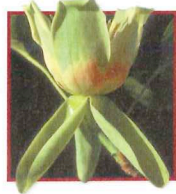
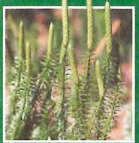


7

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, plants produce carbohydrates from carbon dioxide and water in the presence of chlorophyll inside organelles called chloroplasts. Sometimes the term *plant* is extended to include autotrophic prokaryotic forms, especially the bacterial lineage known as the cyanobacteria (or blue-green algae). Many traditional botany textbooks even include the fungi, which differ dramatically from green plants in being heterotrophic eukaryotic organisms that enzymatically break down living or dead organic material and then absorb the simpler products of digestion. Fungi appear to be more closely related to animals, another lineage of heterotrophs characterized by relatively rapid movement and by eating other organisms and digesting them internally.

In this chapter we first briefly discuss the origin and evolution of several separately derived 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 origin of the land plants (embryophytes), the vascular plants (tracheophytes), the seed plants (spermatophytes), and the flowering plants (angiosperms).

Although knowledge of fossil plants is critical to a deep understanding of each of these shifts, and although we will mention some key fossils, 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 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 in this chapter is to chronicle the evolutionary events leading up to the 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 their diversity is the focus of this book.

Before we proceed, it is important to 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 most of the traditional "green algae." In other cases, different names have been used for the same group; for example, 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 it typically reflects only the traditions of the relevant taxonomic community. Thus taxa assigned to a particular taxonomic rank (such as a 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, mosses, and hornworts. In recent years, however, it has become clear that these groups probably 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 "dicotyledons." 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 containing just the extant "naked-seed plants").

In this chapter we will not refer to taxonomic ranks. Elsewhere in the text, major clades within the 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 for our discussion of green plant phylogeny.

In general, 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." Efforts are under way to provide a new system of names for the major clades of vascular plants (Cantino et al., 2007), and a number of small name changes have been made in this edition of the text for consistency with this treatment. Throughout, we have avoided using names that refer to nonmonophyletic 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 their membranes) and molecular studies establishing that the DNA in plastids is more closely related to that in free-living cyanobacteria than it is to DNA in the nucleus of the same cell.

Endosymbiosis entailed massive reductions in the size and gene content of the plastid genome relative to that of free-living cyanobacteria (Delwiche et al. 2004). For example, the free-living cyanobacterium *Nostoc* has a genome size of some 6400 kilobases and over 6500 genes, whereas a red algal chloroplast has only about 190 kilobases and 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., Martin et al. 2002). There are many more proteins active within plastids (from 500 to 5000) than there are genes, which means that some of these proteins are products of genes that reside outside the plastids.

How many endosymbiotic events have there been? Recent phylogenetic evidence is consistent with just a single primary endosymbiotic event (Palmer 2003; Delwiche et al. 2004; Keeling 2004). For example, recent analyses of eukaryote phylogeny (see Baldauf et al. 2004) recover a clade containing viridophytes (green plants), rhodophytes (red algae), and glaucophytes, sometimes referred to as the archaeplastid clade or primoplantae (Figure 7.1). This result, combined with plastid gene order and composition and the presence of two membranes, suggests that a primary endosymbiotic event occurred in the common ancestor of this clade. In the glaucophytes, the cyanobacterial cell wall still surrounds 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 each other (e.g., in structure and in light harvesting mechanisms), which makes it possible to distinguish with considerable confidence between a red plastid lineage and a green plastid lineage (Delwiche et al. 2004;

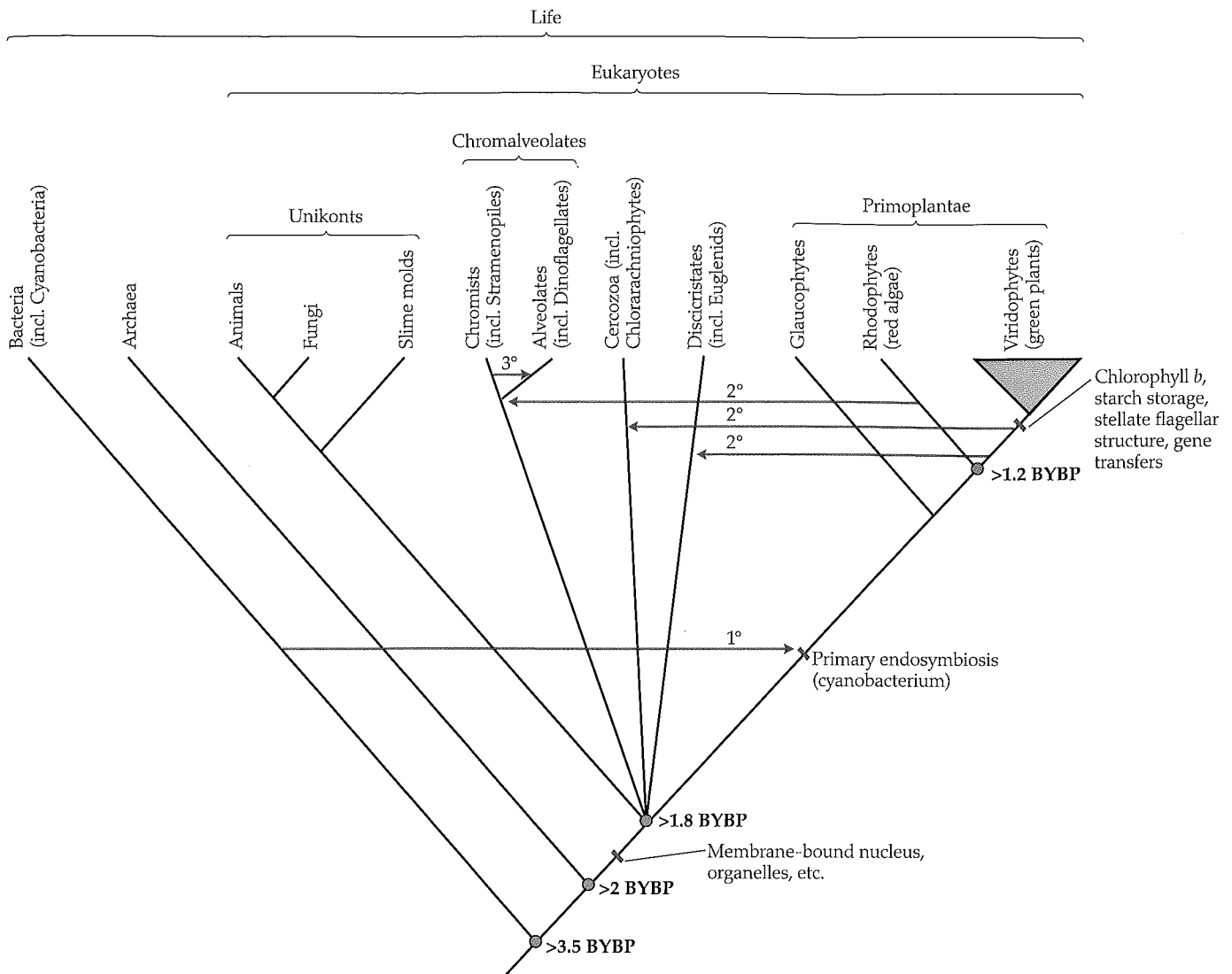


FIGURE 7.1 Phylogenetic tree of life, showing the positions of green plants (viridophytes) and various “algae” among the eukaryotes as well as characters marking several major clades. Red arrows represent primary, secondary, or tertiary endosymbiotic events.

One recent hypothesis for the eukaryotes places their root along the unikont branch, thus separating a clade that initially had one cilium from a clade that initially had two cilia. BYBP, billion years before present. (Adapted from Baldauf et al. 2004.)

Keeling 2004). This distinction helps us to identify instances in which plastids have been acquired by permanent incorporation of either red or green eukaryotes (see Figure 7.1). It appears that red algal chloroplasts were acquired via such secondary endosymbiosis at the base of the chromalveolate clade, which includes a chromists line, with brown algae and diatoms, and an alveolate line, with dinoflagellates and apicomplexans (the later including *Plasmodium*, the malaria parasite, which contains remnant colorless plastids). Secondary endosymbiotic events involving the uptake of green algae appear to account for the chloroplasts in euglenids (within Discicristates) and chlorarachniophytes (within Cercozoa). Dinoflagellates include a mixture of different types of plastids, and the chloroplasts in one subgroup may even have originated via a tertiary endosymbiotic event (Yoon et al. 2002).

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. Before we provide brief descriptions of several of the major groups of “algae,” we must 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 in 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 between 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, including coral reefs (Saunders and Hommersand 2004). 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, and their chloroplasts are descended from the primary endosymbiotic event that pre-dated the divergence of these two lineages.

The **chromalveolates** include the chromists, which in turn include the stramenopiles, and the alveolates, which include the dinoflagellates (see Figure 7.1). **Stramenopiles** include the brown algae and diatoms (and several other groups of algae), along with the water molds (oomycetes), which were formerly considered to be fungi (Andersen 2004). The stramenopile clade (sometimes called the heterokonts) 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 their 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 animals.

There are about 6000 living species of **diatoms** (bacillariophytes), and many more (perhaps as many as 40,000 species) are known from fossils. Owing to their still largely uncharted diversity (Norton et al. 1996), they may be “the insects of the microbial world.” Diatoms are unicellular organisms (though they sometimes 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 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 **alveolates** include the dinoflagellates, ciliates, and apicomplexans (see Figure 7.1) and are characterized by small membrane-bound sacs (alveoli) under the cell surface. **Dinoflagellates** (Hackett et al. 2004) include about 3000 described species, found in both fresh and salt water. They have two flagellae located in characteristic grooves between cellulose plates embedded in the cell wall, 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 coral reefs; for example, the phenomenon known as coral “bleaching” involves the loss of the zooxanthellae. Other dinoflagellates that produce highly toxic substances are responsible for periodic “red tides” or “algal blooms,” which can have dramatic effects on other organisms.

Viridophytes (Green Plants)

As shown in Figure 7.2, the traditional “green algae” are related to the land plants, and together these organisms constitute a clade known as the **green plants** (viridophytes). This clade includes more than 300,000 described species, or over one-sixth of all known extant species on Earth. Molecular evidence, 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), strongly supports the monophyly of the green plants. This clade is also supported by numerous chemical and morphological features, including the loss of phycobilins (found in cyanobacteria, glaucophytes, 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.

Most phylogenetic analyses (e.g., Karol et al. 2001) have supported 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 among the “green algae” (see Figure 7.2). Several lineages of unicellular organisms with distinctive scaly cell walls (so-called micromonads, or prasinophytes) are situated around the base of green plant phylogeny, and one of these, *Mesostigma*, has appeared as either the sister group of all other green plants (Jürmel et al. 2002) or, more often, as the sister of the streptophyte line (Kim et al. 2006).

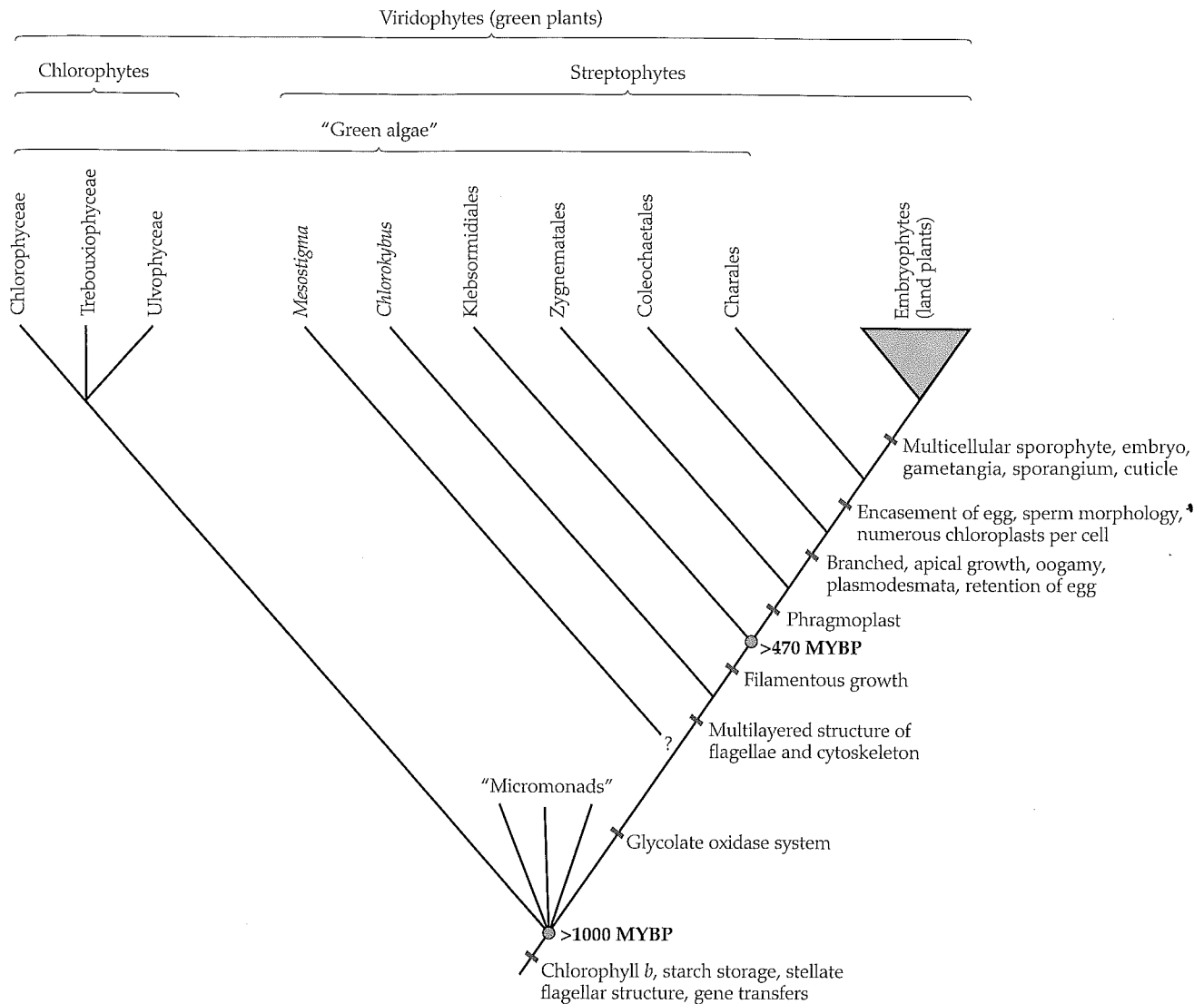


FIGURE 7.2 Green plant phylogeny, showing the separation of chlorophytes from streptophytes, the relationship of some former "green algae" to embryophytes, and characters marking major clades. MYBP, million years before present. (Adapted from Karol et al. 2001 and Delwiche et al. 2004.)

