossils that may be closely related to angiosperms. (A, B) Bennettitales: (A) Habit of *Williamsonia sewardiana*, showing cycad-like trunk and compound leaves; (B) longitudinal section of a flower-like strobilus of *Williamsoniella*. B, bracts; M, microsporophyll with microsporangia; OS, stalked ovules and sterile scales borne on a central axis. (C) Caytoniales (Mesozoic “seed ferns”): (i) palmate leaf, *Sagenopteris phillipsi*; (ii) portion of a microsporophyll, *Caytonanthus*

kochi; (iii) megasporophyll of *Caytonia nathorsti*, showing two rows of cupules; (iv) longitudinal section of a cupule of *Caytonia thomasi*, showing ovules within. (D) Glossopteridales: (i) Ovulte portion of *Denkania indica*, showing six cupule-like structures attached to a leaf; (ii) *Lidettonia mucronata*, showing seeds attached on the lower surfaces of stalked disks borne on a leaf. (A from Taylor and Taylor 1993; B, C:ii–iv, and D from Gifford and Foster 1989; C:i from Stewart 1983.)

It is possible that the angiosperms are quite ancient, whereas the crown angiosperms originated much more recently, perhaps not long before the radiation seen in the fossil record. That the angiosperm line may be quite old is suggested by the fact that all of the likely close relatives of angiosperms have fossil records going back at least to the Triassic. We might, therefore, expect to find them as fossils before the Cretaceous, though perhaps without the full complement of characters found in modern angiosperms. So far, however, putative angiosperm fossils from the Triassic and Jurassic have either

turned out not to be related or are equivocal on the basis of available material.

Estimates based on molecular data are faced with the problem of shifts in the rate of molecular evolution, possibly independently in different lineages. Early molecular clock studies (e.g., Martin et al. 1989) yielded implausibly early ages for crown angiosperms. However, progress has been made in “relaxing” the molecular-clock assumption, and recent estimates place the origin of the angiosperm crown clade between 140 and 190 million years ago (Sanderson and Doyle 2001).

RELATIONSHIP OF ANGIOSPERMS TO OTHER GROUPS

Botanists have long puzzled over the relationship of angiosperms to other seed plants. As noted earlier, this problem is complicated because, in addition to the other extant clades of seed plants (cycads, ginkgos, conifers, and gnetophytes), several extinct groups bear directly on the problem (see Stebbins 1974; Beck 1988; Stewart and Rothwell 1993; Taylor and Taylor 1993). In particular, it has long been hypothesized that flowering plants are most closely related to some group of Mesozoic “seed ferns” (e.g., *Caytonia*, glossopterids), or perhaps to the Bennettitales (also known as “cycadeoids” because of their resemblance to cycads; Figure 7.14A). Bennettitales have been especially attractive candidates because some of them produced large, flower-like reproductive structures with pollen-producing organs surrounding a central stalk that bears the naked seeds (Figure 7.14B).

Regarding the five extant lineages, ideas on relationships have shifted over the years. In the early 1900s (e.g., Arber and Parkin 1907), Gnetales (along with the extinct Bennettitales) were widely believed to be related to angiosperms on the basis of several morphological similarities, such as vessels in the wood, net-veined leaves in *Gnetum*, and flower-like reproductive organs. These views changed by the middle of the twentieth century with the reinterpretation of these characters. For exam-

ple, vessels were interpreted as being derived independently in Gnetales (from tracheids with circular bordered pits) and in angiosperms (from tracheids with scalariform pits). This character, and several others, suggested instead that gnetophytes were related to conifers.

In the mid-1980s, several phylogenetic studies of seed plants were carried out using morphological characteristics (Crane 1985; Doyle and Donoghue 1986). These analyses concluded that angiosperms formed a clade with Bennettitales and Gnetales—a clade referred to as the “anthophytes” to highlight the flower-like reproductive structures (Figure 7.15A). Since then, a number of independent morphological analyses have yielded the same basic result. In some of these studies, the gnetophytes have even emerged as paraphyletic with respect to angiosperms (Taylor and Hickey 1992; Nixon et al. 1994). The characters that have served to unite the anthophytes vary among analyses, but they are mostly rather obscure and in some cases unknown in fossil groups—for example, lignin chemistry, the layering of cells in the apical meristems, and pollen and megaspore features (Donoghue and Doyle 2000).

