



Kathleen M. Pryer
Harald Schneider
Susana Magallón

The Radiation of Vascular Plants

Vascular plants include our major food resources in the form of leaves, stems, roots, fruits, and seeds. They further sustain human life by providing other essentials such as wood, fibers, and medicines. Plants are the dominant primary producers in terrestrial habitats, and by the process of photosynthesis, they actively convert solar energy, water, and carbon dioxide into carbohydrates (sugars) and oxygen, which is vital to all living things. The rise and spread of vascular plants resulted in a dramatic drop in atmospheric carbon dioxide (CO_2) about 400 million years ago during the mid-Paleozoic (Algeo et al. 2001, Berner 2001, Driese and Mora 2001, Raven and Edwards 2001). This decline in atmospheric CO_2 triggered the evolution of vascular plants with more complex body plans, including such organs as leaves, specialized for optimizing photosynthesis (Beerling et al. 2001, Pataki 2002, Shougang et al. 2003). Vascular plants therefore both caused and reacted to global changes in their physical environment early in their evolution. The earliest radiation of vascular plants has been interpreted as one in which rapidly diversifying lineages colonized and shaped different terrestrial habitats (DiMichele et al. 2001). Repeated reciprocation between climatic change and vascular plant radiation is noted throughout the fossil record, with particularly marked changes in floristic patterns occurring at the end of the Permian (Looy et al. 2001), at the Triassic/Jurassic (McElwain et al. 1999) and Paleocene/Eocene boundaries (Tiffney and Manchester 2001), and in the Cretaceous (Friis et al. 2001b).

The advent of terrestrial primary producers capable of forming a huge biomass correlates with the simultaneous rise of terrestrial animals in the Paleozoic, including various groups of arthropods and tetrapods (Coates 2001, Shear and Selden 2001, Carroll 2002). For example, the first known mites are found together with the first vascular plants in Devonian Rhynie Chert beds in Aberdeenshire in the north of Scotland. According to a recent molecular clock estimate, basal groups of insects originated during the Late Devonian (Gaunt and Miles 2002), coinciding with the diversification of vascular plants. The wide spectrum of fossilized insects observed in the Late Carboniferous (Labandeira 2001), including herbivorous groups, also suggests a simultaneous adaptive radiation of vascular plants and insects. The establishment of vascular plants with large and complex body plans in the Carboniferous and Permian resulted in an increased amount and diversity of vegetative biomass that favored the diversification of herbivorous tetrapods in the Permian (Sues and Reisz 1998, Coates 2001). Vascular plants are not only the major nutrient source for the consumers in their ecosystems, but they also play an important role in symbiotic associations with fungi (Brundrett 2002). Rhynie Chert fossils of glomalean mycorrhizal fungi discovered in association with preserved plant shoots exquisitely document complex plant–fungi interactions by the Early Devonian, suggesting that mycorrhizal associations were a critical factor in the early and successful colonization of land by terrestrial plants (Taylor et al. 1995, Blackwell 2000, Cairney 2000,

Hibbett et al. 2000, Redecker et al. 2000, Brundrett 2002; see also ch. 12 in this vol.).

In this review, we summarize the results of various recent studies that have used morphological and/or molecular evidence to infer the phylogeny of living vascular plants, and those that have used morphological/anatomical evidence to understand relationships of fossil plants. These studies differ widely in their taxon sampling, in the parts of the green branch of the Tree of Life they focus on, and also in their methodology. It is a challenging exercise, therefore, to distill from them not only a summary but also a fresh look at our current understanding of the evolution and relationships among both living and extinct vascular plants. It should be noted at the outset that we view the continued traditional application of several taxonomic names and ranks, especially to fossil groups that are clearly not monophyletic (e.g., Rhyniophyta), as hampering progress in our understanding and discussions of vascular plant evolution. Rather than abandon these names entirely, we retain most of them as common names in quotation mark (e.g., "rhyniophytes") to clarify historical usage. In our phylogenetic figures, we attempt to illustrate progress that has been made in discerning the relationships of members of these groups and our best sense of where they "fit in." Also, where we integrate fossils together with living taxa, we try to distinguish between stem and crown groups (see Smith 1994:94–98). Stem groups include taxa that are in fact part of a particular lineage but that lack some character(s) (synapomorphy) that distinguishes the crown group.

We were especially fortunate to be able to build on several thorough reviews that have been published in recent years. For additional information and different perspectives, the reader is referred to Kenrick and Crane (1997b), Bateman et al. (1998), Doyle (1998b), Rothwell (1999), Renzaglia et al. (2000), Donoghue (2002), Judd et al. (2002: ch. 7), and Schneider et al. (2002).

What Are Vascular Plants?

Vascular plants make up the bulk of all the land plant lineages. They are a monophyletic group characterized by the presence of specialized cells, tracheids and sieve elements, which conduct water and nutrients throughout the plant body and provide structural support (Kenrick and Crane 1997a, 1997b, Bateman et al. 1998, Schneider et al. 2002). Land plants are typified by an alternation of generation phases, whereby heteromorphic haploids (gametophytes) and diploids (sporophytes) alternate throughout the plant's life cycle (Kenrick 1994, 2000, 2002b, Mable and Otto 1998, Renzaglia et al. 2000). The gametophytes of nonvascular land plant lineages (mosses, liverworts, and hornworts) are the dominant or more visible phase that bears a comparatively tiny sporophyte with a single sporangium. The recent confirmation of Charales as the green algal lineage most closely related to land plants (Karol et al. 2001) supports the view

that a dominant gametophyte phase is the plesiomorphic (ancestral) condition, whereas a predominant sporophyte phase, which is found in vascular plants, is derived (Mable and Otto 1998, Kenrick 2000). The gametophyte phase is diminutive in vascular plants compared with the highly branched sporophyte that bears more than a single sporangium (polysporangiate). Figure 10.1 contrasts these major differences in morphology and life cycle between nonvascular and vascular plants. Observations from the fossil record (Kenrick 2002b) the reconstruction of life cycle evolution based on living taxa (Schneider et al. 2002: fig. 17.2a) converge on a scenario, suggesting that over time there was a trend from a short-lived sporophyte phase ("bryophytes") to one whereby both the gametophyte and sporophyte phases were essentially codominant (putatively isomorphic in "rhyniophytes") and that eventually the sporophyte phase came to dominate the life cycle in vascular plants. Heterosporous lineages (those that produce two spore types), and especially seed plants, demonstrate this trend most clearly, with the gametophyte phase becoming extremely reduced both in size and in duration.

Unequivocal evidence for the earliest polysporangiate plants dates back to the Rhynie Chert beds of the Late Silurian. Representatives such as *Aglaophyton* (fig. 10.2 inset), *Horneophyton*, and *Rhynia* all had simple and diminutive body plans with dichotomously branched axes and no roots or leaves (Kenrick and Crane 1997a, 1997b, Crane 1999, Edwards and Wellman 2001). The erect axes were terminated by round or ovoid sporangia and possessed water-conducting cells that were either unthickened and unornamented (e.g., *Aglaophyton*) or well-developed tracheids (e.g., *Rhynia*) organized in centrarch protosteles (protoxylem is centrally located in the vascular cylinder and xylem maturation is centrifugal—toward the periphery of the axis). These plants are often referred to as "rhyniophytes," and they were never very diverse either in species number or in morphology and quickly became replaced by plants with a more complex organization. The descendants of these "rhyniophytes" diversified rapidly in the Early Devonian, resulting in a split into two major groups (fig. 10.2), the lycophytes (Lycophytina) and the euphyllophytes (Euphyllophytina). The primary feature that unites these two groups to distinguish them from the "rhyniophytes" is the differentiation of the plant body into aerial (shoot) and subterranean (root) components (Gensel and Berry 2001, Gensel et al. 2001, Schneider et al. 2002), which argues for a single origin of roots rather than several independent origins (Raven and Edwards 2001, Kenrick 2002a).