Chlorophytes

Within the chlorophytes there are three well-supported clades (see Figure 7.2): Chlorophyceae, Ulvophyceae, and Trebouxiophyceae (Lewis and McCourt 2004). Relationships among these clades remain unsettled, but gene order and other molecular characters suggest that the ulvophytes and the chlorophytes may be linked (Pombert et al. 2005).

The **Chlorophyceae** are marked by somewhat obscure ultrastructural features (such as clockwise rotation of the flagellar basal bodies), but they have been supported as a clade in most molecular studies. Included within this line is the so-called volvocine lineage, which encompasses progressively more complex colonies (from 4 cells in *Gonium* to as many as 500–50,000 cells in the hollow spherical

colonies of *Volvox*). These colonies 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.

The **Ulvophyceae** include many marine forms and are marked by the production of multinucleate cells (Figure 7.3D–F). In some, the entire body lacks 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 (apparently derived several times independently) that lack motile cells at any stage. Many of the nonmotile forms live in terrestrial habitats, often in association with lichen-forming fungi or

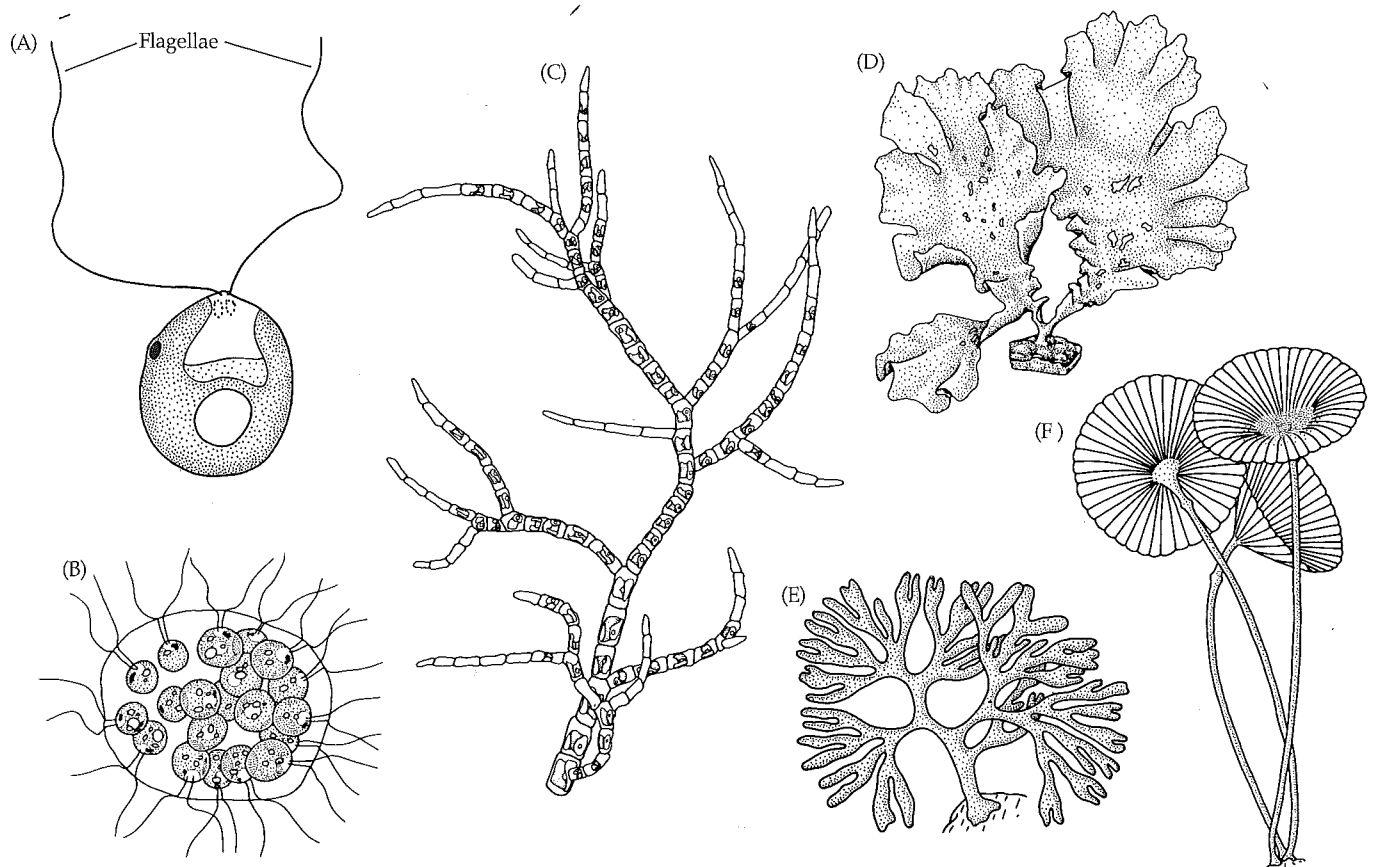


FIGURE 7.3 Morphology of chlorophytes. (A–C) Chlorophyceae: (A) *Chlamydomonas*, showing flagellae. (B) *Eudorina*, a colonial “volvocine” form. (C) *Stigeoclonium*, a branched filamentous form. (D–F) Ulvophyceae: (D) *Ulva*. (E) *Codium*, showing a coenocytic diploid thallus; (F) *Acetabularia*. (From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

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). 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 this phragmoplast occurred in the charophycean algae (or “charophytes”): the Coleochaetales and Charales. These plants show a range of different growth forms (including upright, branching forms, as in *Chara* and *Nitella*, and flattened forms, as in *Coleochaete*) and live in nearshore 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 also belong in the

streptophyte clade, including Klebsormidiales and Zygnematales (Lewis and McCourt 2004). 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 data (Karol et al. 2001; Delwiche et al. 2004), including structural characters such as the movement of genes from the chloroplast to the nucleus. Coleochaetales and Charales possess some functionally important traits that are otherwise found only in land plants, such as flavonoids and the chemical precursors of a 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

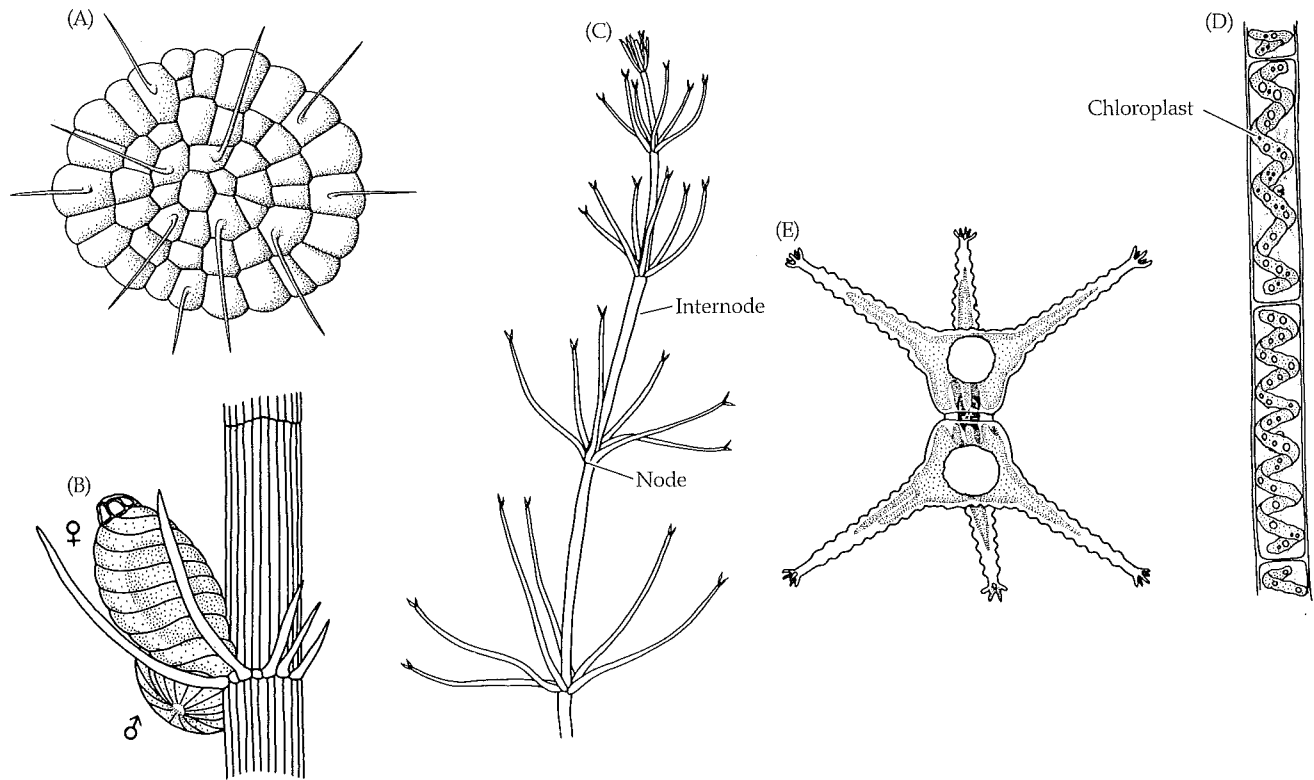


FIGURE 7.4 Morphology of basal streptophytes. (A) *Coleochaete*, showing a haploid discoidal thallus, with setae. (B, C) Charales: (B) *Chara*, showing a node with an egg-bearing structure (above) and a sperm-producing structure (below). (C) *Nitella* habit, showing

node and internode construction. (D, E) Zygnematales: (D) *Spirogyra*, a filamentous form, showing helical chloroplasts. (E) *Staurastrum*, a unicellular desmid, forming two mirror-image semi-cells. (A from Taylor and Taylor 1993; B–E from Scagel et al. 1969.)

volvocine forms explored a lifestyle in which the cells became aggregated into colonies. The larger colonies 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 *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 charophycean lineages plus 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* evolved a life cycle like that of humans, in which gametes are the only haploid cells. In the charophycean lineages, the plants are haploid, and the only diploid cell in the life cycle is the zygote, which results from fertilization of a large non-motile egg by a swimming sperm.

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 evidence (Kenrick and Crane 1997a,b; Karol et al. 2001; Wolf et al. 2005; Qiu et al. 2006). 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 because several algal lineages (e.g., some Trebouxiophyceae) have independently (though less conspicuously) made the transition to life on land. In addition to the embryo, embryophytes are characterized by the production of a multicellular sporophyte, multicellular reproductive structures (gametangia and sporangia), a cuticle, and thick-walled spores with characteristic trilete marks (see Figure 7.7A).

Traditionally, embryophytes have been classified as either bryophytes or vascular plants. There are three major lineages of bryophytes—liverworts, mosses, and hornworts—which we will characterize briefly in the next few paragraphs (see also Shaw and Goffinet 2000; Shaw and Renzaglia 2004). As we will see, it has become increasingly clear that the “bryophytes” are paraphyletic with respect to the vascular plants (see Figure 7.6).

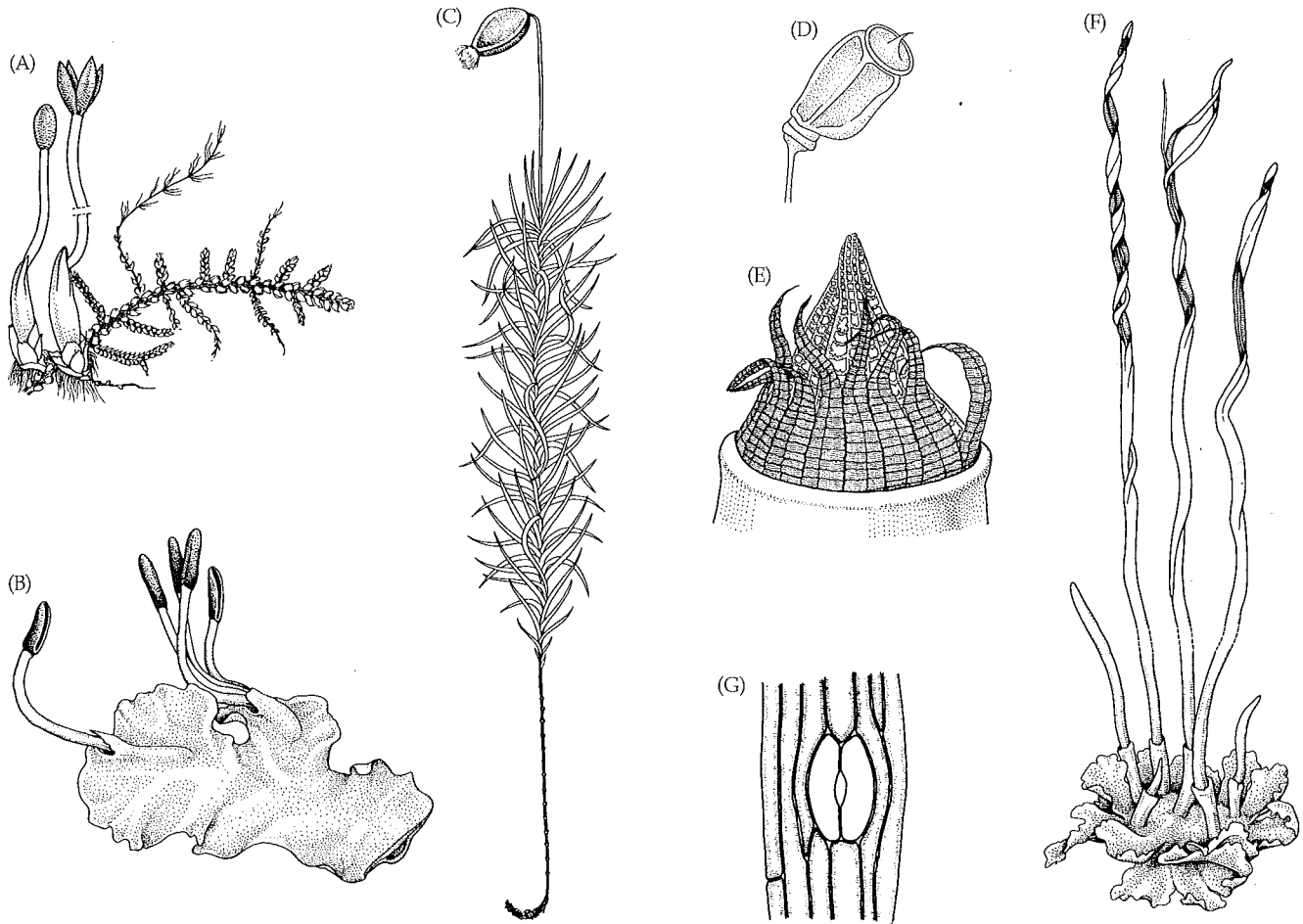


FIGURE 7.5 Morphology of basal embryophytes ("bryophytes"). (A, B) Liverworts: (A) A leafy liverwort, *Lepidozia reptans*, showing dehiscence of the sporangium by four valves. (B) Portion of a thalloid liverwort, *Monoclea forsteri*, showing sporangia with longitudinal dehiscence. (C–E) Mosses: (C) *Dawsonia superba* habit, showing upright, leafy gametophyte and unbranched sporophyte with terminal sporangium. (D) Sporangium (capsule) of a