However, the repeated recovery of the anthophyte clade favored a return to the view that gnetophytes and angiosperms are closely related. In turn, this conclusion influenced the interpretation of morphological evolution. Perhaps most notably, double fertilization (reported

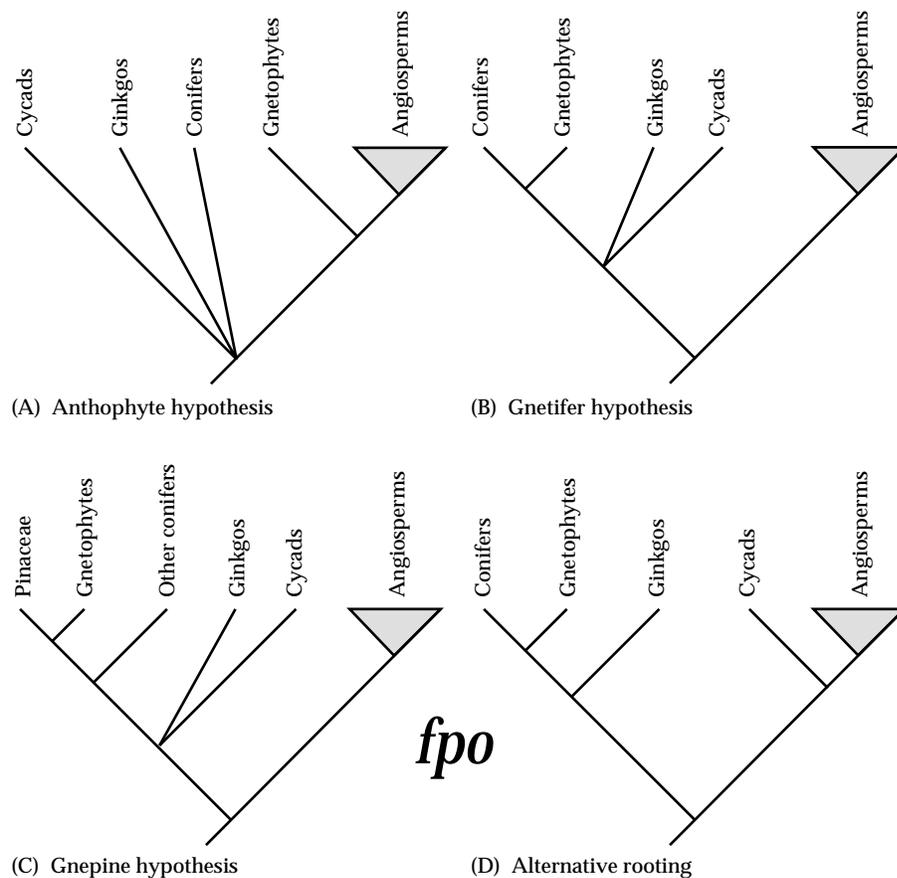


Figure 7.15 Alternative hypotheses of relationships among the five major extant lineages of seed plants. (A) In the anthophyte hypothesis, gnetophytes are most closely related to angiosperms. (B) In the gnetifer hypothesis, gnetophytes are most closely related to conifers. (C) In the gnepine hypothesis, gnetophytes are most closely related to Pinaceae within the conifers. (D) An example of a tree that is difficult to reject with current data (see text).

for *Ephedra* in the early and mid-1900s, but recently clearly documented in *Ephedra* and *Gnetum* (Friedman 1990; Carmichael and Friedman 1996) was interpreted as having evolved in the common ancestor of gnetophytes and angiosperms, with polyploid endosperm evolving later in the angiosperm line (see Donoghue and Scheiner 1992; Friedman and Floyd 2001).