Lycophytes and Zosterophytes (Lycophytina)

The earliest lycophyte lineages diversified in the Early Devonian and are referred to here as "protolycophytes" (fig. 10.3), plants characterized by mostly dichotomously branching axes that are either naked or covered by spiny appendages. The aerial axes mostly possess an exarch pro-

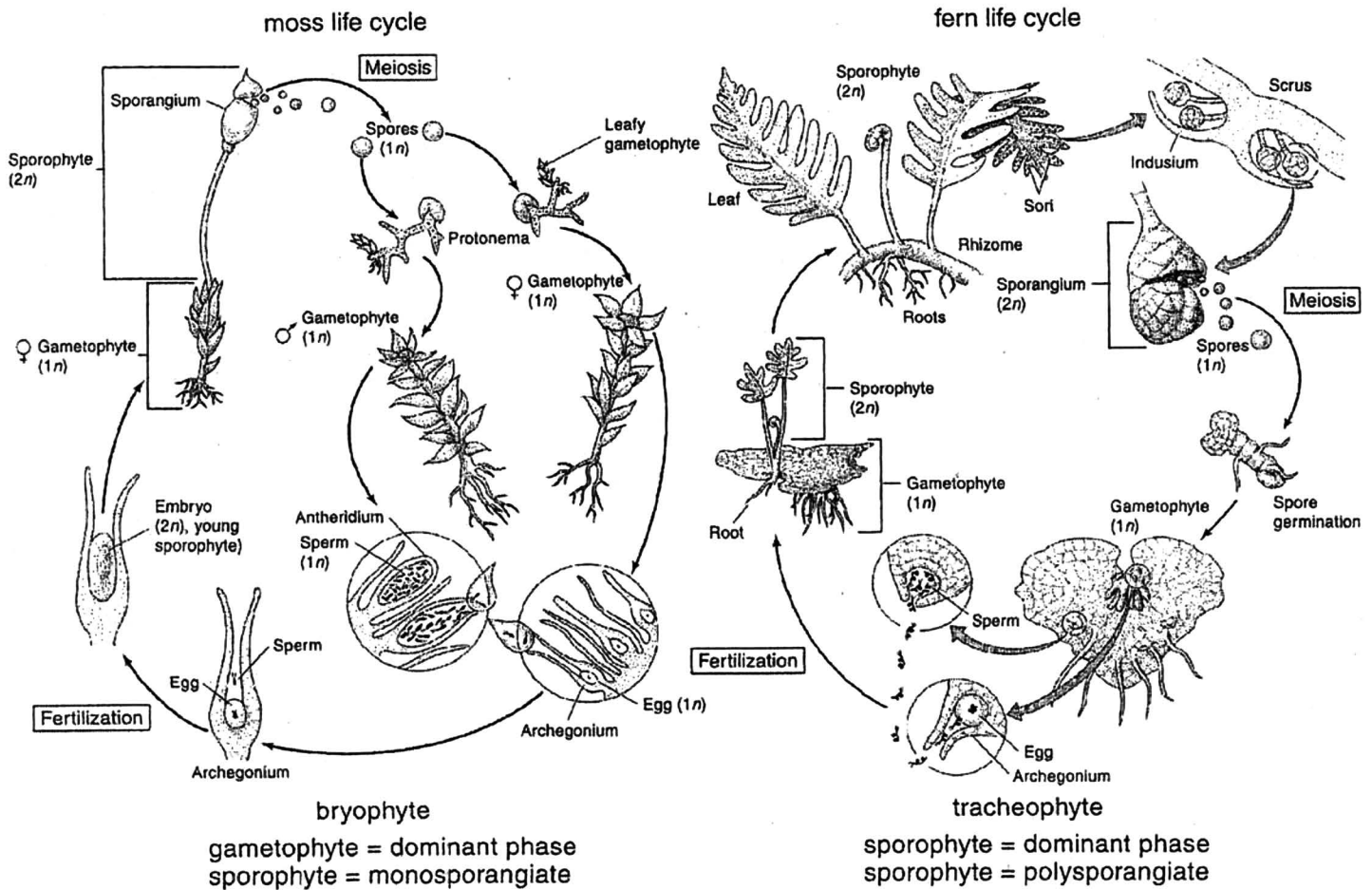


Figure 10.1. Comparison of alternation of generation phases between representative "bryophyte" and tracheophyte life cycles to illustrate the evolutionary transition from a dominant autotrophic gametophyte and a nutritionally dependent monosporangiate sporophyte in "bryophytes" to a dominant autotrophic polysporangiate sporophyte in tracheophytes. In ferns, the gametophytes are independent of the sporophytes; in seed plants, the microgametophytes are independent but the megagametophytes are retained on the sporophyte. Figure modified from Singer (1997).

tostele (protoxylem is located at the edge of the vascular cylinder and xylem maturation is centripetal—toward the center of the axis) and bear dorsiventral sporangia (often kidney-shaped) that open into two equal-sized valves via transverse dehiscence. These sporangia are laterally inserted either on terminate or nonterminate axes (Kenrick and Crane 1997a). Zosterophytes [e.g., *Zosterophyllum* (fig. 10.3 inset), *Sawdonia*] and prelycophytes (e.g., *Asteroxylon*, *Drepanophycus*) were a dominant component of the landscape until they became extinct in the Early Carboniferous. Their descendants, which include three extant lineages of lycophytes—Lycopodiales, Selaginellales, and Isoëtales (fig. 10.3)—bear lycophylls, leaves that develop exclusively by intercalary growth (Crane and Kenrick 1997, Kenrick 2002b; Schneider et al. 2002). Intercalary growth is characterized by meristematic activity that is not apical but rather is more diffusely organized toward the base of the lycophylls.

These three lineages diversified in the Late Devonian and Carboniferous and can be easily distinguished by both reproductive and vegetative features (Kenrick and Crane 1997a, Judd et al. 2002). The Lycopodiales are homosporous (pro-

duce spores of a single type) and are sister to a clade of heterosporous (producing two spore types) lycophytes, Selaginellales and Isoëtales, which bear a sterile leaflike appendage (ligule) on the adaxial (facing toward main axis) leaf surface. The heterosporous lycophytes were morphologically and ecologically diverse throughout the Carboniferous, including arborescent forms with a unique type of secondary xylem, such as the isoetalean lycophyte *Lepidodendron* (fig. 10.3, inset), but declined drastically starting in the Upper Carboniferous (Pigg 2001, DiMichele and Phillips 2002) and continuing throughout the Mesozoic. Today the lycophyte representatives that remain are diminutive in stature and diminished in diversity (<1% of extant vascular plants).

"Trimerophytes" and Euphyllophytes (Euphyllophytina)

Euphyllophytes are the sister group to the lycophytes. Although the euphyllophytes encompass an astonishing morphological diversity, they all share several features in common,

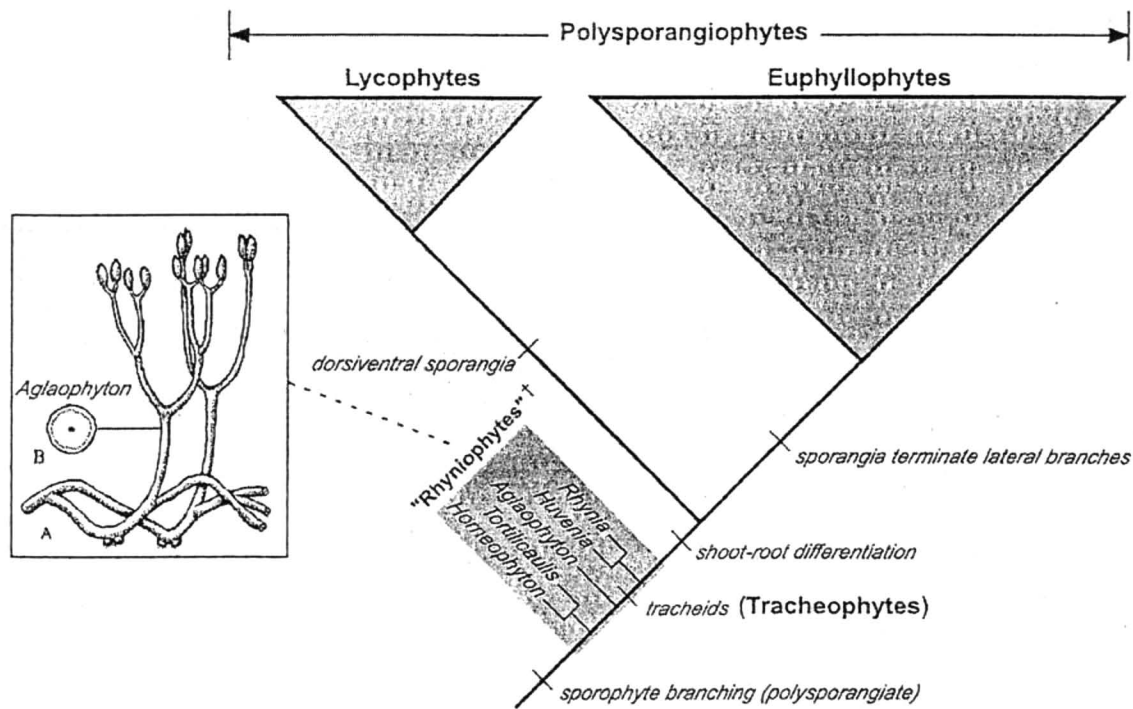


Figure 10.2. Vascular plant phylogeny: relationships of early polysporangiate taxa. Gray triangles indicate extant lycophyte and euphyllophyte crown groups; shaded box highlights extinct (†) “rhyniophyte” stem group with some representative taxa. Critical synapomorphies are indicated on the branches. Phylogeny based largely on Kenrick and Crane (1997:129, fig. 4.31) and Meyer-Berthaud and Gerrenne (2001). Inset, Sketch of a representative early Devonian “rhyniophyte,” *Aglaophyton*: A, dichotomously branched creeping and erect axes, the latter terminated by ovoid sporangia; B, tiny central strand of unthickened water-conducting cells. Plant drawing from Fischer et al. (1998).