moss prior to dehiscence. (E) Apex of the dehiscing sporangium of a moss, *Fontinalis antipyretica*, showing the peristome teeth. (F, G) Hornworts: (F) *Phaeoceros laevis* habit, showing the thalloid gametophyte and dehiscing sporangia of the sporophyte. (G) Stoma, with guard cells, from the sporangium wall of *Anthoceros*. (A–B, D–G from Scagel et al. 1969; C from Barnes 1998.)

Liverworts

There are about 8000 species of **liverworts**, which come in a thalloid form or, more commonly, a derived leafy form (Figure 7.5A,B). Unlike mosses and hornworts, liverworts lack stomata, 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 been interpreted as ancestral within land plants.

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.

Mosses

Mosses are probably the most familiar bryophytic plants, and with some 10,000 species, they are also the most diverse. The upright, leafy gametophyte is the dominant phase in the moss life cycle (Figure 7.5C). The sporophyte forms a single unbranched stalk terminated by a sporangium (or capsule) (Figure 7.5D). 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 protonema 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; Qiu et al. 2006). The enigmatic *Takakia*, which was considered to be a liverwort until the recent discovery of the sporophyte phase, now appears to be related to *Sphagnum*. The sporangium of *Andreaea* opens by four vertical slits, and that of *Takakia* by a single helical slit, in contrast to the lidlike operculum found in the vast majority of mosses. The operculum of most mosses is also characterized by a distinctive row of toothlike structures, which together make up the peristome (Figure 7.5E).

Hornworts

There are only about 100 species of hornworts (Figure 7.5F,G), which are encountered much more rarely than either mosses or liverworts. One presumably derived feature of this entirely thalloid group is the presence of a meristem in the sporophyte located at the base of the capsule. The activity of this meristem accounts for the contin-

ued upward growth of the capsule, which is quite extensive in some groups (e.g., *Anthoceros*).

Phylogenetic Relationships within Embryophytes

Phylogenetic analyses of land plants that have included an adequate sampling of species have found that the "bryophytes" are paraphyletic. However, the exact relationships are still controversial. Early morphological analyses supported a basal split between the liverwort lineage and everything else (Figure 7.6A), and placed the mosses as the sister group to the vascular plants (Mishler and Churchill 1985). Under this view, stomata 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, were interpreted as precursors of the water- and nutrient-conducting cells found in vascular plants. Mosses and vascular plants both have sporophytes that increase in height through cell divisions in an apical meristem, and the first vascular plants had upright gametophytes, as mosses do.

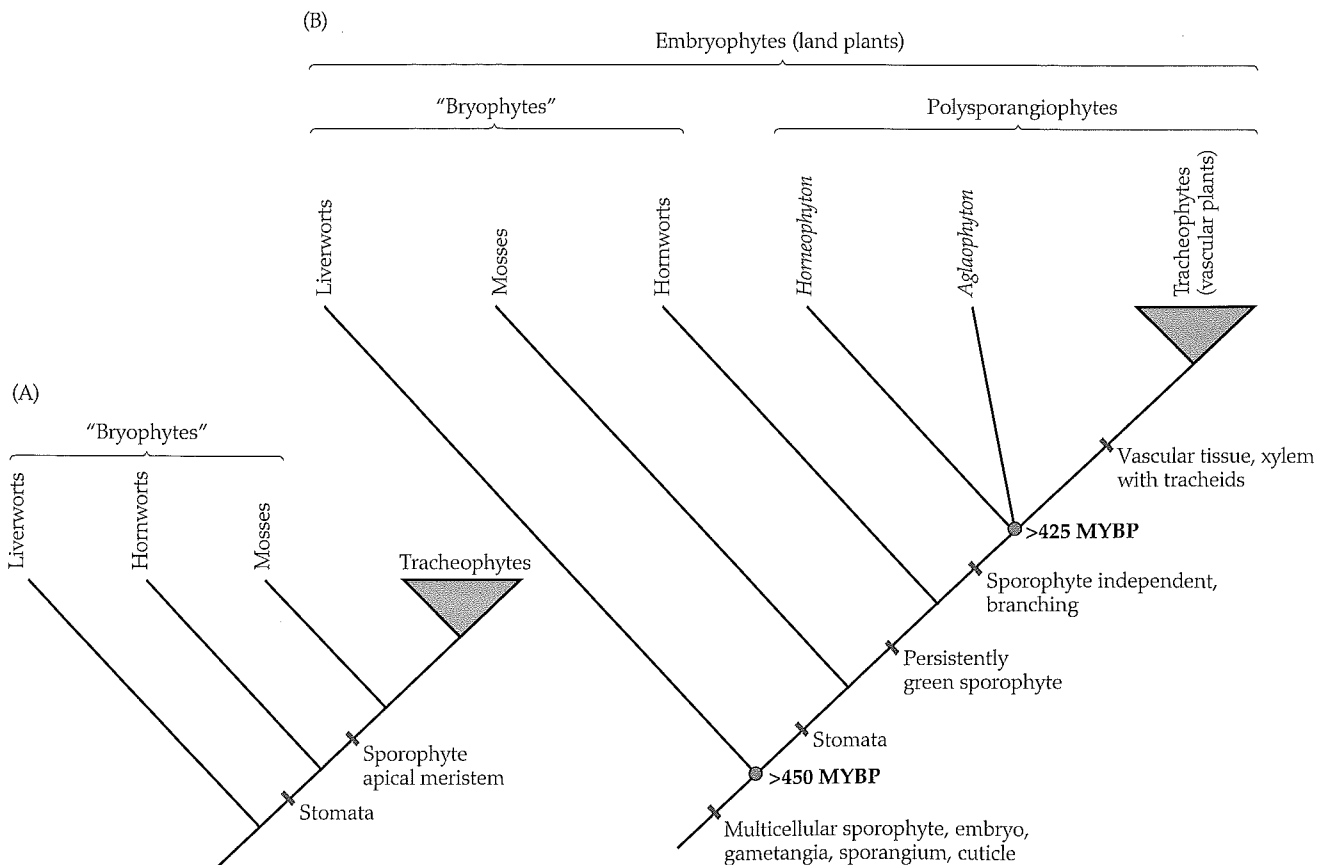


FIGURE 7.6 Phylogenetic relationships at the base of the embryophytes (land plants), showing characters that mark major clades under two hypotheses of how the bryophytic lineages (liv-

erworts, mosses, and hornworts) are related to the vascular plants. MYBP, million years before present. (A adapted from Mishler and Churchill 1985; B adapted from Qiu et al. 2006.)

Several recent molecular studies, however—alone and in combination with a variety of ultrastructural characters (especially sperm ultrastructure)—have supported alternative hypotheses. In some trees, hornworts appeared as the sister group of all other extant land plants, and a clade containing mosses and liverworts was sister to the vascular plants (e.g., Renzaglia et al. 2000). The most recent analyses (e.g., Qiu et al. 2006) support the view depicted in Figure 7.6B, in which liverworts are sister to all other embryophytes and hornworts are sister to the vascular plants. This hypothesis remains consistent with a single origin of stomata, although hydroids and leptoids in mosses probably are not homologous with tracheids and sieve cells in vascular plants (Ligrone et al. 2000) and the stalk of the moss sporophyte may not be homologous with the stem in vascular plants (Kato and Akiyama 2005).

Transition to Land

This phylogenetic knowledge illuminates the origin of several key adaptations to life on land (Graham 1993; Waters 2003). Cuticle and sporopollenin (present in the thick spore wall) appear to be evolutionary responses to desiccation. Gas exchange is facilitated by small pores in the epidermis or by genuine stomata with guard cells that can open or close them depending on environmental conditions, thereby regulating water loss. Flavonoids help plants absorb damaging long-wavelength UV radiation. A glycolate oxidase system helps them cope with the inhibition of carbon dioxide fixation by oxygen, which is present in much higher concentrations in 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 (in which they are ubiquitous). The precursors of many of these adaptations can be found among the Coleochaetales and Charales, which therefore appear to have been preadapted to make the transition to land (Graham 1993).

Knowing 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 generations (Graham 1993). In Coleochaetales and Charales, the egg is retained on the haploid parent plant, and, 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 including the charophycean 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. Sperm are produced and protected by a multicellular structure called an antheridium. Initially, the gametophyte phase was dominant, as it is today in liverworts, mosses, and hornworts, and the sporophyte remained attached to, and was nutritionally dependent on, the gametophyte (though perhaps less so in hornworts; Qiu et al. 2006). In vascular plants, the sporophyte became dominant and nutritionally independent, and there was progressive reduction in gametophyte size (Kenrick and Crane 1997a,b).

These findings also help us interpret the absolute timing of events in embryophyte evolution (see Figures 7.1, 7.2, and 7.6). Green plants may be a billion or more years old, and some major green plant lineages existed in the Precambrian (Heckman et al. 2001). A variety of chlorophyte fossils have been found in the Cambrian (about 550 million years ago), such as well-preserved, lime-secreting Ulvophyceae, including 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 began in the mid-Ordovician, some 470 million years ago (Wellman et al. 2003; Sanderson 2003). Dispersed spores have been found from that time (and possibly even earlier, in the Cambrian), sometimes in envelope-enclosed tetrads or dyads (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 (Figure 7.7A) have been recovered from the early Silurian. It is probable, therefore, that liverworts, mosses, hornworts, and vascular plants were all in existence by the late Ordovician. Somewhat later, beginning in the mid-Silurian, well-preserved macrofossils representing the vascular plant lineage are found. The occupation of land was certainly in full swing by then.

Tracheophytes (Vascular Plants)

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 7.7B,C). These plants had no leaves or roots. In some cases (e.g., *Aglaophyton*, formerly known as *Rhynia*, from the Rhynie chert in Scotland), the preservation of these plants is spectacular, and it is possible to discern many anatomical details, including stomata, spores, and vascular tissue inside the stem. These fossils revealed that the first **polysporangiophytes**—plants with branching sporophytes—did not actually produce specialized water-conducting cells (**tracheids**) in the xylem tissue and

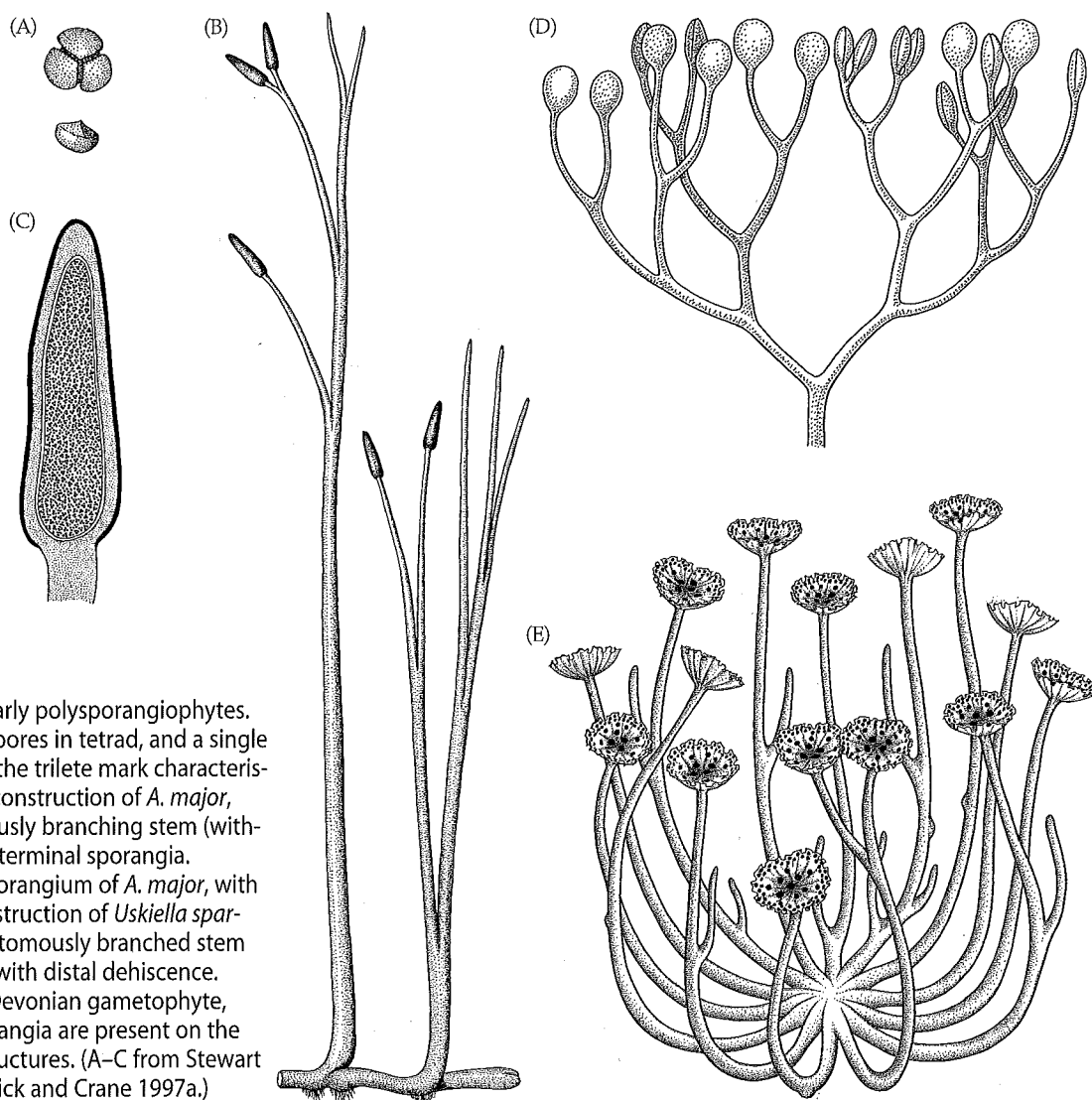


FIGURE 7.7 Fossils of early polysporangiophytes. (A) *Aglaophyton major* spores in tetrad, and a single thick-walled spore with the trilete mark characteristic of land plants. (B) Reconstruction of *A. major*, showing the dichotomously branching stem (without leaves or roots) and terminal sporangia. (C) Enlarged terminal sporangium of *A. major*, with spores inside. (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.)

must therefore have depended on turgor pressure to remain upright (Kenrick and Crane 1997a). True water-conducting cells evolved somewhat later and characterize the true vascular plants: the **tracheophytes** or **Tracheophyta**.