The first molecular phylogenetic studies of the problem yielded a variety of results and were viewed as possibly being consistent with the anthophyte hypothesis (see Donoghue and Doyle 2000). Within the last few years, however, several major studies (especially those based on mitochondrial genes or on a combination of genes from different genomes) have cast serious doubt on the existence of an anthophyte clade (e.g., Goremykin et al. 1996; Bowe et al. 2000; Chaw et al. 2000; Frohlich and Parker 2000; but see Rydin et al. 2002). These analyses suggest instead that extant gymnosperm groups form a clade that is sister to the angiosperms, and that Gnetales are related more directly to conifers (the gnetifer hypothesis; see Figure 7.13B) or may even be nested within the conifers as the sister group of the Pinaceae (the gnepine hypothesis; see Figure 7.13C). Detailed analyses of the molecular data sets (e.g., Graham and Olmstead 2000; Sanderson et al. 2000) have revealed several different signals; some partitions of the data even favor placing the gnetophytes as sister to all other extant seed plant groups.

Unfortunately, at the present time these issues remain unresolved. It has become clear, however, that there are several potentially separate issues at stake. One important question is whether an anthophyte clade exists, or whether, instead, gnetophytes may be directly related to conifers. A second issue is the rooting of the seed plant tree, especially of the portion that includes the extant lineages. One possibility is a basal split into the angiosperms on the one hand and the extant gymnosperms on the other. Other possibilities are difficult to rule out on the basis of presently available data, such as placement of the root in the vicinity of cycads and ginkgos (see Figure 7.15D).

There is a distinct possibility that no living group of seed plants is very closely related to angiosperms. Recent results therefore accentuate the importance of fitting fossils into the picture, which will depend on more and better fossils and more attention to the phylogenetic analysis of morphological characters (Donoghue and Doyle 2000; Frohlich and Parker 2000).

Enormous progress has recently been made in understanding phylogenetic relationships at the base of the angiosperms themselves (Figure 7.16). Until very recently, the problem of identifying the root of the angiosperms and relationships among the basal branches looked intractable (Donoghue 1994). Over the last few years, however, several different lines of evidence have converged on the same answer. These new findings are having a major impact on our interpretation of early

angiosperm evolution and the factors that account for the enormous success of flowering plants.

Most students of angiosperm evolution have held that the first flowering plants were among the “Magnoliidae”—a paraphyletic group including magnolias, avocados, water lilies, and black peppers, among others (Cronquist 1988; Thorne 1992; Takhtajan 1997). Even if true, however, this conclusion is not very helpful in deriving an image of the first flowering plants because these plants display an impressive range of morphological forms. Some are woody plants and some are small herbs. Moreover, some, like magnolias, have large flowers, with many flower parts (stamens, carpels) spirally arranged on an elongate axis, while others, such as black peppers, have tiny flowers with few parts in distinct whorls. In fact, some phylogenetic results have suggested that the first flowering plants were woody with large flowers; others have implied that they were herbaceous with tiny flowers (see Doyle and Donoghue 1993).

Since 1999, several independent molecular studies have concluded that the first split within modern angiosperms was between a lineage that now includes just the single species *Amborella trichopoda* (and possibly also the water lilies, Nymphaeales) and all the rest of the approximately 257,000 species (Mathews and Donoghue 1999; Qiu et al. 1999; Soltis et al. 1999; Barkman et al. 2000; Zanis et al. 2002; see also Zimmer et al. 2000). *Amborella trichopoda* is a shrubby plant from the island of New Caledonia with rather small flowers and a limited number of spirally arranged parts (Endress and Igersheim 2000b). Pollen-producing flowers are borne on some plants and seed-producing flowers on others. The presence of staminodes in the carpellate flowers, however, implies that this species evolved from ancestors with bisexual (perfect) flowers. Unlike almost all other angiosperms, the water-conducting cells in the xylem of *Amborella* are tracheids (Feild et al. 2000), supporting the view that the first angiosperms lacked vessels (see Figure 7.16).

The water lilies (Nymphaeales) form another very early branch of the angiosperm tree (Friis et al. 2001), as do Austrobaileyales (including Illiciaceae). Interestingly, the female gametophytes of plants in these lineages have just four cells and form diploid endosperm tissue, which may prove to be ancestral for angiosperms (Williams and Friedman 2002). Along with *Amborella*, these two lineages subtend a clade including all of the rest of the flowering plants, which we refer to as the **core angiosperms**.