such as sporangia that terminate some lateral branches (figs. 10.2 and 10.4), a distinctively lobed primary xylem strand (Stein 1993, Kenrick and Crane 1997a) and a 30-kilobase chloroplast inversion (Raubeson and Jansen 1992a). Early members of the euphyllophyte lineage, such as *Psilophyton* (fig. 10.4 inset), are referred to as “trimerophytes” and were homosporous and leafless plants restricted to the Devonian. They exhibited pseudomonopodial branching (overtopping) resulting in a differentiation of the shoot system whereby one axis is dominant with indeterminate growth (main axis continues to grow) and the lateral axes were determinate (terminated by sporangia). Later during the evolution of this lineage the determinate axes were transformed into euphylls—leaves that develop with an apical and/or marginal meristem resulting in a gap being formed in the stele (stem vascular cylinder) above the point of leaf insertion (Schneider et al. 2002), which argues for a single origin of euphylls, rather than several independent origins (Boyce and Knoll 2002). Therefore, as early as the Devonian there was a major transition from vascular plants without leaves to those that possessed euphylls (Beerling et al. 2001, Shougang et al. 2003).

During the evolution of the Euphyllophytina there was a split in the early-mid Devonian into two major clades, monilophytes and lignophytes (Pryer et al. 2001). The monilophytes (= Infradivision Moniliformopses, *sensu* Kenrick and Crane

1997a; Judd et al. 2002: ch. 7) include horsetails, eusporangiate and leptosporangiate ferns, and whisk ferns (*Psilotum* and relatives). The lignophytes include all seed plants and their closest relatives (Doyle 1998b). The ancient radiation of these two divergent lineages gave rise to what now is 99% of extant vascular plant diversity.

Monilophytes

The monilophytes comprise five major extant lineages (fig. 10.5A): Equisetopsida (horsetails), Polypodiidae (leptosporangiate ferns), Psilotidae (whisk ferns), Marattiidae (marattiaceous ferns), and Ophioglossidae (moonwort ferns). Previous assessments of relationships among these lineages were contradictory and often placed one or more of them as sister to the seed plants, implying that vascular plant evolution had proceeded in a progressive and steplike fashion. Recent recognition that these lineages are clustered together in a single clade that is sister to seed plants has helped to stabilize this pivotal region of the vascular plant phylogeny (Kenrick and Crane 1997a, 1997b, Nickrent et al. 2000, Renzaglia et al. 2000, Pryer et al. 2001, Rydin et al. 2002).

Among the extant monilophytes, the earliest-diverging lineages are those with the poorest fossil record—the Psiloti-

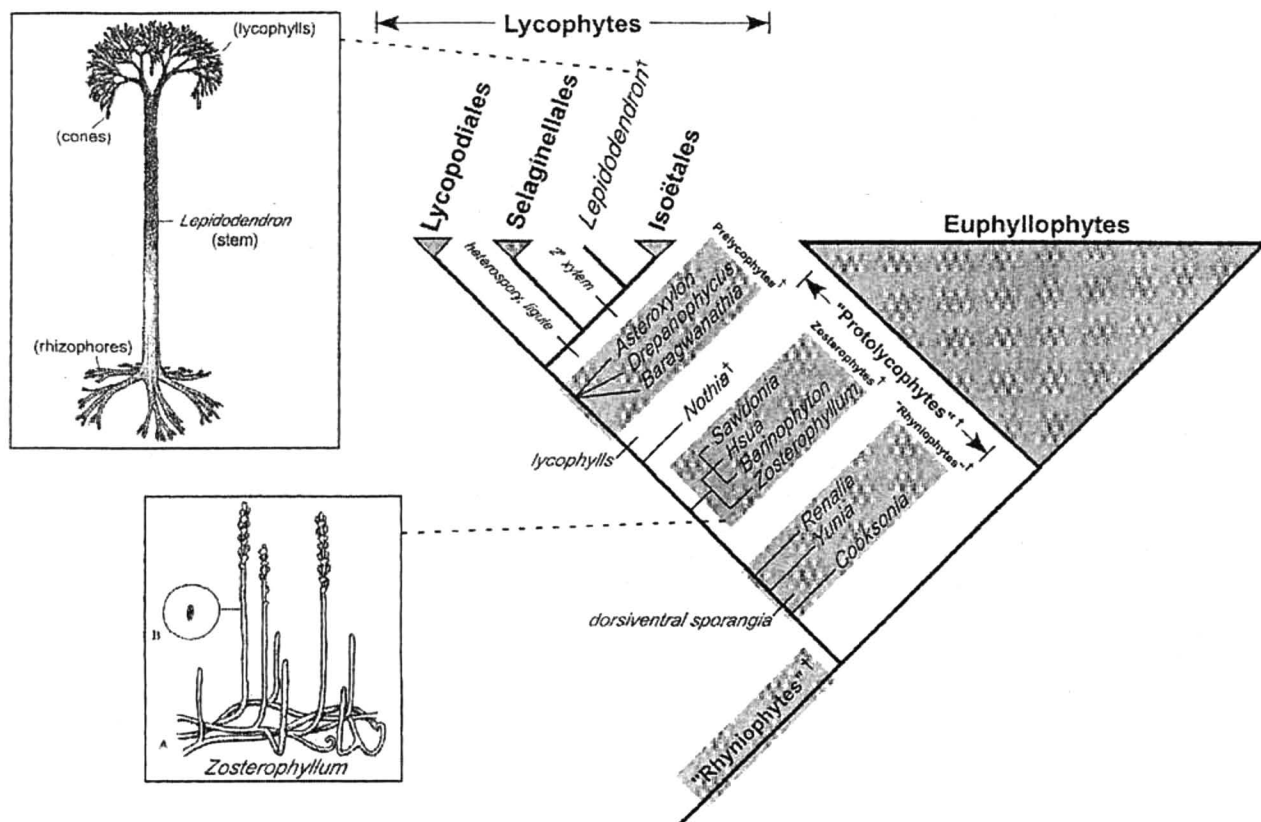


Figure 10.3. Vascular plant phylogeny: relationships of lycophytes. Phylogeny based largely on Kenrick and Crane (1997a:129, fig. 4.31) and Meyer-Berthaud and Gerrienne (2001); extinct taxa are indicated with a dagger (†). Early in the evolution of the lycophyte lineage there was a transition to sporangia that had a dorsoventral organization and that opened with transverse dehiscence. The crown group of lycophytes shares a single origin of leaves (lycophylls) that develop by an intercalary meristem. Bottom inset, Sketches of a representative early Devonian lycophyte, *Zosterophyllum*: A, dichotomously branched axes, erect axes bearing lateral dorsoventral sporangia; B, Tiny central vascular strand (protostele) composed of tracheids. Plant drawing from Arens et al. (1998a). Top inset, *Lepidodendron*, typical arborescent lycopsid. Plant drawing from Arens et al. (1998b). Taxonomic issues: *Hsua* = "rhyniophyte" sensu Banks (1975, 1992) = putative zosterophyte sensu Kenrick and Crane (1997a); *Nothia* = "rhyniophyte" sensu Banks (1975, 1992) = putative zosterophyte sensu Kenrick and Crane (1997a); *Barinophyton* = *incertae sedis* sensu Banks (1975, 1992) = zosterophyte sensu Kenrick and Crane (1997a); *Cooksonia* = "rhyniophyte" sensu Banks (1975, 1992) = polyphyletic, with some species part of Lycophytina stem group sensu Kenrick and Crane (1997a).

dae and Ophioglossidae (fig. 10.5B)—eusporangiate ferns (produce thick-walled sporangia containing numerous spores) with such radically different phenotypes that their recognition as sister taxa became apparent only after the accumulation of data from a number of molecular markers (Nickrent et al. 2000, Pryer et al. 2001). Morphological characters that support this relationship are exceedingly difficult to discern given the extreme simplification that one observes in both their vegetative and reproductive structures. However, these two monilophyte lineages share a reduction in root systems, whereby Ophioglossidae have no root hairs and Psilotidae have lost roots altogether, with both lineages relying on endomycorrhizal associations for nutrient absorption (Schneider et al. 2002).