Tracheids are elongated 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, the tracheids were of a distinctive type, in which the cell wall had only a very thin decay-resistant layer (conferred by lignification of cellulose fibers). Cell walls that are much more decay-resistant characterize an included clade, which contains 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.

In recent years, careful paleobotanical studies have revealed that some early land plant fossils are actually haploid gametophytes, bearing antheridia and archegonia, apparently on separate plants (Remy et al. 1993; Taylor et al. 2005). These fossils are remarkable because they are relatively large, upright, and branched, and in some ways resemble the sporophyte phase of the life cycle (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 comparison to the bryophytic groups, it seems that both the gametophyte and the sporophyte generations were initially 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, a condition retained today in the “free-sporing” lineages such as ferns and lycophytes. With the evolution of seed plants, however, the gametophyte became much further reduced and eventually became completely dependent on the sporophyte.

Viewed in this context, the “bryophyte” groups (especially the mosses) and the vascular plants appear to have explored different mechanisms to increase the number of spores produced per fertilization event (Mishler and Churchill 1985). In mosses, this increase in spore production was accomplished by intercalation of a filamentous protonemal stage that could produce numerous unbranched leafy gametophytes, each bearing a single unbranched sporophyte terminated by a single sporangium. In contrast, in the vascular plant lineage the number of sporangia was increased by the branching of the sporophyte so that each branch tip could bear a sporangium.

What factors might have favored the elaboration of the sporophyte phase as opposed to the gametophyte phase (which became increasingly specialized for sexual reproduction)? One hypothesis invokes the buffering of diploid organisms against deleterious mutations. But an alternative hypothesis is that the sporophyte was free to become larger (which was advantageous in competing for light and may also have enhanced spore dispersal), whereas the gametophyte was dependent on water for fertilization as long as the sperm needed to swim to the egg.

Phylogenetic relationships among the major lines of extant vascular plants are shown in Figure 7.8. These conclusions are based on morphological and molecular evidence, and most of them are now quite strongly supported (Doyle 1998; Pryer et al. 2004a). The basal split, which occurred in the early to mid-Devonian (before 400 million years ago), separated a clade that includes the modern lycop-

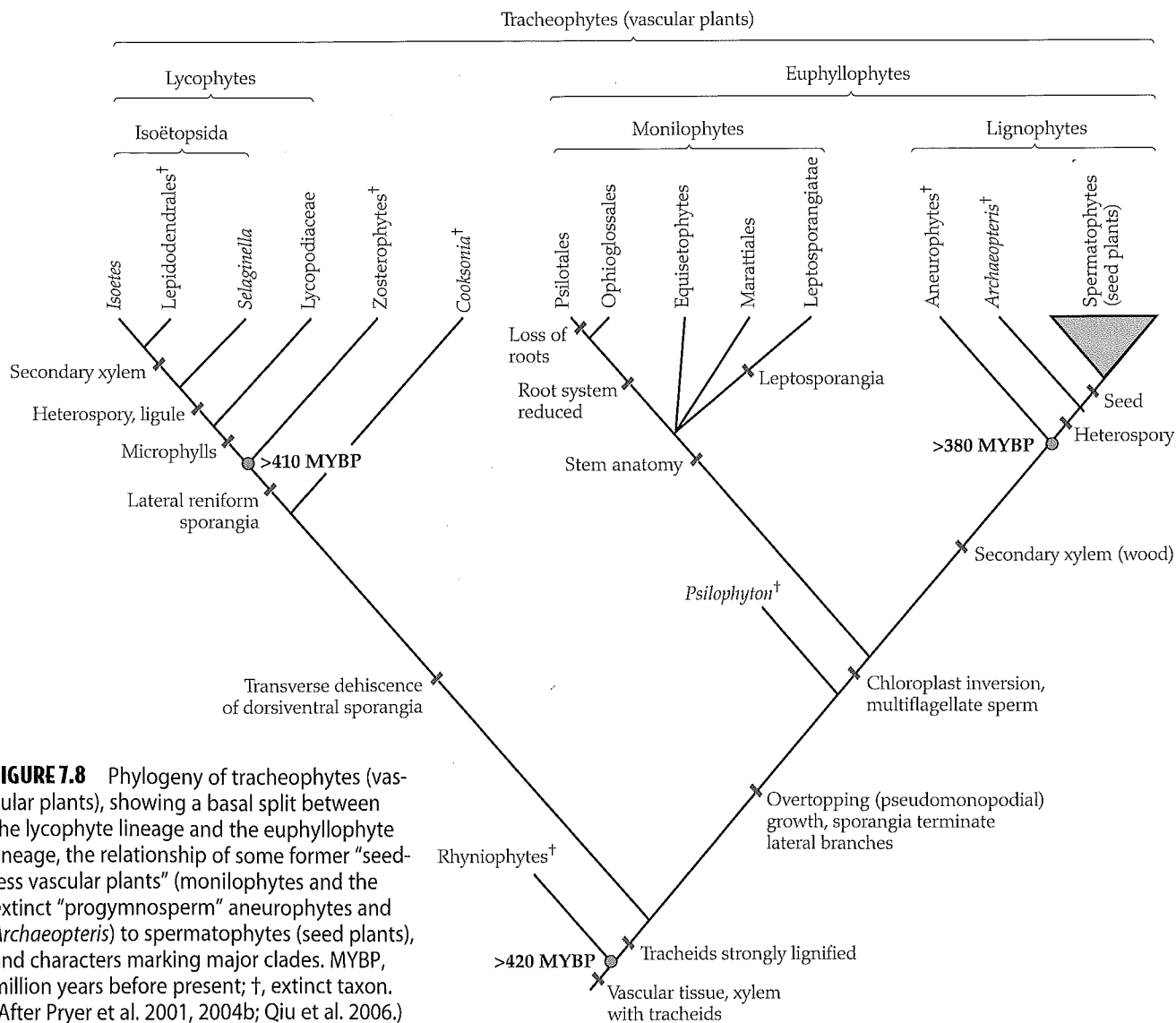


FIGURE 7.8 Phylogeny of tracheophytes (vascular plants), showing a basal split between the lycophyte lineage and the euphyllophyte lineage, the relationship of some former “seedless vascular plants” (monilophytes and the extinct “progymnosperm” aneurophytes and *Archaeopteris*) to spermatophytes (seed plants), and characters marking major clades. MYBP, million years before present; †, extinct taxon. (After Pryer et al. 2001, 2004b; Qiu et al. 2006.)

phyte lineage from another clade, known as the euphyllophytes, that contains all of the other extant vascular plant lineages. This split is marked by a variety of morphological features. One noteworthy feature is the presence of multiflagellate sperm in the euphyllophytes, as opposed to biflagellate sperm in the bryophytic lineages and in the lycophytes (except in *Isoetes* and *Phylloglossum*, in which multiflagellate sperm evolved independently). One compelling bit of molecular evidence is the derived presence in modern euphyllophytes of a 30-kilobase inversion in the chloroplast DNA (Raubeson and Jansen 1992; Wolf et al. 2005).

Lycophytes

The lineage that includes the modern **lycophytes**, or **Lycopodiophyta** (Lycophyta) (Figures 7.8 and 7.9A–C; see also Figures 8.1 and 8.2), appeared in the fossil record very soon after the first appearance of vascular plants. It is marked by the lateral position, reniform (kidneylike) shape, and transverse dehiscence of the sporangia. **Microphylls** (small 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, dominating coastal swamps of tropical lowlands (Bateman et al. 1998). The remains of these plants account for our major coal deposits.

Some lycophytes, such as *Lepidodendron*, became large trees, with secondary growth allowing an increase in girth (Figure 7.9D). The stems of these plants were covered by microphylls, which left the distinctive leaf bases seen in fossils (Figure 7.9E). These plants also evolved so-called stigmairian 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, but they may have grown very slowly in height at first (while the root system became established) and later elongated rapidly, and may have died after producing strobili (cone-like structures) at the tips of all the branches simultaneously (Phillips and DiMichele 1992; see Donoghue 2005).

Today there are some 1200 species of lycophytes belonging to several major lines (see Figure 7.8 and 7.9). Rhizomatous species of *Huperzia* 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 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 (Isoëtopsida; see Figure 7.8), which is also united by the association of a leaflike 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* and the other very large lycophyte trees. *Isoetes* has retained the cambium and some secondary growth, and it has rootlets that resemble those of the extinct trees (Figure 7.9J).

Euphyllophytes

The lineage that includes the modern **euphyllophytes**, or **Euphyllophyta** (see Figure 7.8), is marked by differentiation between a main axis and side branches (pseudomonopodial growth), a key development first seen in a variety of Devonian fossils known as trimerophytes (Figure 7.10A; see Donoghue 2005). According to the “telome theory” (Zimmermann 1965), **megaphylls** (the large leaves characteristic of the euphyllophytes) were derived from flattened lateral branch systems. This derivation involved planation (flattening) 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 and euphyllophyte lines. Even within the euphyllophytes, it appears that laminated megaphylls originated several times independently (e.g., in ferns, equisetophytes, and seed plants), in each case through the activity of a meristem located at the margin of the developing organ (Boyce and Knoll 2002).

Living euphyllophytes appear to belong to two major clades (see Figure 7.8): the seed plants (**spermatophytes** or **Spermatophyta**) and a clade that includes several “fern” lineages, the horsetails, and the whisk ferns (the **monilophytes** or **Monilophyta**). This new view of euphyllophyte relationships is supported by analyses of morphological characters and both chloroplast and nuclear genes (Pryer et al. 2004b; Rothwell and Nixon 2006). Within the monilophytes there are five major lineages, each discussed only briefly here: (1) leptosporangiate ferns (Leptosporangiales), (2) Marattiales, (3) Ophioglossales, (4) Psilotales, and (5) equisetophytes (see also Chapter 8).

The common name *fern* is applied to the members of three of these major lineages: Leptosporangiales, Marattiales, and Ophioglossales. These plants are superficially similar in usually having large (often highly dissected) frondlike 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 (Figure 7.10B,C) and the Ophioglossales are so-called eusporangiate ferns. These plants appear to have retained the ancestral condition, in which the sporangium develops from several initial cells and has a mature wall that is more than one cell layer thick. These eusporangia also tend to contain large num-