Whereas in the basal-most lineages the carpels are typically sealed by a secretion, in members of the core clade the carpels usually are sealed by postgenital fusion of epidermal layers (Endress and Igersheim 2000a). In the three basal lineages, and also in Chloranthaceae (which may be at the base of the core angiosperms; Doyle and Endress 2000), the carpels are ascidiate, meaning that the primordium is U-shaped at first, and grows

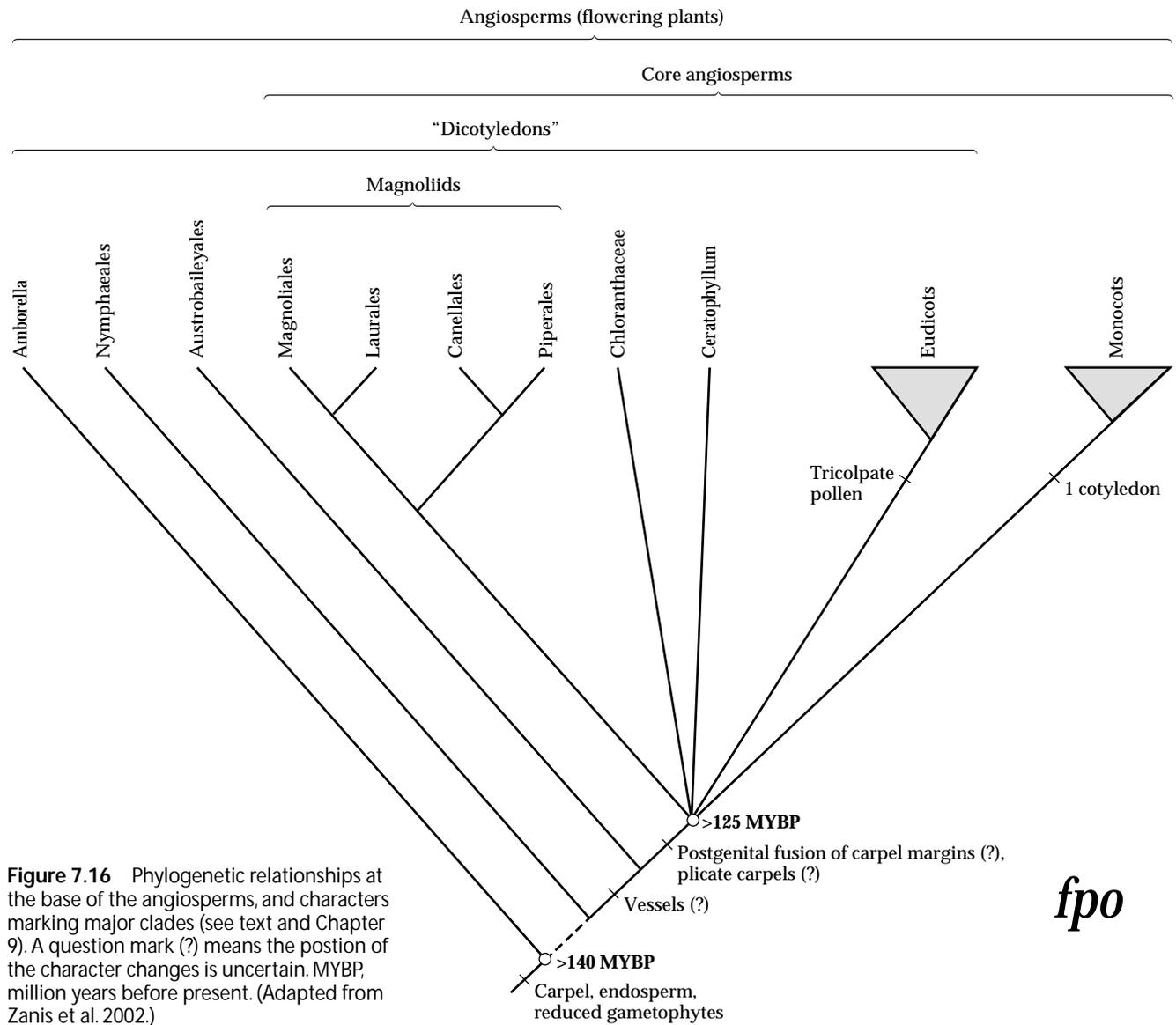


Figure 7.16 Phylogenetic relationships at the base of the angiosperms, and characters marking major clades (see text and Chapter 9). A question mark (?) means the position of the character changes is uncertain. MYBP, million years before present. (Adapted from Zanis et al. 2002.)