How the remaining lineages of extant monilophytes (Equisetopsida, Polypodiidae, and Marattiidae) are related to

one another is still unclear. Extant Equisetopsida (15 species; Des Marais et al. 2003) and Marattiidae (300 species; Hill and Camus 1986) are relatively species poor, but both these groups have very rich fossil records in the Late Paleozoic and Early Mesozoic (fig. 10.5B; Bateman et al. 1998, Rothwell 1999, Liu et al. 2000, Berry and Fairon-Demaree 2001). In contrast, the Polypodiidae have had a rich fossil record from the Late Paleozoic until the Recent period, with extant taxa numbering greater than 10,000 species (Collinson 1996, Skog 2001). Polypodiidae share the notable characteristic of being leptosporangiate—having sporangia with a wall that is a single cell layer thick and containing relatively few meiospores (<1000, usually 64).

Continued emphasis on increasing the availability of molecular markers will likely improve resolution among these deep branches in the monilophyte clade. However, it

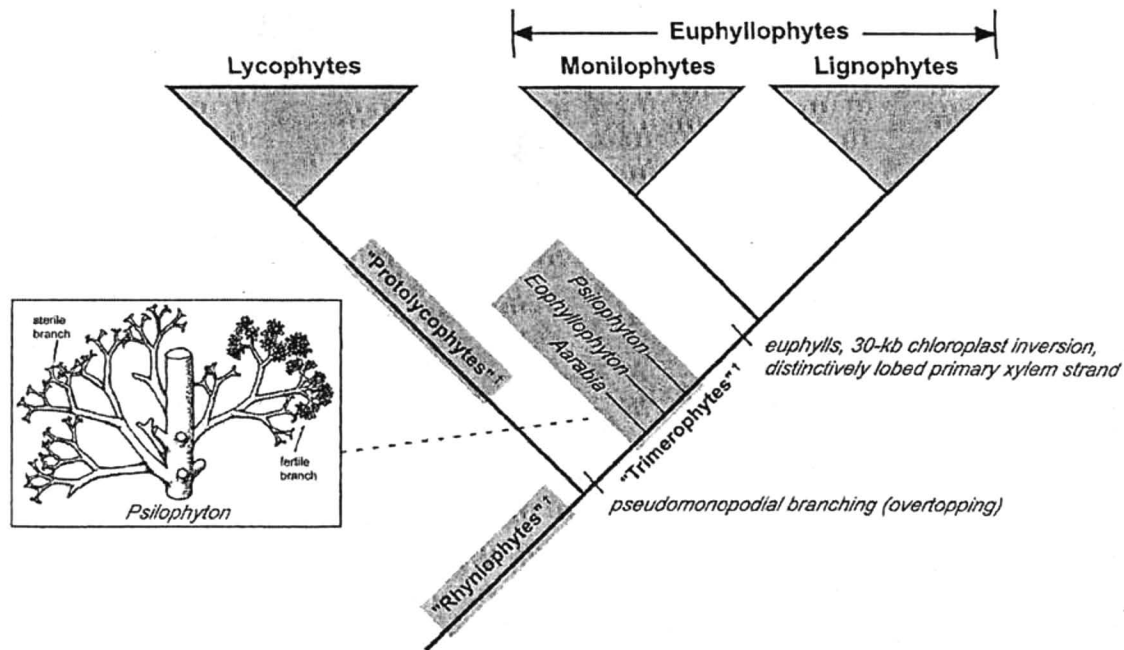


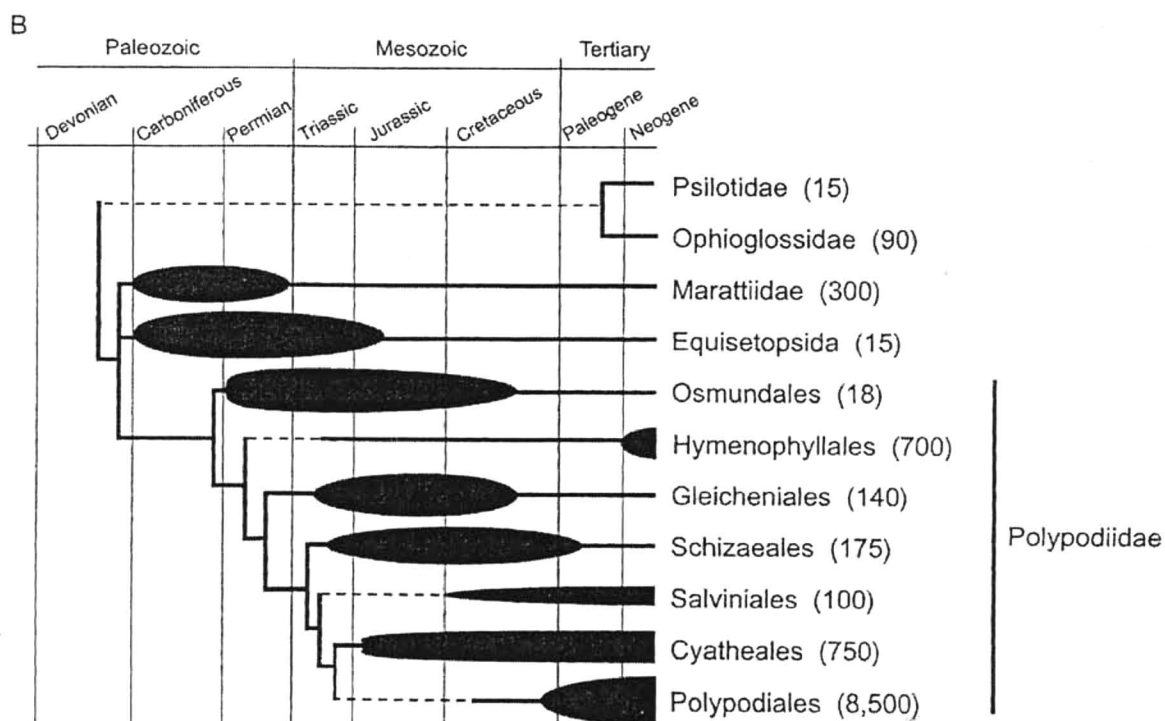
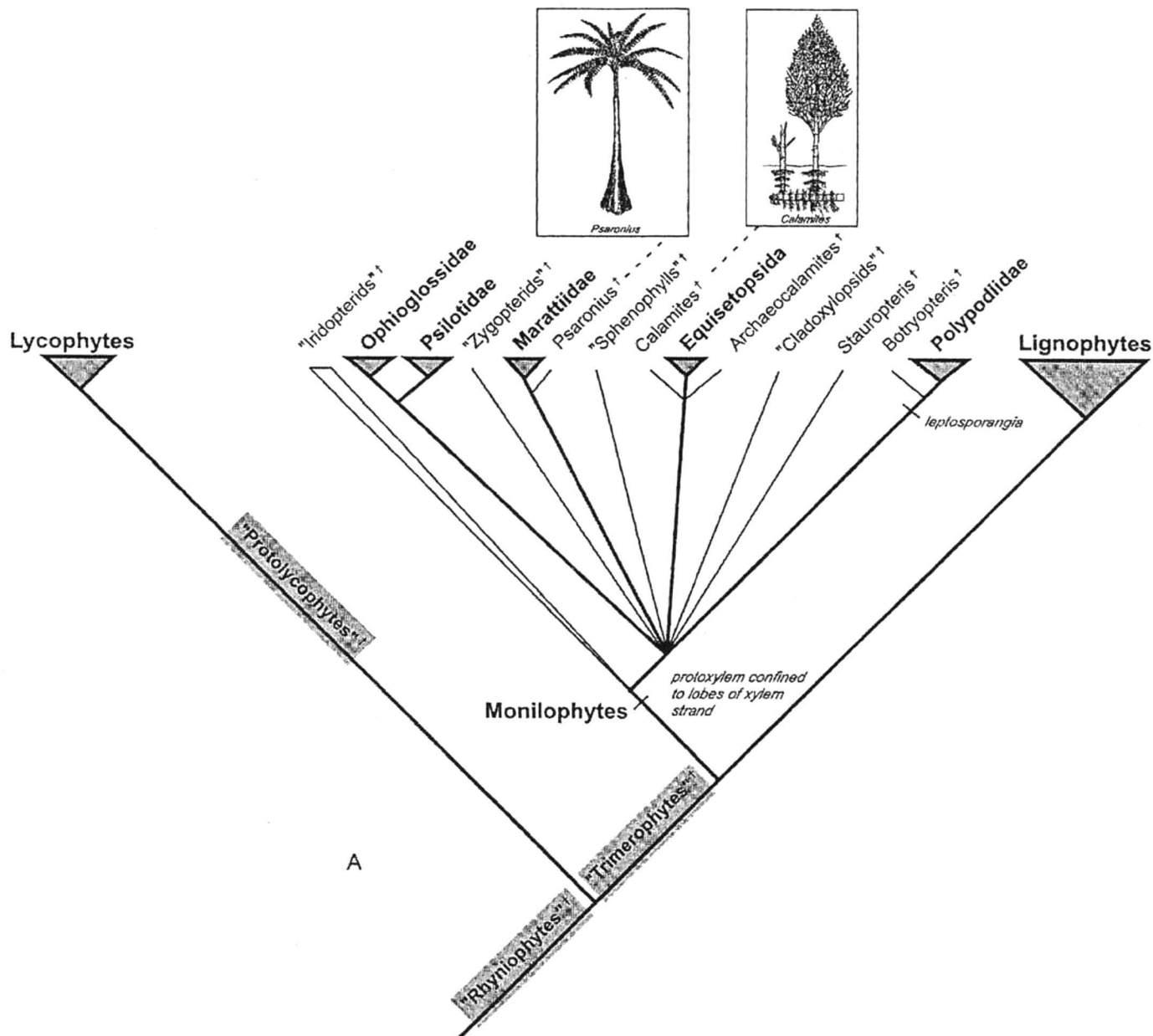
Figure 10.4. Vascular plant phylogeny. Relationships of "trimerophytes" and euphyllophytes (= monilophytes + lignophytes). Phylogeny based largely on Kenrick and Crane (1997a:240, fig. 7.10) and Meyer-Berthaud and Gerrienne (2001). Extinct (†) taxa are in shaded boxes. The transition to "trimerophytes" is marked by a change to pseudomonopodial branching, whereby a main indeterminate axis develops and overtops lateral determinate axes. Euphyllophytes share a common origin of leaves (euphylls) that develop by an apical and/or marginal meristem, a 30-kilobase inversion in the chloroplast genome organization, and a distinctively lobed primary xylem strand. Inset, sketch of *Psilophyton* shows sterile axes with forked tips and fertile lateral axes terminated by sporangia. Plant drawing from Arens et al. 1998c).