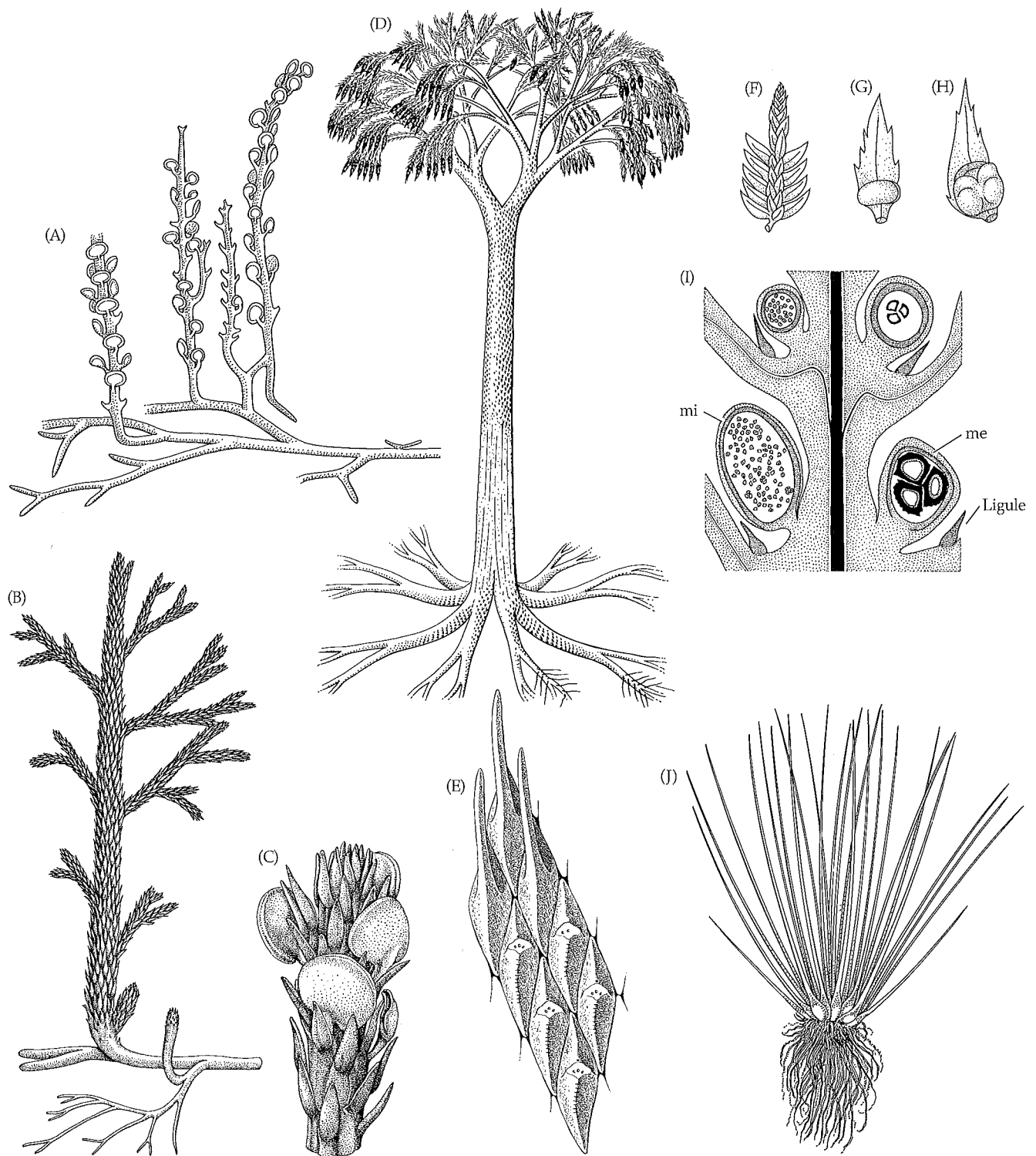


FIGURE 7.9 Morphology of lycophytes and their relatives. (A) Reconstruction of the extinct *Zosterophyllum deciduum*, showing prostrate rhizome bearing leafless upright axes with lateral reniform sporangia. (B) Reconstruction of the extinct *Asteroxylon mackiei*, showing upright dichotomously branching stems covered by microphylls, as well as 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 *Lepidodendron* sp.,

showing three attached microphylls and the scars left by the abscission of five others. (F) Tip of a branch of *Selaginella*, showing microphylls 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.)

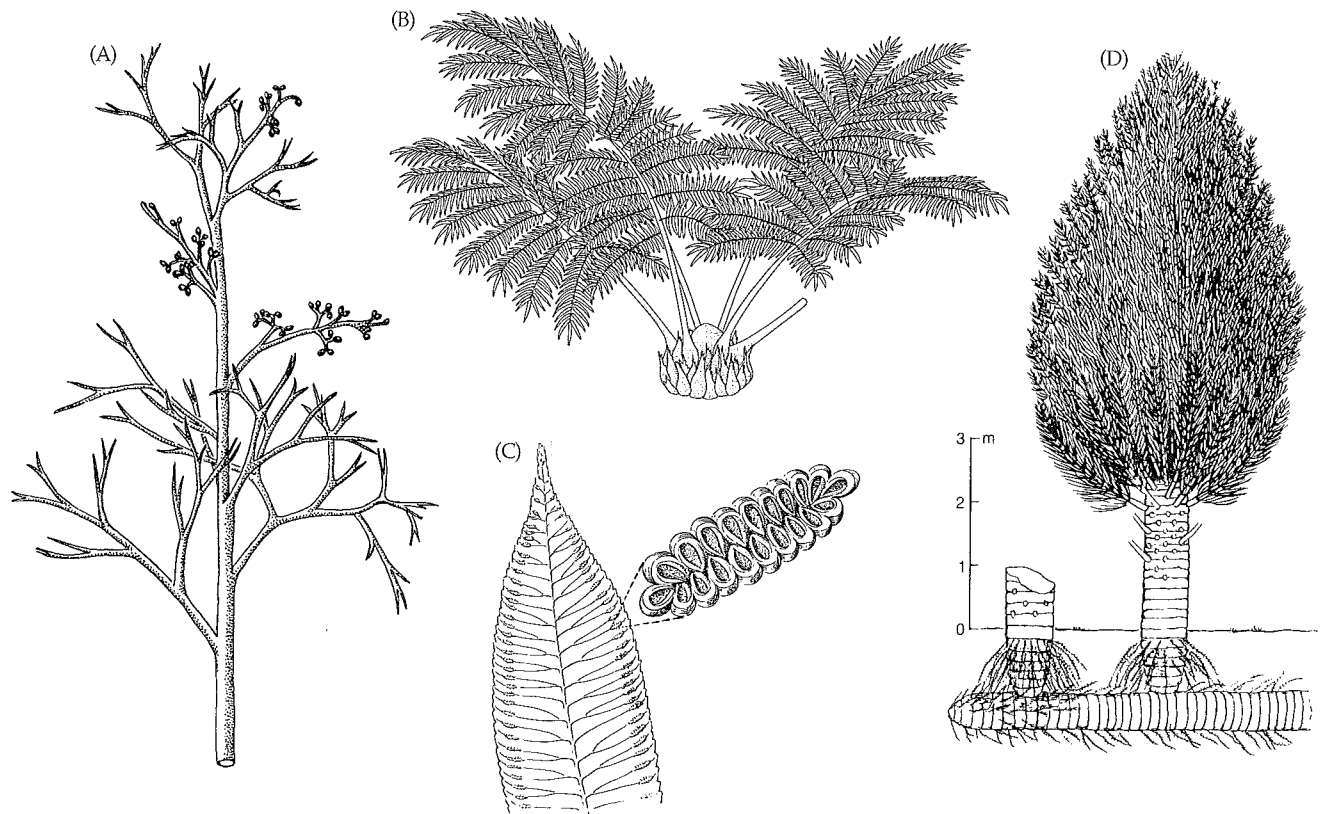


FIGURE 7.10 Morphology of various euphyllophytes. (A) The extinct trimerophyte *Psilophyton forbesii*, showing pseudomonopodial growth (differentiation between a main trunk and side branches). (B) Large, arching leaves of *Angiopteris* (Marattiales). (C) The lower (abaxial) surface of a fertile leaflet of

Angiopteris, showing a cluster of eusporangia. (D) Schematic representation of an extinct treelike equisetophyte, *Calamites*, showing the stout rhizome and tall, upright, branching shoot. (A from Stewart 1983; B from Barnes 1998; C and D from Gifford and Foster 1989.)

bers of haploid spores at maturity. In contrast, the leptosporangiates are characterized by a derived development in which the sporangium arises from a single cell and has a mature wall only one cell layer thick. These leptosporangia are borne on a distinct stalk and have a characteristic structure called an **annulus**, consisting of a row of cells with thickened inner walls and thin outer walls (see Figure 8.13). The leptosporangia of most species contain a relatively small and definite number of haploid spores (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 **Leptosporangiatæ**, of which there are more than 12,000 living species (see Figures 8.4 and 8.8–8.19). Many of these plants have highly dissected pinnate leaves, of the type we commonly associate with ferns, but leaf form is actually extremely variable within this group, and some species even have simple, undissected leaves. The sporangia are typically produced in small clusters called **sori** (singular **sorus**) on the undersides of the leaves. The sori are often covered by a flap of tissue called an **indusium** (plural **indusia**), 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 lineage, recent morphological and molecular studies have identified several noteworthy clades (Pryer et al. 2004b; Smith et al. 2006). 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 (Cyathaceae), and another contains all 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 8.9), the existence of fossil intermediates also supports the monophyly of the group (Rothwell 1999).

The **Marattiales**, which are mainly plants of the wet tropics, tend to have very large pinnate fronds with thick-

walled eusporangia in distinctive clusters (sometimes fused) on the lower surfaces (see Figure 7.10B,C). There are perhaps 150 living species in this clade, most of which belong to *Angiopteris* or *Marattia*, but it has a long fossil record, and extinct relatives (especially *Psaronius*) were important components of Carboniferous swamps. Consistent with their relative morphological stasis, these plants may also have a decelerated rate of molecular evolution (Soltis et al. 2002).

The **Ophioglossales** (with perhaps 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, tuberlike structures that are associated with an endophytic fungus.

The **Psilotales**, or **psilophytes**, include 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 studies have established with considerable certainty that neither of these ideas is correct (Pryer et al. 2001, 2004b). Instead, it appears that the Psilotales are most closely related to the Ophioglossales, with which they share some similarities in gametophytes, in the reduction (or loss) of roots, and in the development and position of the sporangia. Under this view, the tiny leaves and the absence of true roots in the psilophytes are derived conditions.

Today there are only about 15 species of **equisetophytes**, or horsetails, all placed in *Equisetum* (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 to 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 (Figure 7.10D). The position of equisetophytes within the monilophytes remains uncertain (Pryer et al. 2004a).

Spermatophytes (Seed Plants)

The **Spermatophytes**, or **Spermatophyta**, 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 of this clade is axillary branching, as compared with the unequal dichotomous branching that preceded it within euphyllophytes.

Major Characteristics of Spermatophytes

To understand the seed, it helps to think about how it evolved (see Figure 7.11C–E). Seed plants are nested well within a lineage characterized by homosporous (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 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 (see Figure 7.11D), except for a little hole left open at the apex, called the micropyle. In seed plants other than 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 also helpful to consider the developmental events leading to a mature seed in a plant such as a cycad or a pine tree. Within the ovule (young seed) a single meiotic division occurs within the megasporangium, three of the resulting haploid products disintegrate, and the female gametophyte develops within the remaining spore. 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 may be 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 on page 171), the pollen tube is haustorial, ramifying slowly through the megasporangium wall, and two very large multiflagellate sperm are eventually produced. 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 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, the differentiation of the first (primary) xylem, situated toward the inside of the plant axis, and of phloem, situated toward the outside, occurs. 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 toward both 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 as thick-walled as xylem cells. Additionally, phloem cells have to be alive to carry out their function of transporting carbohydrates and nutrients upward and downward in the plant body.

It is interesting to note that in contrast to the bifacial cambium of seed plants, the giant lycophytes and most equisetophytes of the Carboniferous seem to have had unifacial cambia, producing secondary xylem toward the inside of the stem, but not secondary 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

(e.g., Cichan and Taylor 1990). The details of cambium function in these plants translated into a variety of highly unusual growth and life history strategies as compared with the familiar seed plants of today (Donoghue 2005).

Early Evolution of Spermatophytes

With this background on the seed and on wood, let us briefly consider the origin and early evolution of seed plants (Figures 7.11 and 7.12; see also Figure 7.8). 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” (Figure 7.11A,B).

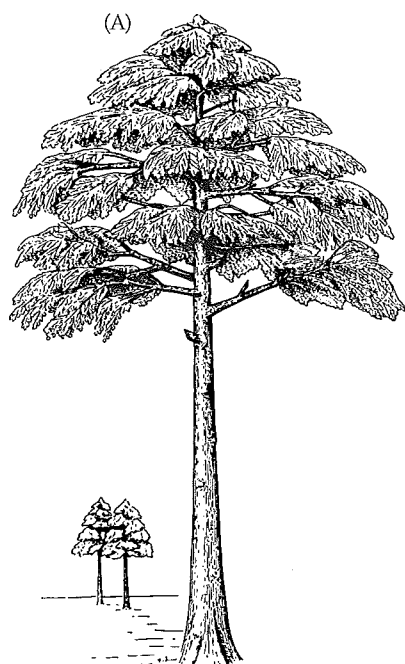
Recall that the differentiation of a main trunk and side branches had already evolved in the euphylllophyte lineage. One first sees the appearance of very large trunks, with wood rather similar in structural detail to that of modern conifers, in *Archaeopteris*, a “progymnosperm” of the late Devonian. Its trunk was connected to large, frondlike branch systems bearing many small leaves (Figure 7.11A). *Archaeopteris* 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), 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 plus “progymnosperms” has been called the **lignophytes** (Doyle and Donoghue 1986) or **Lignophyta**, in reference to the production of wood (see Figure 7.8).

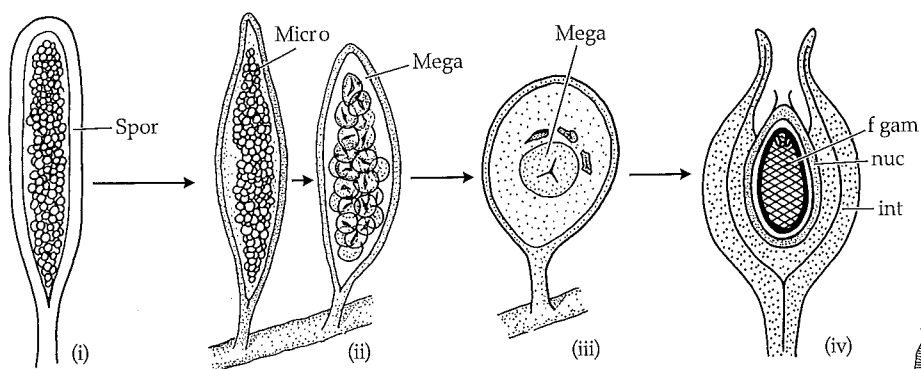
The term *seed fern* is applied to a wide variety of early seed plants with large, frondlike leaves, resembling those seen in ferns today, but bearing bona fide seeds (Stewart and Rothwell 1993; Taylor and Taylor 1993) (Figure 7.11B). It is now clear that these plants are not all most closely related 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 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 (e.g., Serbet and Rothwell 1992). This structure presumably functioned in pollen grain capture (Figure 7.11D). 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 (Figure 7.11E).