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up like a tube, whereas in core angiosperms the carpels are plicate, like a leaf folded down the middle. Although these observations clarify the basal carpel condition in angiosperms, they leave open the controversial issue of whether the carpel was derived from a leaf or instead is a compound structure derived from a reduced branch and its subtending leaf (see Doyle 1994).

Within the core angiosperm clade, relationships are still poorly resolved, with the placement of several enigmatic groups still uncertain, especially the Chloranthaceae and *Ceratophyllum*. However, several major clades are rather well supported. First, a restricted **magnoliid clade** includes the Magnoliales plus Laurales, and the Canellales plus Piperales (including the Aristolochiaceae and Lactoridaceae). Winteraceae, a vessel-less group, is in the Canellales, implying that vessels may actually have been lost in some cases (see also “Trochodendraceae” in Chapter 9).

A second major lineage of core angiosperms, containing the remainder of the former dicotyledons, has been called the **eudicots**. This lineage was first recognized in morphological analyses and was initially called the tricolpate clade (Donoghue and Doyle 1989), in reference to the main morphological character marking the group—namely, the production of pollen grains with three colpi, or germinal furrows (and a variety of derivative forms; see Figure 4.46). Many eudicots also have flowers with parts in fours or fives, or in multiples of these numbers.

Altogether there are perhaps 160,000 species of eudicots. This huge group contains a number of very speciose lineages, including legumes (about 16,000 species) and composites (about 20,000 species), as well as buttercups, roses, oaks, mustards, tomatoes, mints, and snapdragons, to list only a few familiar names among the groups discussed in detail in Chapter 9.

A third major clade, with some 65,000 species, corresponds to the traditional **monocotyledons**. Almost half of the species of monocots are either orchids (about 20,000 species) or grasses (about 9000 species), but this group also includes palms, bromeliads, bananas, aroids, lilies, irises, and many other familiar and important plants (see Chapter 9).

Many of the features traditionally cited in support of the monocot clade may be ancestral angiosperm conditions, including flower parts in threes and monosulcate pollen. Other features may unite the monocots, such as scattered vascular bundles and loss of vascular cambium, parallel leaf venation, and development of the leaf blade from the basal part of the leaf primordium, but this depends on exactly what their relatives turn out to be and on relationships within the monocots. In the end, the presence of one seed leaf, or cotyledon, may be the morphological character that best distinguishes the monocotyledons (see Figure 4.42).

Note that the view of relationships we have just outlined is at odds with standard classifications in which flowering plants are divided into two major groups: the monocotyledons and the dicotyledons. Instead, the monocots make up a clade that is nested within the paraphyletic “dicots.”

POLLINATION, DISPERSAL, AND HABIT

Much of the diversity of flowers is related to pollination biology (see Chapter 4). Insect pollination is known from several other seed plant lineages: the modern cycads and the gnetophytes, as well as the fossil Bennettitales and possibly some Mesozoic “seed ferns.” Insect pollination was apparently established by the origin of crown-group angiosperms and was probably first carried out by pollen-eating or pollen-collecting insects, especially beetles and flies. Flowers pollinated by nectar-collecting insects evolved later. This conclusion is supported by the morphology of early angiosperm fossils, as well as by knowledge of pollination mechanisms in extant members of basal lineages (Friis et al. 1987; Thien et al. 2000).

It is unclear how much pollination by insects stimulated the early diversification of angiosperms, but the evolution of flowering plants apparently did not have a major impact on the origin of the major insect lineages, which evolved much earlier. It is abundantly clear, however, that diversification within some angiosperm and insect lineages has been causally linked.

Variation in fruit morphology is largely related to the use of different dispersal agents (see Chapter 4). Cretaceous fossil fruits and seeds are generally quite small, and there is no direct evidence of specialized dispersal by mammals or birds (see Friis et al. 1987). Adaptations for dispersal by frugivorous and granivorous animals apparently did not appear until later in the Cretaceous, and in most lineages probably originated in the Tertiary. Not until the Early Tertiary do we first see evidence of complex rain forests, and the major radiation of birds

and mammals occurred during the same time. The evolution of large colorful fruits and seeds was linked to the evolution of these groups.