will also be critical for future studies to incorporate morphological data from fossil members pertinent to this clade if we really are going to improve our understanding of the evolution of monilophyte lineages through time and clarify ideas concerning homology. These include arborescent relatives of Equisetopsida, such as *Archaeocalamites* and *Calamites* (fig. 10.5A); fossil relatives of Marattiidae, such as *Psaronius* (fig. 10.5A), which was an important tree-fern-like component of Carboniferous landscapes; and extinct Polypodiidae, such as *Botryopteris*, which although less abundant and more diminutive (Bateman et al. 1998, DiMichele et al. 2001), were opportunistic and scandent members of the terrestrial ecosystem, much as their living relatives are today.

As to the relationships of other fossil monilophytes of the Devonian with highly divergent morphologies, such as "iridopterid" (*Ibykya*), "cladoxyloids" (*Calamophyton*, *Pseudosporochnus*), and "zygopterid" ferns (*Rhacophyton*), much work remains to be done (Bateman et al. 1998, Rothwell 1999, Berry and Farion-Dermaret 2001). These fossil plants have been discussed as relatives to horsetails and ferns in the broad sense, but with no clear picture emerging as to which are stem group or crown group members (fig. 10.5A). Integrating these taxa into a phylogeny of living members will certainly improve our understanding of evolutionary transitions in morphology in this group.

Within the leptosporangiate ferns (Polypodiidae), our knowledge of extant fern relationships has dramatically improved over the last 10 years (Hasebe et al. 1995, Pryer et al.

1995, 2001, Schneider 1996, Wolf et al. 1998). A few highlights include the determination that Osmundaceae is the earliest-diverging leptosporangiate family; gleichenioid and dipteroid ferns together with *Matonia* are a monophyletic early-diverging group and not, as was once thought, a paraphyletic grade of basal ferns; the heterosporous ferns (Marsileaceae and Salviniaceae) are sister group to a large clade of derived homosporous ferns that includes tree ferns and the species-rich "polypodiaceous" ferns; the most derived lineage of ferns including dennstaedtioid, ptendoid, dryopteridoid, and polypodioid ferns, once thought to be polyphyletic (Smith 1995), are now known to be monophyletic. Extant lineages differ enormously in their diversity and history, including their time of origin, time of greatest diversity, and time of decline (fig. 10.5B). Osmundaceous ferns, the most basal lineage of leptosporangiate ferns, are a small group today, but they were highly diverse from the Permian and throughout the Mesozoic until they began to decline in the Upper Cretaceous (Skog 2001). Other basal Polypodiidae lineages, such as the gleichenioid and schizaeoid ferns, followed a similar pattern (fig. 10.5B). In stark contrast, the clade of ferns (Polypodiales; fig. 10.5B) with the greatest diversity today (>80% of all extant leptosporangiate ferns) might have originated as early as the Cretaceous (Skog 2001; but see Collinson 1996) and has diversified throughout the Cenozoic (Collinson 2001). The origin and diversification pattern observed in this clade of ferns parallels that observed in the angiosperms, albeit at a relatively smaller scale



(H. Schneider, E. Schuettpelz, K. M. Pryer, R. Cranfill, S. Magallón, and R. Lupia, unpubl. obs.).

Lignophytes

The lignophytes (Doyle and Donoghue 1986, Rothwell and Serbet 1994, Bateman et al. 1998, Doyle 1998b) include all plants that reproduce via seeds (spermatophytes), together with their immediate "seed-free" precursors (fig. 10.6). Spermatophytes are the only living lignophytes, and with more than 260,000 species, they constitute the most diverse group of extant plants. The overwhelming majority of this diversity belongs to angiosperms (flowering plants), which produce their seeds enclosed within carpels (modified leaves). The remaining spermatophytes are "gymnosperms," represented by four extant lineages (fig. 10.6): Cycadophyta (cycads, ~130 species), Gnetophyta (gnetophytes or gnetales, ~70 species), Ginkgophytes (*Ginkgo biloba*, a single living species), and Coniferophyta (conifers, ~550 species). All "gymnosperms" produce naked seeds, that is, not enclosed within a carpel.

Lignophytes share the capability of forming wood by means of a bifacial cambium—a region of persistent cell division in their stems that produces secondary phloem toward the outside and secondary xylem toward the inside. At maturity, these secondary xylem cells form wood. Lignophyte precursors share a tetrastichous branch arrangement and a distinctive form of protoxylem ontogeny (= Infradivision Radiatopses, *sensu* Kenrick and Crane 1997a; Schneider et al. 2002; fig. 10.6). *Pertica*, formerly regarded as a "trimerophyte" (*sensu* Banks 1975, 1992), and *Tetraxlopteris*, a "progymnosperm," have been tentatively identified as lignophyte precursors (Kenrick and Crane 1997a; fig. 10.6). The earliest lignophytes had a gymnospermous wood-producing stem anatomy, and some were large trees. Unlike gymnosperms, however, these woody plants did not produce seeds, but rather were free-sporing. Collectively, these plants are known as

"progymnosperms" and were important components of the mid-Paleozoic vegetation (Meyer-Berthaud et al. 1999). Early representatives of this group, such as the Middle Devonian (Eifelian) *Aneurophyton*, produced a single type of spore (homospory). Younger "progymnosperms" produced two different types of spores (heterospory), microspores and megaspores, which gave rise to microgametophytes/sperm cells and megagametophytes/egg cells, respectively. The megagametophyte and microgametophyte phases of the life cycle of these fossils are believed to have been retained within the walls of the megaspore and the microspore, respectively (endospory), which is the condition observed in all known living heterosporous plants. The heterosporous "progymnosperms," including the Late Devonian *Archaeopteris* (fig. 10.6, inset), are considered to be the closest relatives to the seed plant lineage (spermatophytes).