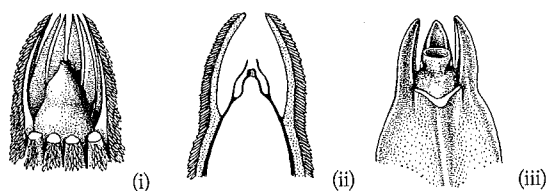
Through much of the last century, extant and extinct seed plant lineages were commonly divided into two major groups: the cycadophytes and the coniferophytes. The **cycadophytes**, including modern cycads, were distinguished by rather limited production of wood with wide rays (manoxylic wood) and by large, frondlike 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 needlelike, and the seeds are biradially symmetrical (platyspermic, or flattened). This distinction suggested



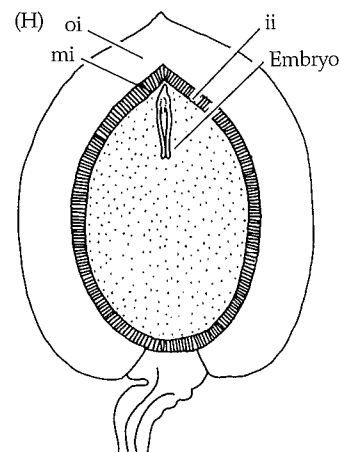
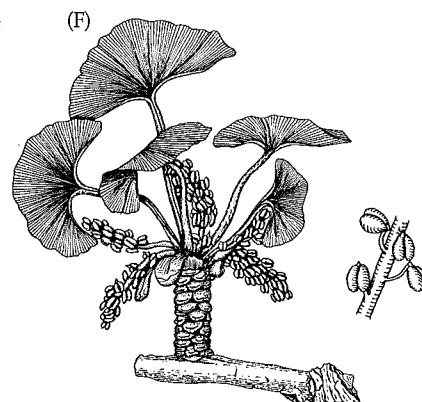
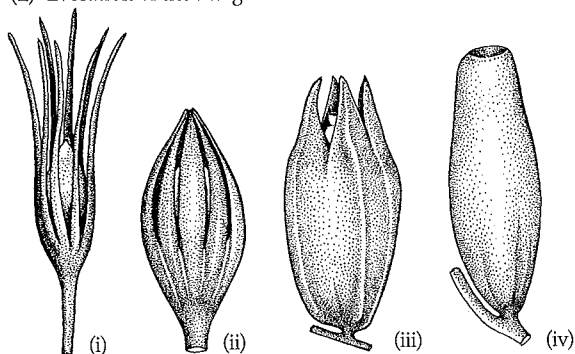
(C) Probable steps of seed evolution



(D) Pollen-receiving structures



(E) Evolution of the integument



◀ **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) homosporous 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 the megasporangium (endospory); (iv) envelopment of the megasporangium by integument tissue, leaving a micropyle at the apex. Spor, sporangium; Micro, microspores; Mega, megaspores; f gam, female gametophyte; int, integument; nuc, nucellus or megasporangium wall. (D) Pollen-receiving structures at the apex of the ovule in early seeds (all extinct): (i) *Physostoma elegans*; (ii) *P. ele-*

gans, longitudinal section showing pollen chamber within; (iii) *Eurystoma angulare*, showing cup-shaped opening. (E) Stages in the evolution of the integument in early seeds (all extinct): (i) *Genomosperma kidstoni*, (ii) *G. latens*, (iii) *Eurystoma angulare*, (iv) *Stamnostoma huttonense*. (F) Portion of long shoot and spur shoot of the extant ginkgophyte, *Ginkgo biloba*, showing axillary microsporangiate 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 (ii, inner layer of integument; mi, middle layer of integument; oi, outer layer of integument). (A, F, and G from Bold 1967; B and D from Gifford and Foster 1989; C and H from Scagel et al. 1969; E from Stewart 1983.)

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, frondlike leaves. In coniferophytes, on the other hand, the individual leaves of a precursor like *Archaeopteris* might have been modified into needlelike 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 Figure 7.8 and Figure 7.12 (e.g., Doyle 1998, 2006). These studies imply that the seed evolved just once, and that the first seed plants were cycadophytic, at least in having large, dissected leaves and radially symmetrical seeds. Specifically, it appears that a series of Devonian–Carboniferous “seed ferns” (*Elkinsia*, *Lyginopteris*, and medullosans) are situated at the base of the seed plant phylogeny and that coniferophytes are nested well within the tree, in a platyspermic clade. This arrangement implies a later shift to small, needlelike 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, ginkgos, conifers, gnetophytes, and flowering plants (angiosperms). The first four groups are often called gymnosperms, in reference to their naked seeds, as opposed to angiosperms, in which the seeds are enclosed inside 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. 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, as well as several other “seed fern” lineages from the later Permian and Mesozoic, some of which appear to be on the line leading to modern angiosperms (Doyle 2006). 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 (Cycadophyta or 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 8.21). 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 male gametophytes and gigantic multiflagellate 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 (e.g., Rai et al. 2003). *Cycas* has retained the presumed ancestral condition (seen in some fossil relatives, such as *Taeniopteris*) of having several ovules borne on rather leaflike 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 inward toward the axis of the strobilus.

Ginkgos There is just one surviving species, *Ginkgo biloba*, within ginkgophytes (or Ginkgoales; 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

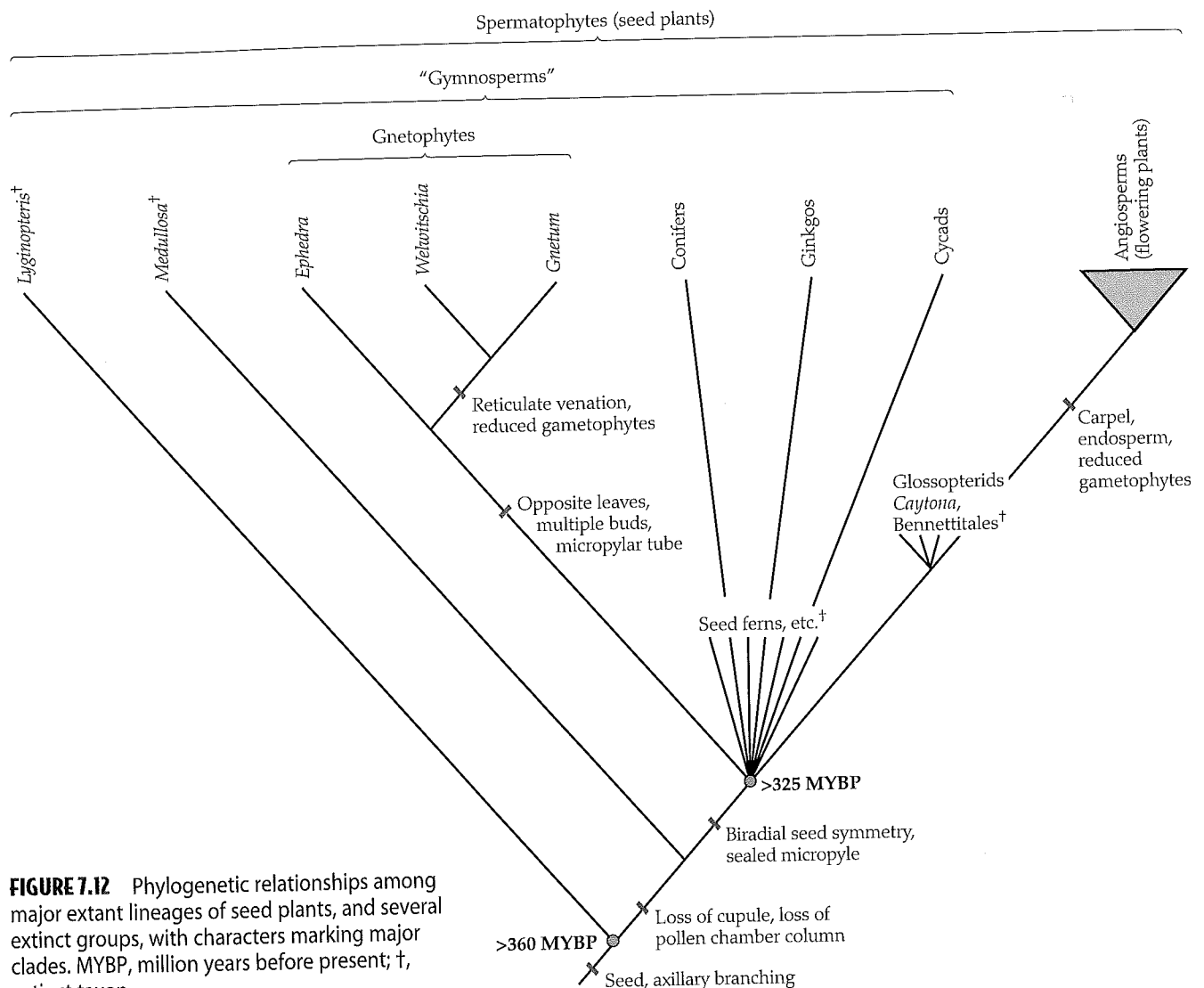


FIGURE 7.12 Phylogenetic relationships among major extant lineages of seed plants, and several extinct groups, with characters marking major clades. MYBP, million years before present; †, extinct taxon.

modern times it has been spread by humans as a street tree. Perhaps the most characteristic feature of the modern ginkgo is its production of deciduous, fan-shaped leaves with dichotomous venation. Ginkgophytes are well known in the fossil record, in which a greater diversity of leaf shapes is seen.

Like cycads, ginkgos are dioecious (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). Like cycads, ginkgos retain several ancestral characteristics, including haustorial male gametophytes and swimming sperm.

Conifers There are approximately 600 living species of **conifers** (**Coniferae** or **Coniferales**) (see Figures 8.24–8.27). These plants are shrubs or small trees with well-developed wood and often needlelike leaves. In most cases 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 stomata. In some 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 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 saclike appendages, but these seem to have been lost in several lineages.

In the seed cones, 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

through the wall of the megasporangium to deliver two sperm. The phenomenon of "polyembryony" is fairly common in conifers. Multiple embryos may be produced in an ovule 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 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*), in which the cone scale is produced in the axil of a prominent three-pronged bract (Figure 7.13C). 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 the other conifers, the **Cupressophyta** (Cantino et al., 2007). The Pinaceae are distinguished by several features, including inversion of the ovules (with the micropyle facing the axis of the cone; Figure 7.13D) and the derivation of the wing of the seed from the cone scale. Within the Cupressophyta, 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. As noted on page 176, several recent molecular analyses have called into question the monophyly of the Coniferae, placing the gnetophytes within the conifers as the sister group of the Pinaceae (see Figure 7.15C).

Gnetophytes The fourth major extant lineage of seed plants is the **gnetophytes** (**Gnetophyta** or Gnetales) (Figure 7.13F–I; see also Figure 8.28). This group contains only about 75 living species, which belong to three quite distinct lineages. *Ephedra* (with about 40 species in deserts around the world) has very reduced scalelike leaves (see Figure 8.28). *Gnetum* (with about 35 species in tropical forests of

the Old and New Worlds) has broad leaves (Figure 7.13F–H), 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 7.13I).

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 layer forms a micropylar tube that exudes the pollen droplet, and the outer layer is derived from a fused pair of bracts (Figure 7.13H). Molecular studies also strongly support the monophyly of this group.

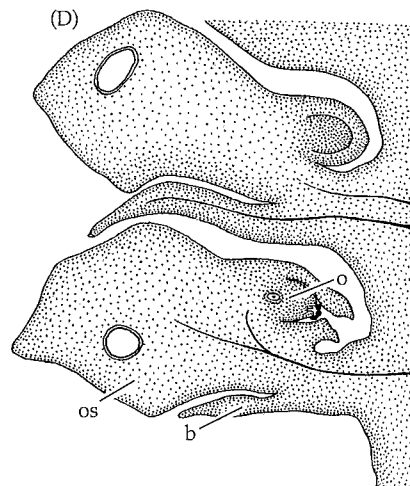
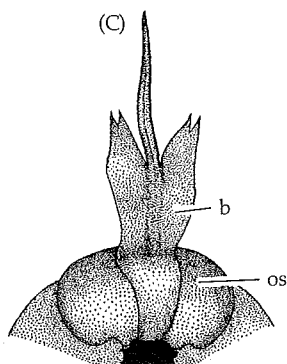
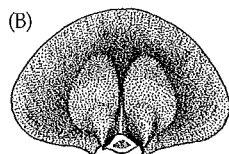
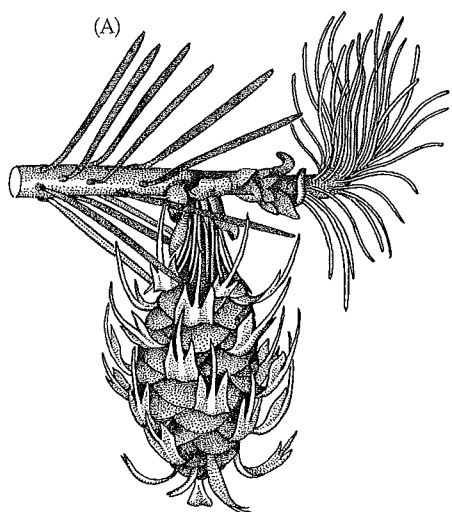
Within the gnetophytes, *Gnetum* and *Welwitschia* form a well-supported clade. Morphological synapomorphies include reticulate leaf venation, further reduction of the male gametophyte, and aspects of female gametophyte structure (tetrasporic development, loss of archegonia, free nuclei functioning as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

Aside from fossil pollen, the fossil record of the gnetophytes is rather limited (Crane 1996), with relatively few macrofossils described until recently (e.g., Rydin et al. 2004; reviewed in Won and Renner 2006). 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.