Finally, it is interesting to contemplate the evolution of growth form within angiosperms and what effects this might have had on diversification. Most recent studies position woody plant lineages near the base of the tree. *Amborella* and Austrobaileyales are mostly shrubs or small trees, though they show a tendency toward vine-like growth. Modern representatives, at least, live in forest understory environments, and they show various adaptations to rather low-light environments (Feild et al. 2001). A major exception among the early lineages is the water lily clade, in which the plants are herbaceous and live in high-light aquatic environments. The extinct *Archaeofructus*, whose relationships are poorly resolved, was also probably an aquatic plant (Sun et al. 2002).

The herbaceous habit evolved early in angiosperm evolution, probably several times independently—for example, in Nymphaeales, Chloranthaceae, Piperales, *Ceratophyllum*, and monocotyledons. In several cases this development appears to be correlated with movement into aquatic habitats. Larger woody forms have also re-evolved from herbaceous plants on some occasions, though the evolution of “normal” wood was precluded in the monocots by the loss of the cambium. Within the monocots, large stature has instead been attained in several other ways—for example, through a specialized thickening mechanism in the apical meristem of palms; enlarged, stiffened leaf bases in the bananas and their relatives; and an anomalous form of cambial activity in the Rusceae, Agavaceae, and a few of their relatives (see Chapter 9).

Within the eudicots we see enormous variation in habit, but again there have been many shifts from woody to herbaceous growth form, some of these quite early in the evolution of the group. For example, herbaceous poppies (Papaveraceae) and buttercups (Ranunculaceae) may have evolved early, and independently, within one of the first major eudicot branches, the Ranunculales. *Nelumbo*, the water lotus, presents another early example involving a shift to the aquatic environment.

An important trend within eudicots has been the derivation of herbaceous lineages of temperate climate zones from within tropical woody plant lineages (Judd et al. 1994). These transitions often appear to be correlated with upward shifts in the rate of diversification (Judd et al. 1994; Magallon and Sanderson 2001), and taken together they have had a profound impact on angiosperm diversity.

Summary

The tremendous progress made over the last few decades in establishing phylogenetic relationships is now having a major impact on our understanding of

green plant evolution. Recent phylogenetic analyses have shown that some traditionally recognized groups are not monophyletic. For example, we appreciate that “plants” (autotrophic eukaryotes) originated independently through several separate endosymbiotic events. Within the green plant clade, traditional “green algae” are paraphyletic with respect to land plants, as are “bryophytes” with respect to vascular plants, “seedless vascular plants” with respect to seed plants, “gymnosperms” with respect to flowering plants, and “dicotyledons” with respect to monocots. As such groups are dismantled, major new clades are being identified, such as the streptophytes (some “green algae” plus embryophytes) and euphyllophytes (some “seedless vascular plants” plus spermatophytes).

A variety of long-standing phylogenetic questions have also recently been answered with considerable confidence. For example, the whisk ferns (*Psilotaceae*) are not remnants of the first vascular plants but instead are part of the monilophyte clade. Perhaps most surprising-

ly, the very base of the angiosperm tree is finally being resolved, with the *Amborella* and water lily branches diverging before a core angiosperm clade that includes the eudicots and the monocots.

Although phylogenetic progress has been rapid, many key questions remain unresolved. For example, we are more uncertain today than we were a decade ago about relationships at the base of the embryophytes, as well as among the major seed plant lineages. Where do the gnetophytes fit, and what really are the closest relatives of the flowering plants? And within core angiosperms, what are the closest relatives of the monocots and the eudicots?

These important questions are proving to be very difficult to resolve, but the successes of the last few decades suggest that answers will eventually be forthcoming. Experience also implies that analyses integrating evidence from a wide variety of sources—molecular data, morphology, development, and the fossil record—stand the best chance of lasting success.

Literature Cited and Suggested Reading

References marked with an asterisk (*) are other reviews focused on phylogenetic relationships and are especially recommended for additional information and viewpoints. References marked with a number symbol (#) are standard texts on comparative plant anatomy, morphology, physiology, and paleobotany that can be consulted for background information on specific characters and groups of organisms. These sources are not specifically cited in the text of this chapter, but they provide the basis for discussions of life cycles and morphological evolution. The symbol @ identifies recent symposia on gnetophyte and angiosperm phylogeny.

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