Although heterospory evolved several times in different tracheophyte lineages, only in the lineage leading to spermatophytes was it accompanied by a sophisticated suite of innovations and modifications involving the structure and function of megagametophytes, microgametophytes, and associated sporophytic tissues, giving rise to the complex structures that are seeds (Bateman and DiMichele 1994). The fossil record indicates that the series of steps leading from heterospory to seeds occurred a single time in the evolution of plants (Crane 1985, Doyle and Donoghue 1986, Nixon et al. 1994, Rothwell and Serbet 1994). Several Late Devonian (Famennian) reproductive structures, such as in *Elkinsia* and *Archaeosperma* (fig. 10.6), exhibit some of the early steps in the evolution of the seed, but lack several critical attributes found in later forms. These structures consisted of an unopened (indehiscent) megasporangium that retained within its walls a single functional megaspore with an endosporic megagametophyte. Partially fused protective lobes of sporophytic origin (integumentary lobes) enveloped the indehiscent megasporangium, thereby retaining the megasporangium on the sporophyte parent plant.

Subsequent spermatophyte lineages had seeds with a completely fused envelope (integument) that enclosed the

Figure 10.5. Vascular plant phylogeny: relationships of ferns and horsetails (monilophytes). (A) Phylogeny based largely on Pryer et al. (2001) and Kenrick and Crane (1997a). The monilophytes share the positional and ontogenetic characteristic of having their protoxylem confined to the outer lobed ends of the xylem strand ("necklacelike," *L. moniliformis*). The greatest species diversity within the monilophytes (~12,000 species) is found in the Polypodiidae clade, which shares the derived leptosporangiate condition: thin-walled sporangia that produce a low number of spores (generally 64). Sketch of representative extinct crown group monilophytes: left inset, *Psaronius*, Pennsylvanian marattialean "tree fern." Plant drawing from Arens et al. (1998d); right inset, *Calamites*, Carboniferous arborescent relative of the modern horsetail, *Equisetum*. Plant drawing from Arens et al. (1998c). By integrating extant taxa (Pryer et al. 2001) together with their fossil (†) relatives (Kenrick and Crane 1997a, Berry and Fairon-Demaret 2001, Meyer-Berthaud and Gerrienne 2001) in this phylogeny, we hope to demonstrate that much of the morphological diversity that once existed in this clade is not represented in studies that consider only the living taxa. The representative fossils (†) encompass several groups: "cladoxyllopsids" (*Calamophyton*, *Pseudosporochnus*), "iridopterids" (*Hyenia*, *Ibyka*), "sphenophylls" (*Sphenophyllum*, *Bowmanites*), "zygopterids" (*Rhacophyton*, *Zygopteris*), and *Stauropteris*. (B) Phylogeny of extant monilophytes (Pryer et al. 2001) plotted onto a geological time scale (Geological Society of America 1999) to illustrate the diversification of leptosporangiate ferns through time (Skog 2001). Dashed lines indicate ghost lineages—lineages without a corresponding fossil record (a striking example is the branch that unites Psilotidae and Ophioglossidae); continuous lines indicate congruence between fossil record and phylogeny. Thickened areas only generally approximate the relative diversity of groups through time.

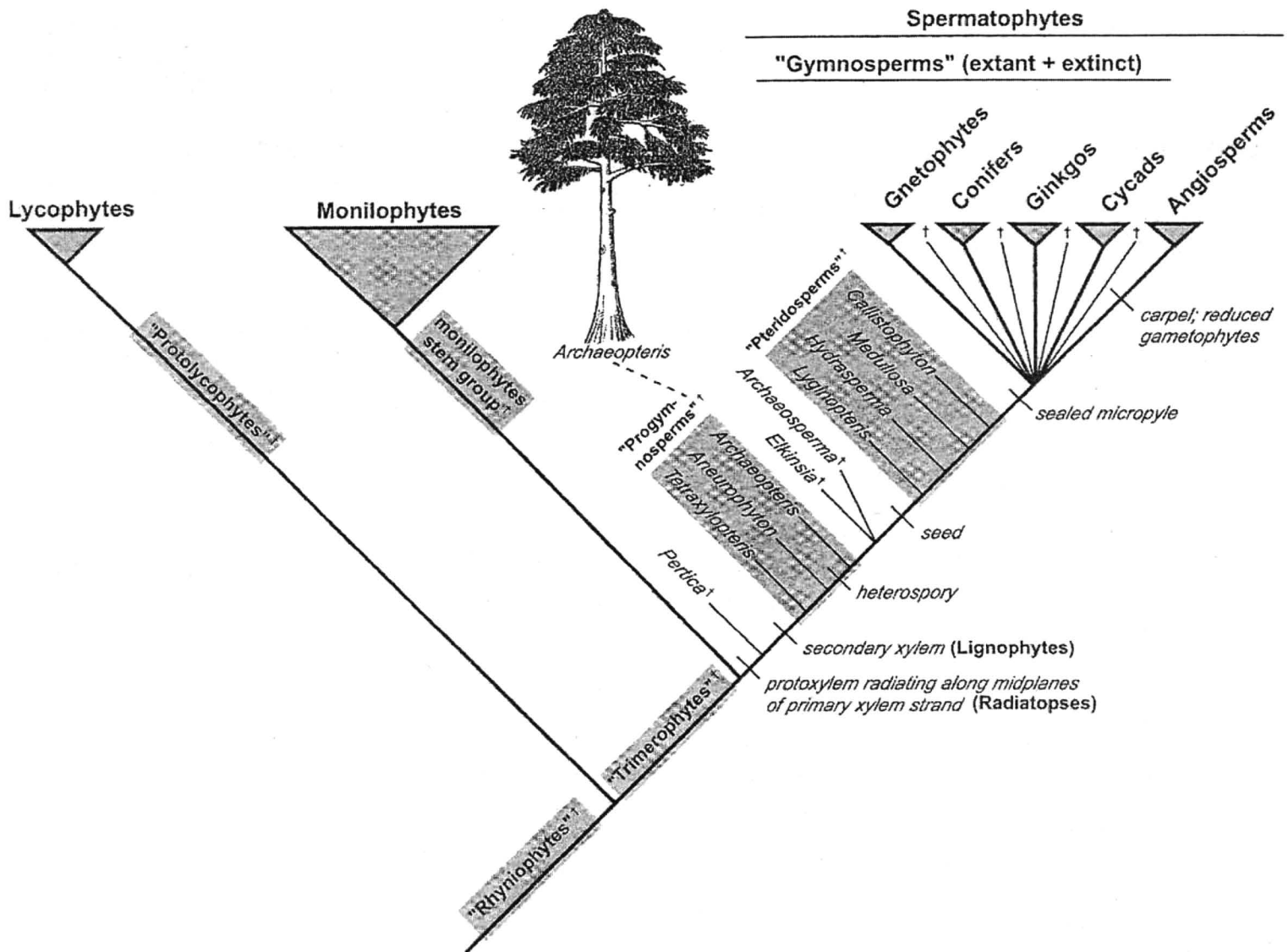


Figure 10.6. Vascular plant phylogeny: relationships of seed plants and the extinct "progymnosperm," "pteridosperm," and derived "trimerophyte" stem group lineages. Phylogeny based primarily on Kenrick and Crane (1997a). Members of this clade share the positional and ontogenetic characteristic of having protoxylem with multiple strands occurring along the midplanes of the lobed primary xylem ribs, corresponding to the "radiate protoxylem" group of Stein (1993) (= Infradivision Radiatopses in Kenrick and Crane 1997a). The greatest species diversity within this clade is found in the angiosperms (~260,000 species), which share several derived characters, including a carpel that encloses the seed and highly reduced male and female gametophytes. Critical synapomorphies (e.g., secondary xylem, heterospory, seed, sealed micropyle) are plotted onto the topology at positions we believe best reflect our current understanding of the evolution of these features. A "seed" is a complex structure and is defined here as a megasporangium containing a single functional megaspore enclosed in one or more integuments of sporophytic origin. Inset, Sketch of representative extinct "progymnosperm": *Archaeopteris*. Plant drawing from Arens et al. (1998f). Relationships among all five major extant seed plant lineages remains elusive with no consensus as to the closest relative to the angiosperms. The figure attempts to illustrate that taking into account all the lineages (extinct and extant) that produce naked seeds ("gymnosperms") as a whole, results in "gymnosperms" being a paraphyletic assemblage, regardless of how the modern groups turn out to be related (i.e., even if all four living lineages are a monophyletic sister group to the angiosperms). Extinct (†) lineages interspersed among the five extant lineages of seed plants represent such groups as Bennettitales, Pentoxylales, Caytoniales, Corystospermales, and Cordaitales.