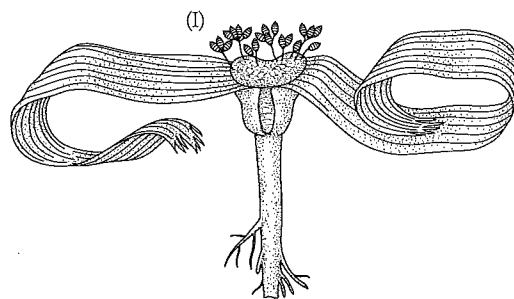
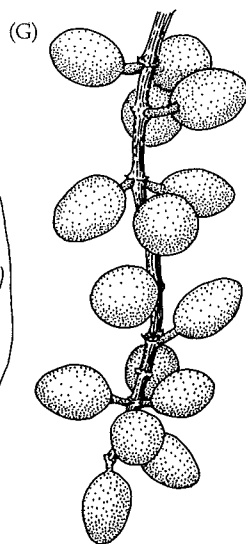
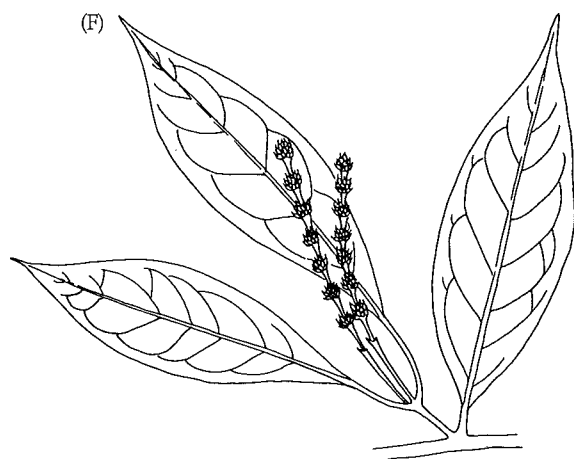
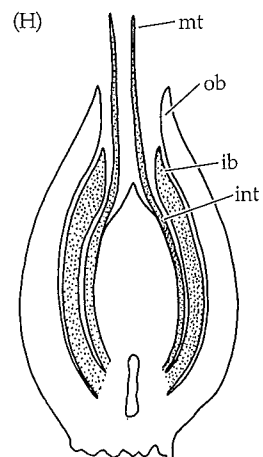
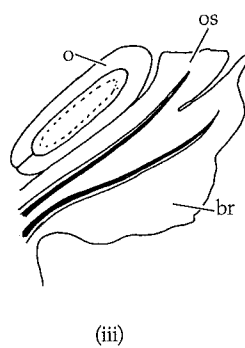
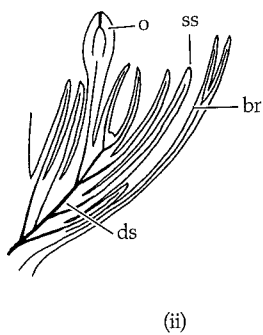
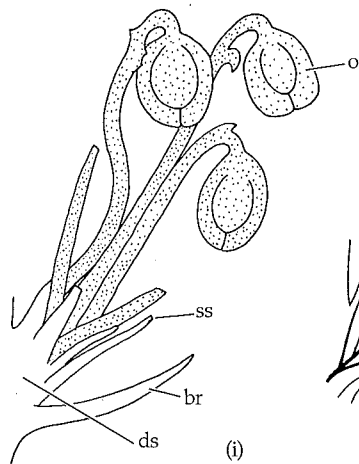
Like the angiosperms, the gnetophytes shortened the life cycle (and probably became herbaceous) and evolved insect pollination (found in some living species). In marked contrast to flowering plants, however, gnetophytes never became significant components of the vegetation at mid- and high paleolatitudes, 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** (**Angiospermae**) 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,



(E) Steps in ovuliferous cone scale evolution



◀ **FIGURE 7.13** Morphology of conifers and gnetophytes. (A) *Pseudotsuga*, 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 exerted 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 *Cordaitea*, with several ovules (o) and sterile scales (ss) attached to a dwarf shoot (ds) in

the axil of a bract (br); (ii) the extinct *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) Leaves and compound microsporangiate strobili of *Gnetum*. (G) Mature seeds of *Gnetum*. (H) 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). (I) General habit of the gnetophyte *Welwitschia mirabilis*, showing the short woody stem with two large leaves, axillary position of the multiple strobili, and taproot. (A–D from Stewart 1983; E–H from Scagel et al. 1969; I from Barnes 1998.)

leading to the formation of a typically triploid nutritive tissue called endosperm.

Several derived vegetative characteristics are also noteworthy. Almost all angiosperms produce **vessels** in the xylem tissue, though this feature probably 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 4.33). 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 enucleated 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, for example, might also 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 portion (filament) and a tip portion (anther) bearing two pairs of microsporangia (pollen sacs). The angiosperm carpel is typically differentiated into a lower portion (ovary) that encloses the ovules and an elongated portion (style) that elevates a surface receptive to pollen (stigma). The angiosperm ovule is unusual in several ways (see Figures 4.41 and 4.42). 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, in which 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 a compatible 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 4.42). Ultimately the egg is situated toward the micropylar end of the female gametophyte, along with two other cells (synergids) that 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, 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 diploid zygote develops into an embryo, and the triploid product undergoes a series of mitotic divisions to produce endosperm, which serves as the nutritive tissue in the seed.

Time of Origin of Angiosperms

When did the flowering plants originate and radiate? It appears from the fossil record (which includes pollen, leaves, flowers, and fruits) that angiosperms underwent a major radiation starting in the early Cretaceous (Friis et al. 1987; Doyle and Donoghue 1993; Crane et al. 1995). The oldest unequivocal angiosperm fossils are pollen grains from about 135 million years ago. Extraordinarily complete macrofossils from China were first described as being from the late Jurassic (Sun et al. 2002), but are now interpreted as early Cretaceous. Many major angiosperm lineages can be recognized by the mid-Cretaceous (water lilies, Chloranthaceae, Winteraceae, and eudicots were present by 125 million years ago). Other Cretaceous fossils are difficult to assign to modern lineages (Friis et al. 2005). In any case, by the end of the Cretaceous, angiosperms had diversified extensively and were the dominant plants in many terrestrial environments (see Magallón and Sanderson 2001; Bell et al. 2005).

In discussing the age of the angiosperms (or any other group), it is important to distinguish clearly between the ori-

gin of the stem lineage—the line leading to the modern group (i.e., when this lineage split from its sister lineage that includes extant organisms)—and the origin of the crown clade—the least inclusive clade that contains all of the extant members. The clade that includes the angiosperm stem lineage has been referred to as the “angiophytes” (Doyle and Donoghue 1993), and more recently as the Pan-Angiospermae (Cantino et al., 2007), to distinguish it from crown-clade angiosperms (Angiospermae).

It is possible that the angiophytes are quite ancient, whereas the crown angiosperms originated much more recently, perhaps not long before the radiation seen in the Cretaceous fossil record. That the Pan-Angiospermae 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 stem-lineage 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 to the angiosperms 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 yielded implausibly early ages for crown angiosperms. Progress has been made in “relaxing” the molecular clock assumption, however, and recent estimates place the origin of the angiosperm crown clade between 140 and 190 million years ago (Sanderson and Doyle 2001; Bell et al. 2005), somewhat before the unequivocal appearance of angiosperms in the fossil record.

Relationships of Angiosperms to Other Groups

Botanists have long puzzled over the relationships of angiosperms to other seed plants. 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 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 attractive candidates because some of them produced large, flowerlike reproductive structures, with pollen-producing organs surrounding a central stalk bearing naked seeds (Figure 7.14B).

Regarding the five extant lineages, ideas on relationships have shifted over the years (see Soltis et al. 2005). In the early 1900s (e.g., Arber and Parkin 1907), gnetophytes (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 flowerlike reproductive organs. These views had changed by the middle of the twentieth century with the reinterpretation of these characters. For example, vessel elements 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 characters (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 flowerlike reproductive structures (Figure 7.15A). A number of independent morphological analyses yielded the same basic result, though in some the gnetophytes were paraphyletic with respect to angiosperms (Taylor and Hickey 1992; Nixon et al. 1994). The characters that appeared to unite the anthophytes varied among analyses, but they were mostly rather obscure and in some cases unknown in fossil groups—for example, lignin chemistry, the layering of cells in the apical meristem, and pollen and megaspore features (Donoghue and Doyle 2000).

In any case, 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 (first reported for *Ephedra* in the early and mid-1900s) was interpreted as having evolved in the common ancestor of gnetophytes and angiosperms, with polyploid endosperm evolving later in the angiosperm line (see Friedman and Floyd 2001).

The first molecular phylogenetic studies of the problem yielded a variety of results and were viewed as at least consistent with the anthophyte hypothesis (see Donoghue and Doyle 2000). Starting in the late 1990s, however, a variety of molecular studies (especially those based on mitochondrial genes or on a combination of genes from different genomes) cast serious doubt on the existence of an anthophyte clade (e.g., Bowe et al. 2000; Chaw et al. 2000). These analyses suggested instead that the extant gymnosperm groups form a clade that is sister to the angiosperms, and that gnetophytes are related more directly to conifers (the gnetifer hypothesis; Figure 7.15B) or may even be nested within the conifers as the sister group of the Pinaceae (the gnepine hypothesis; Figure 7.15C). Detailed analyses of the molecular data sets (e.g., Graham and Olmstead 2000; Sanderson et al. 2000; Magallón and Sanderson 2002; Burleigh and Mathews 2004) have revealed several different signals, with some partitions of the data even favoring the placement of gnetophytes as sister to all other extant seed plant groups.

Unfortunately, these questions 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, gneto-

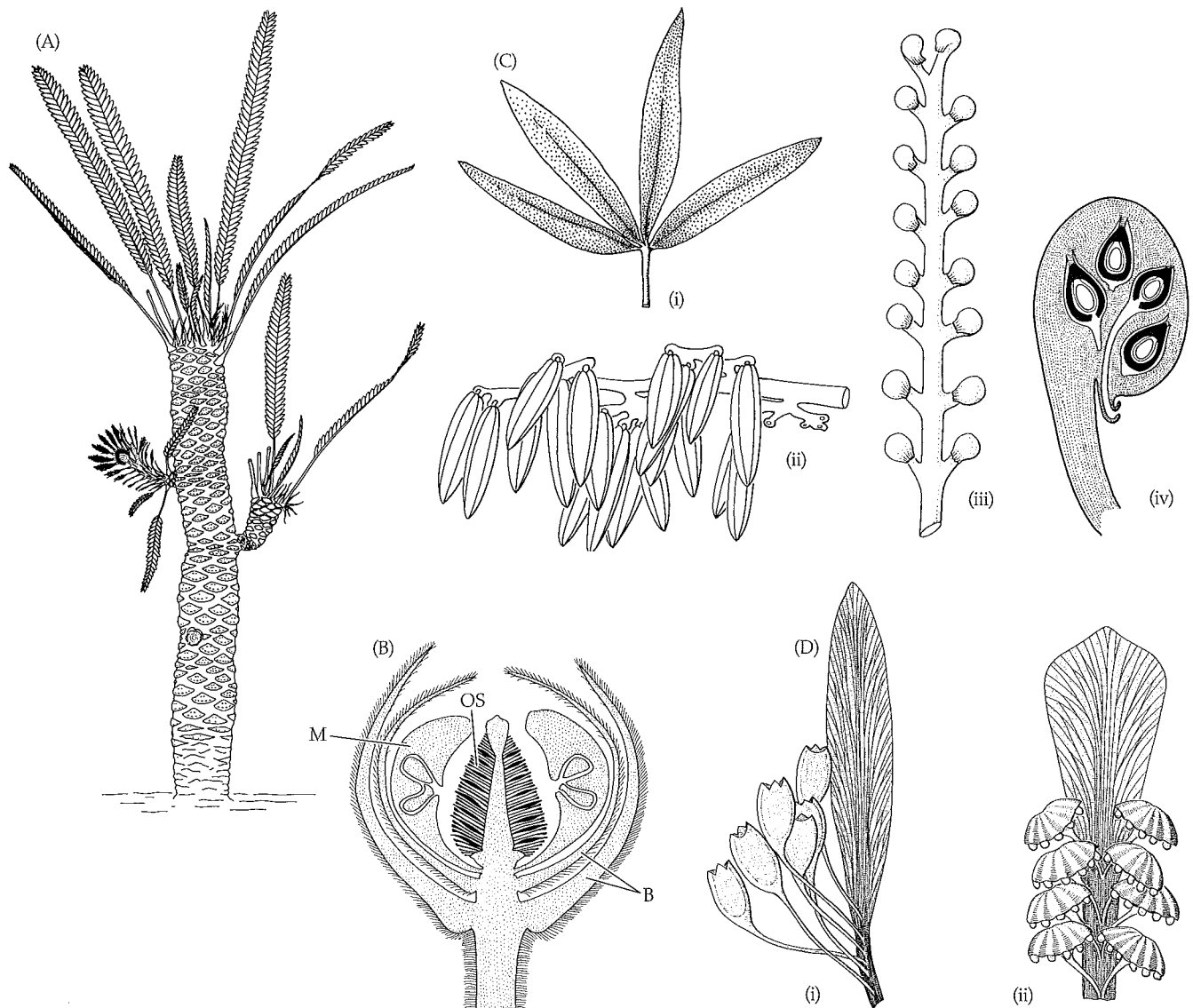


FIGURE 7.14 Reconstructions of Mesozoic fossils that may be closely related to angiosperms. (A, B) Bennettitales: (A) Habit of *Williamsonia sewardiana*, showing cycadlike trunk and compound leaves. (B) Longitudinal section of a flowerlike strobilus of *Williamsoniella*. B, bracts; M, microsporophyll with microsporangia; OS, stalked ovules and sterile scales borne on a central axis. (C) Caytoniales: (i) palmate leaf, *Sagenopteris phillipsii*; (ii) portion of a microsporophyll, *Caytonanthus kochii*; (iii) megasporophyll

of *Caytonia nathorstii*, showing two rows of cupules; (iv) longitudinal section of a cupule of *Caytonia thomasii*, showing ovules within. (D) Glossopteridales: (i) ovulate portion of *Denkania indica*, showing six cupulelike 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.)

phytes are directly related to conifers. The bulk of the evidence now favors the latter view. A second issue is the rooting of the portion of the seed plant tree 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. But 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 (Figure 7.15D). In any case, it is important to appreciate that “gymnosperms” (including Paleozoic and Mesozoic fossils) are paraphyletic with respect to angiosperms. To avoid con-

fusion, it will probably be best to apply a different name to the hypothesized clade including all extant groups of seed plants without carpels; Cantino et al. (2007) have proposed Acrogymnospermae for this purpose.

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; Doyle 2006).

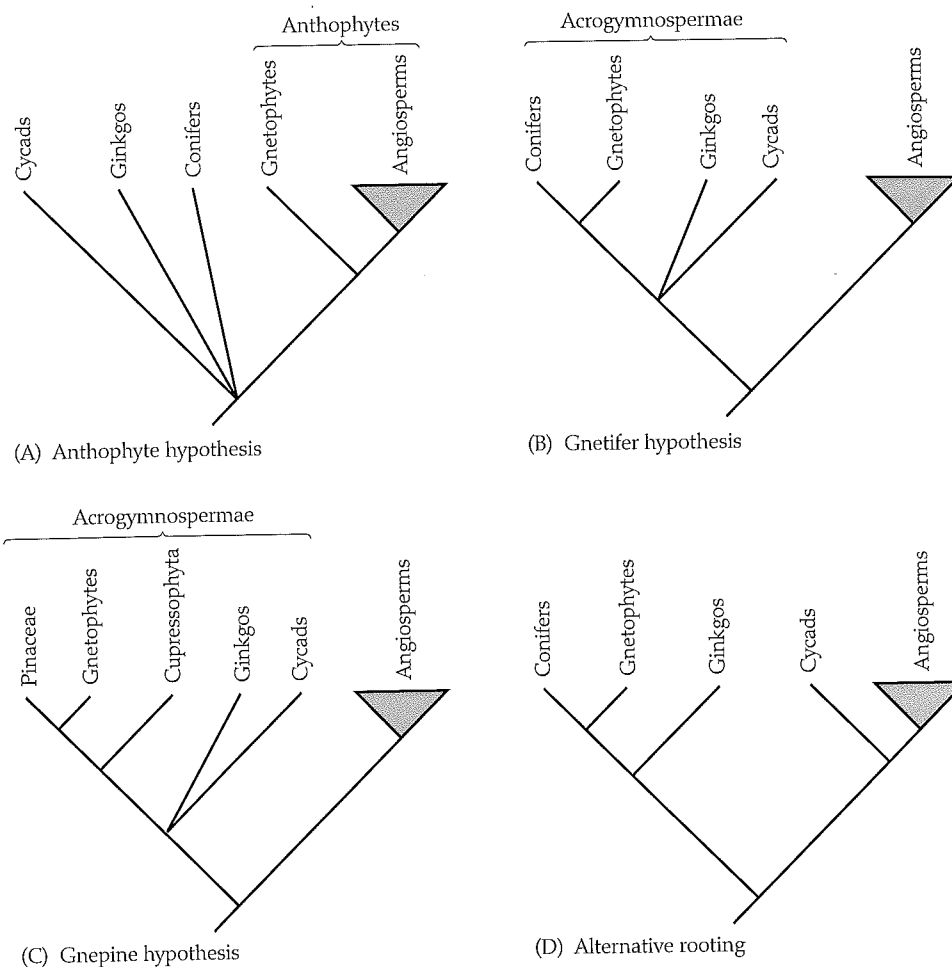


FIGURE 7.15 Alternative hypotheses of relationships among the five major extant lineages of seed plants. (A) According to the anthophyte hypothesis, gnetophytes are most closely related to angiosperms. (B) According to the gnetifer hypothesis, gnetophytes are most closely related to conifers. (C) According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

Relationships within Angiosperms

Enormous progress has recently been made in understanding phylogenetic relationships at the base of the angiosperms themselves (Figure 7.16). Until quite recently, the problem of identifying the root of the angiosperms and the relationships among the basal branches looked intractable. Over the last decade, however, several different lines of evidence have converged on the same answer. These new findings are having a major effect on our interpretation of early angiosperm evolution and the factors that account for the enormous success of flowering plants (see Soltis et al. 2005).

Most students of angiosperm evolution have held that the first flowering plants were among the “Magnoliidae” (*sensu* Cronquist 1988; Takhtajan 1997)—a paraphyletic group including magnolias, avocados, water lilies, and black peppers, among others. 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, such as magnolias, have large flowers with many flower parts (stamens, carpels) spirally arranged on an elongated axis, while others, such as black

peppers, have tiny flowers with few parts arranged in distinct whorls. Some early phylogenetic analyses suggested that the first flowering plants were woody with large flowers, while others implied that they were herbaceous with tiny flowers (see Doyle and Donoghue 1993).

Starting in 1999, a variety of molecular phylogenetic studies concluded that the first split within modern angiosperms was between a lineage that now includes a single species, *Amborella trichopoda* (and possibly also the water lilies, Nymphaeales), and all the rest of the extant angiosperm species (Mathews and Donoghue 1999; Qiu et al. 1999; Soltis et al. 1999; Parkinson et al. 1999; Barkman et al. 2000; Zanis et al. 2002). This conclusion has since been confirmed in all studies that have included a sufficient sample of taxa (e.g., Leebens-Mack et al. 2005). *Amborella trichopoda* is a shrubby plant from the island of New Caledonia with rather small flowers that have 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 those in almost all other angiosperms, the water-conducting cells in the xylem of *Amborella* are tracheids (Feild et al. 2000), supporting the

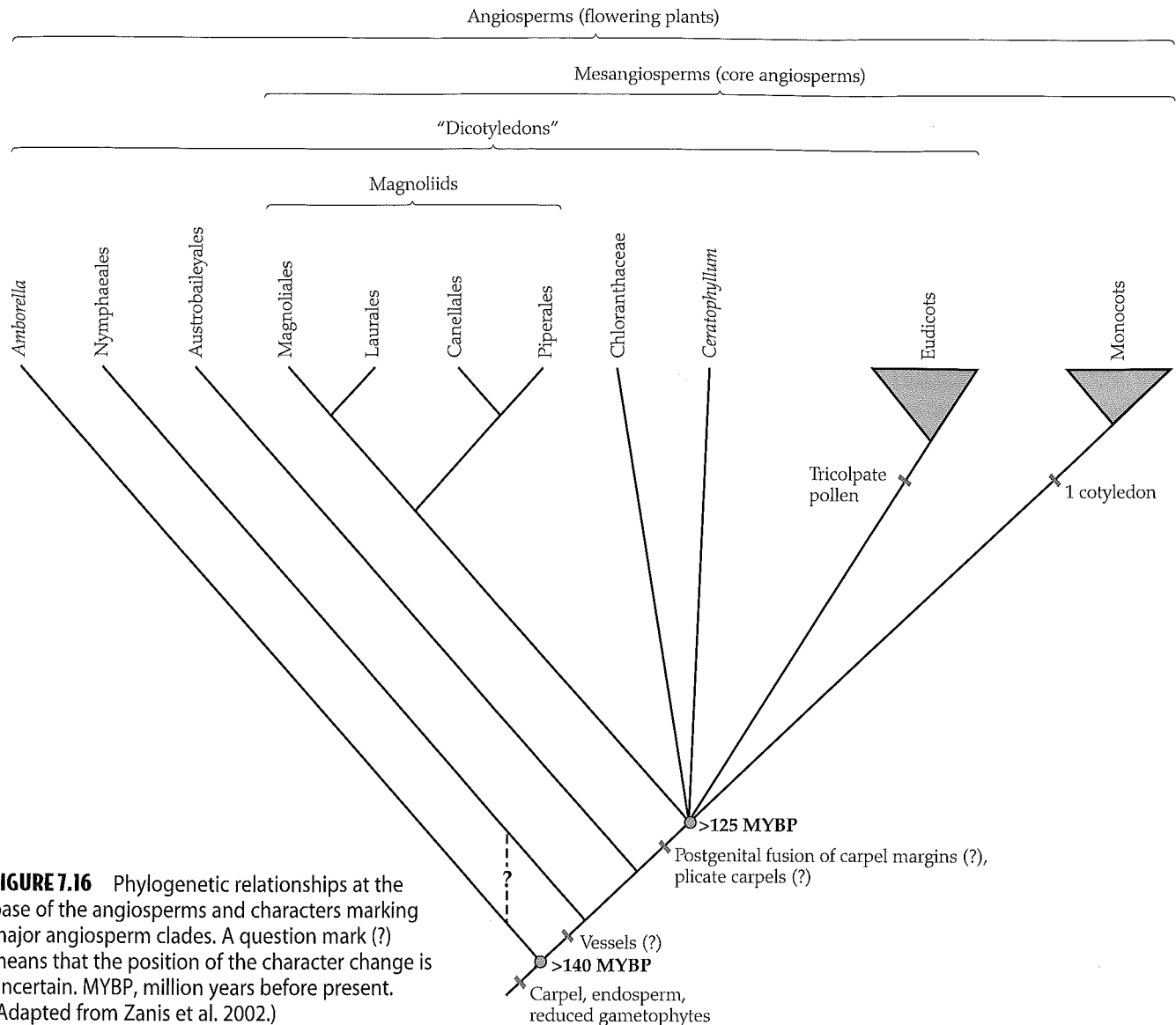


FIGURE 7.16 Phylogenetic relationships at the base of the angiosperms and characters marking major angiosperm clades. A question mark (?) means that the position of the character change is uncertain. MYBP, million years before present. (Adapted from Zanis et al. 2002.)

view that the first angiosperms lacked vessels (see Figure 7.16). *Amborella* female gametophytes are also highly unusual in having three, rather than two, synergid cells with the egg cell at the micropylar end (hence a total of nine nuclei in eight cells, as opposed to eight nuclei in seven cells as in most angiosperms; Friedman 2006).

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 in these two lineages have just four cells and form diploid endosperm tissue (Friedman and Williams 2004). Along with *Amborella*, these two lineages subtend a well-supported **core angiosperm** clade that includes all the rest of the flowering plants, which Cantino et al. (2007) have named the **Mesangiospermae**.

Whereas in the basalmost lineages the carpels are typically sealed by a secretion, in members of the core angiosperm clade the carpels are usually sealed by post-

genital 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 then grows up like a tube, whereas in almost all Mesangiospermae the carpels are plicate, like a leaf folded down the middle. Although these observations help us to visualize 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 2006).

Relationships within the core angiosperm clade are still poorly resolved, with the placement of several enigmatic groups still uncertain, especially the Chloranthaceae and *Ceratophyllum* (Qiu et al. 2005). However, several major clades are rather well supported. First, a restricted **magnoliid** clade (**Magnoliidae**) includes the Magnoliales plus

Laurales and the Canellales plus Piperales. 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** (or **Eudicotyledonae**). 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, pollen grains with three colpi, or germinal furrows (and a variety of derivative forms; see Figure 4.48), which were derived from monosulcate forms (Doyle 2005). The additional germinal furrows may help to ensure contact between at least one germination site and the stigma surface (Furness and Rudall 2004). The appearance of tricolpate pollen grains in the fossil record at around 125 million years ago has provided a key calibration point for dating the radiation of flowering plants. Many eudicots also have flowers with parts in fours or fives, or in multiples of these numbers (Judd and Olmstead 2004). This major shift in flower organization within the eudicots appears to be correlated with duplications of genes encoding several transcription factors that play a key role in specifying organ identity and flower symmetry (Kramer and Hall 2005; Howarth and Donoghue 2006).

Altogether there are perhaps 160,000 species of eudicots. This huge group contains a number of species-rich 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 groups among those discussed in detail in Chapter 9.

A third major clade, with some 65,000 species, corresponds to the traditional **monocotyledons** (or **Monocotyledonae**). 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 monocots—such as flower parts in threes and monosulcate pollen—probably pre-dated the origin of this clade (Soltis et al. 2005). 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 will depend on exactly what their relatives turn out to be and on relationships within the monocot clade. In the end, the presence of one seed leaf, or cotyledon, may still be the morphological character that best distinguishes the monocotyledons (see Figure 4.44).

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.”

Angiosperm Pollination, Dispersal, and Growth Habits

Much of flower diversity relates to pollination biology (see Chapter 4). Insect pollination is known from several non-angiosperm 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 time the crown angiosperms originated. It was probably first carried out by pollen-eating or pollen-collecting insects, especially beetles and flies; flowers pollinated by nectar-collecting insects evolved later. These conclusions are supported by the morphology of early angiosperm fossils as well as by knowledge of pollination mechanisms in extant members of early-diverging angiosperm 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 effect 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 specialization for 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 it probably originated in the Tertiary. Although angiosperm-dominated rain forest vegetation may have come into existence in the Cretaceous (Davis et al. 2005), fossil evidence indicates that it did not become widespread until the early Tertiary, at about the time when the radiation of modern birds and mammals occurred. 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 the angiosperms and what effects it might have had on their 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 vinelike growth. Their modern representatives, at least, live in moist forest understory environments, and they show various adaptations to low-light environments. It has been argued that the first angiosperms grew in disturbed understory habitats or in shady streamside settings, and that movement out into more diverse environments might have stimulated diversification within the core angiosperms (Feild et al. 2004). A major exception among the early lineages is the water lily clade, whose members are herbaceous and live in high-light aquatic environments. The extinct *Archaeofructus*, whose relationships remain poorly resolved, was also probably an aquatic plant (Sun et al. 2002; Friis et al. 2003).

The herbaceous habit evolved early in angiosperm evolution, and originated several times independently—for

example, in Nymphaeales, Chloranthaceae, Piperales, and monocotyledons. In several cases, this development appears to be correlated with movement into aquatic habitats. Larger woody forms have reevolved 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 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 Ruscaceae, 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 forms, 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 adapted to temperate climate zones from 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; Magallón and Sanderson 2001), related perhaps in part to the geographic spread of many such lineages (e.g., around the Northern Hemisphere throughout the Tertiary; see Donoghue and Smith 2004). Taken together, all of these factors have had a profound effect on angiosperm diversity.

Summary

The tremendous progress made over the last few decades in establishing phylogenetic relationships is 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 (Psilotales) are not remnants of the first vascular plants, but instead are part of the monilophyte clade. Moreover, 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 among the major seed plant lineages. Where do the gnetophytes really fit, and what really are the closest relatives of the flowering plants? And within the core angiosperms, what are the closest relatives of the monocots and the eudicots?

These important questions have been very difficult to resolve, but the successes of the last few decades suggest that the 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 READINGS

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texts on comparative plant anatomy, morphology, and paleobotany that can be consulted for background information on specific characters and groups of organisms.

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