megasporangium except at its apex, where a small opening remained. Through this aperture (the micropyle), pollen grains entered the pollen chamber and released either sperm cells or formed pollen tubes to establish contact with the megagametophyte and, eventually, with the egg cells. The earliest seeds with a completely fused integument and a well-defined micropyle are known from the lowermost Carboniferous (e.g., *Stamnostoma*; Long 1960). Spermatophyte diversity increased dramatically during the Carboniferous, giving rise to several lineages with fernlike foliage, collectively known as “pteridosperms” or “seed ferns” (fig. 10.6). These plants encompass an extremely broad array of seed morphology and reproductive biology, but they all have seeds with a micropyle that did not seal following pollen grain capture. How “pteridosperm” lineages are related is incompletely understood (fig. 10.6); however, it appears that the earliest-diverging lineages were composed of forms such as *Lyginopteris*, in which pollen reception involved sophisticated elaborations of the megasporangium wall apex, but in later forms, such as in *Medullosa* and *Callistophyton*, the function of pollen reception was taken up by the micropyle formed by the integuments. The Mesozoic “glossopterids” are putative “pteridosperms,” although some authors have indicated that they may be more closely allied with members of the seed plant crown group (Doyle 1998b, Willis and McElwain 2002).

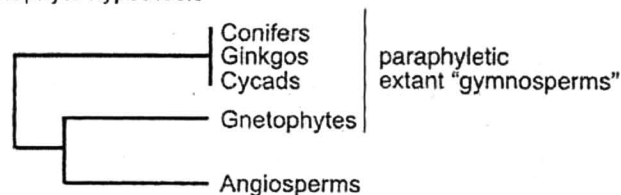
Plants in which the micropyle became sealed after pollen grain capture gave rise to the clade that includes the five major groups of living spermatophytes, as well as many other lineages that are now extinct (fig. 10.6). Included among these are some Mesozoic plants that various authors have previously called “seed ferns.” In this chapter, we restrict the use of “seed ferns” to seed plants without a sealed micropyle; therefore, taxa previously regarded as “seed ferns” that have a sealed micropyle, such as the Caytoniales, no longer fit this definition and are regarded here as part of the seed plant crown group. Discerning relationships among major living spermatophyte clades and their extinct relatives has proven to be extremely problematic, due, at least in part, to the old age of most of the lineages involved (except probably for the angiosperm crown group), and to the scant proportion of overall spermatophyte diversity represented by the living members. The use of morphological and molecular data in phylogenetic studies has resulted in dramatically different views. Morphological studies benefit from incorporating information about extinct clades but are affected by the problematic interpretation of homologies for insufficiently known characters. Molecular studies are severely impacted by the relatively meager taxonomic representation of overall spermatophyte diversity that is provided by living representatives.

Analyses of morphological data have recognized a clade (the anthophytes) that includes angiosperms and gnetophytes, together with the extinct Bennettitales and Pentoxylales (Crane 1985, Doyle and Donoghue 1986, Rothwell and Serbet 1994). As a result, the idea that, among living spermatophytes, angiosperms and gnetophytes are most closely related (anthophyte

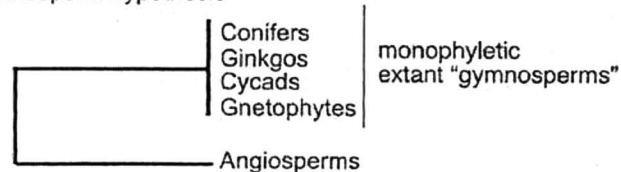
hypothesis, fig. 10.7A) prevailed for more than a decade (Donoghue and Doyle 2000). However, increasing evidence from studies based on molecular data has now rejected the phylogenetic closeness between angiosperms and gnetophytes (Donoghue and Doyle 2000), although, at this writing, none of these studies have yet converged on an alternative, well-supported scheme of relationships among the living major clades of spermatophytes. The conflict spans not only analyses based on morphological versus molecular data, but also analyses based on different types of molecular data and on different approaches to analytical methods and taxon sampling (e.g., Sanderson et al. 2000, Magallón and Sanderson 2002, Rydin and Källersjö 2002, Rydin et al. 2002).

Several studies based on different genes and gene combinations place angiosperms as the sister to all other living spermatophytes (gymnosperm hypothesis; fig. 10.7B), suggesting that angiosperms are not closely related to any one of the extant groups of gymnosperms. Most molecular-based studies indicate a close association between gnetophytes and conifers, some even placing gnetophytes *within* conifers, thus rendering the conifers a paraphyletic assemblage (e.g., Chaw et al. 2000, Gugerli et al. 2001, Magallón and Sanderson 2002, Soltis et al. 2002). The suggestions of extant gymnosperm monophyly and conifer paraphyly are unexpected and should be viewed as provisional. Still other studies (e.g.,

A. “Anthophyte hypothesis”



B. “Gymnosperm hypothesis”



C. “Gnetophyte hypothesis”

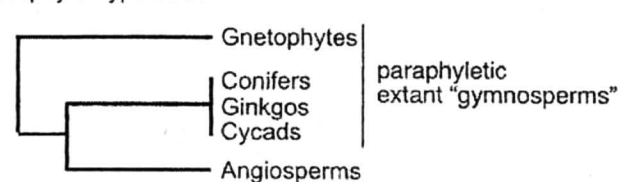


Figure 10.7. Alternative hypotheses of relationships (A, B, C) among five major extant lineages of seed plants. The anthophyte hypothesis places the gnetophytes as sister to the angiosperms. This hypothesis is based mostly on morphological evidence (Crane 1985, Doyle and Donoghue 1986), but most recent molecular studies (e.g., Barkman et al. 2000) have not supported any evidence for an anthophyte clade (but see Rydin et al. (2002).

Graham and Olmstead 2000, Sanderson et al. 2000) have shown that sometimes gnetophytes can be placed as sister to all other extant seed plant groups (gnetophyte hypothesis; fig. 10.7C).

A close proximity between gnetophytes and conifers has been proposed previously on the basis of various anatomical and morphological similarities (Coulter and Chamberlain 1917, Bailey 1953, Bierhorst 1971, Carlquist 1996), but the placement of gnetophytes within the conifers has disturbing implications from a traditional perspective on conifer evolution. Conifers show remarkable homogeneity in their vegetative and reproductive morphological attributes, including a growth form that is nearly always a monopodial tree, mostly needle-shaped leaves, gymnospermous wood, simple pollen cones, and usually compound seed cones with a distinctive organization, whereas gnetophytes display extraordinary variability in each of these characters. A molecular character often cited in support of conifer monophyly is the loss of one of the inverted repeat (IR) copies of the chloroplast genome, which is shared exclusively by all conifers (Raubeson and Jansen 1992b).

Although it is certainly possible that angiosperms are not closely related to any one lineage of living gymnosperms, it is important to keep in mind that molecular evidence alone simply cannot provide information regarding the relationship of angiosperms to any of the extinct groups of gymnosperms. Regardless of how the issue of relationships among the five extant seed plant lineages is finally resolved, "gymnosperms" in the broad sense, which include the early-diverging fossil lineages, are not monophyletic (fig. 10.6). It is highly likely that at the base of the lineage leading to modern angiosperms, there were some gymnosperms that are now extinct.

Taken as a whole, there have been remarkable improvements in our understanding of relationships within the major living spermatophyte lineages. Well-supported examples include the determination that *Cycas* is the sister to all other cycads; among living gnetophytes, *Gnetum* and *Welwitschia* are more closely related to one another than either is to *Ephedra*; Pinaceae is the earliest-diverging clade among living conifers; and Araucariaceae plus Podocarpaceae is sister to a clade that includes Taxaceae (yew), Taxodiaceae (redwood), and Cupressaceae (cypress) (Barkman et al. 2000, Chaw et al. 2000, Gugerli et al. 2001, Magallón and Sanderson 2002, Rydin et al. 2002).

A number of significant innovations originated on the lineage leading to angiosperms, including the carpel, which encloses the seeds, a second integumentary layer around the seed, and an extreme reduction of the megagametophyte (Bateman et al. 1998, 1998b, Theissen et al. 2002). Although our understanding of relationships within the angiosperms has improved dramatically over recent years (Qiu et al. 1999, 2000, Soltis et al. 1999, 2000; see ch. 11 in this vol.), the nature and homology of several characters unique to angiosperms are still unclear.

Vascular Plants, the Phylogenetic and Genomic Revolutions, and Fossils

Our understanding of the phylogeny of vascular plants has changed tremendously in the last 20 years due to the introduction of molecular techniques (Soltis and Soltis 2000) into plant sciences and the concomitant application of explicit phylogenetic methods to both molecular and morphological data. Before that time (and to some extent even in the present), an Aristotelian interpretation of relationships prevailed, one that promoted a linear and unidirectional transition in vascular plant evolution from simple to complex organization. For example, it was commonly thought that the whisk fern *Psilotum* was a "living fossil" or remnant of the earliest lineage of vascular plants, given its remarkable superficial resemblance to the dichotomously branched "rhyniophyte" fossils (Parenti 1980, Gifford and Foster 1989, Rothwell 1996, 1999, DiMichele et al. 2001). We now know that *Psilotum* is well embedded within the euphyllophytes and that its scalelike leaves and lack of roots do not indicate an ancient origin, but are rather the result of morphological simplification during the evolution of these plants (Schneider et al. 2002).

Although there has been remarkable progress in our understanding of plant evolution, some relationships are still enigmatic. For example, relationships among the major seed plant lineages, recently thought to be close to resolution (Donoghue and Doyle 2000), are now under renewed scrutiny, and we are almost no farther along than we were 20 years ago in identifying the closest relatives to the angiosperms. Molecular data appear to have rejected the anthophyte hypothesis (fig. 10.7A)—gnetophytes sister to angiosperms—but they continue to be ambiguous about the position of gnetophytes: either within the putatively monophyletic extant gymnosperms (gymnosperm hypothesis; fig. 10.7B), or sister to all other living seed plants (gnetophyte hypothesis; fig. 10.7C; (Goremykin et al. 1997, Doyle 1998, Barkman et al. 2000, Frohlich and Parker 2000, Sanderson et al. 2000, Magallón and Sanderson 2000, Rydin and Källersjö 2002, Rydin et al. 2002).

Papers on vascular plant phylogeny are now being published that include in excess of eight or more genes (Graham and Olmstead 2000, Soltis et al. 2002), but a clear picture of branching relationships resulting from the deep seed plant radiation is still not emerging. Two approaches are currently favored to resolve these persistently stubborn questions. The first promises to take advantage of the exceptional progress in our ability to sequence large pieces of whole genomes under the assumption that the accumulation of large amounts of genetic information and, in particular, data about structural mutations within the genome may provide a breakthrough. The second favors the integration of more than 100 years of accumulated knowledge of fossils into a modern phylogenetic framework. Exactly how to go about doing this,

integrating data from molecules together with morphological characters from both living and extinct taxa, is one of the exciting challenges now facing us (Doyle and Donoghue 1987, Wilkinson 1995, Nixon 1996, Wiens 1998, O'Leary 2000, Kearney 2002). The latter approach reflects a rather surprising renaissance in how to view morphological data in modern phylogenetic studies. Pushed aside in the early days of DNA sequencing, when molecules were thought to be the holy grail for sorting out all questions on early land plant evolution, they are now back in favor once again as a valuable resource in more synthetic approaches. In addition, there has been a recent notable increase in the description of exciting new plant fossils (e.g., Sun et al. 1998, 2002, Friis et al. 2001a).

Because recent advances in our understanding of vascular plant relationships are due mostly to the introduction of molecular data, our interpretations are nearly exclusively restricted to living taxa. When one stops to ponder the vascular plant tree through hundreds of millions of years, one is struck not only by the large number of taxa that have come before and that are no longer extant (and that are not available for DNA sequencing studies), but also the extent of morphological diversity that is no longer represented in living plants. Extinctions have wiped out major parts of whole lineages that contributed heavily to plant diversity in the Paleozoic and Mesozoic. For example, extant monilophytes consist of five distinct and ancient lineages. With the exception of leptosporangiate ferns (Polypodiidae), these lineages are not rich in either species number or morphological diversity. However, some of these lineages, such as the horse-tails, were among the more diverse and dominant groups in the Upper Paleozoic and Early Mesozoic. Although horse-tails have managed to survive until today with one species-poor lineage, *Equisetum*, other groups of monilophytes, such as Cladoxydopsidales and Zygopteridales, have gone completely extinct. On the surface, this would seem to support the idea that terrestrial ecosystems have witnessed a sequential replacement of lineages through time whereby, for example, such groups as the lycophytes, which were dominant in the Paleozoic, came to be superseded in diversity by the euphyllophytes, especially seed plants (Niklas et al. 1985). This has led to the seemingly popular notion that once such lineages "crash": they either go extinct or experience a prolonged period of stasis. However, some of these "superseded" lineages have undergone subsequent radiations, as observed in lycophytes (Late Tertiary; Wikström and Kenrick 2001) and derived leptosporangiate ferns (Late Cretaceous-Early Tertiary; H. Schneider, E. Schuettpelz, K. M. Pryer, R. Cranfill, S. Magallón, and R. Lupia, unpubl. obs.).

The recent implementation of highly sophisticated genetic tools to study the plant genome and the expression of its genes has generated a new breed of studies that integrate the study of plant development with evolution (Cronk 2001, Cronk et al. 2002, Schneider et al. 2002). This approach can

be used to explore the evolution of critical morphological characters, such as the origin of leaves, for example, that have been the subject of long-standing controversies (Langdale et al. 2002, Schneider et al. 2002). Incorporating data from fossils and plant development in integrative and comparative studies promises to help us to overcome our currently incomplete knowledge of vascular plant relationships through time. The results of such studies will inform our understanding of the evolution of these extinct taxa, will afford us clearer insights into the morphological evolution of extant plants, and will even permit us to interpret fundamental changes in global ecology—including climate—throughout the last 450 million years (McElwain et al. 1999, Beerling et al. 2001, Berner 2001, Driese and Mora 2001, Willis and McElwain 2002).

Acknowledgments

We thank Joel Cracraft and Michael J. Donoghue for inviting us to participate in this symposium and for their patience and encouragement during manuscript preparation. Support from the National Science Foundation to the "Deep Time" Research Coordination Network initiative has been helpful in bringing the coauthors and others together to discuss several points made in this chapter. K.M.P. and H.S. gratefully acknowledge grant support from the NSF (DEB-0089909). An exceptional website on early land plants, developed by Nan C. Arens and Caroline Strömberg, was useful to us (available at <http://www.ucmp.berkeley.edu/IB181/HpageIB181.html>). It was the source of several plant drawings by C. Strömberg, reproduced here courtesy of the University of California Museum of Paleontology.

Literature Cited

- Algeo, T. J., S. E. Scheckler, and J. B. Maynard. 2001. Effects of the Middle to Late Devonian spread of vascular plants on weathering regimes, marine biotas, and global climate. Pp. 213–236 in *Plants invade the land: evolutionary and environmental perspectives* (P. G. Gensel and D. Edwards, eds.). Columbia University Press, Cambridge, MA.
- Arens, N. C., C. Strömberg, and A. Thompson. 1998a. Lab V—lycophytes. In *Virtual paleobotany laboratory*. Available: <http://www.ucmp.berkeley.edu/IB181/VPL/Lyco/Lyco1.html>. Last accessed 10 March 2003.
- Arens, N. C., C. Strömberg, and A. Thompson. 1998b. Lab V—lycophytes. In *Virtual paleobotany laboratory*. Available: <http://www.ucmp.berkeley.edu/IB181/VPL/Lyco/Lyco2.html>. Last accessed 10 March 2003.
- Arens, N. C., C. Strömberg, and A. Thompson. 1998c. Lab VII—the origin of seed plants. In *Virtual paleobotany laboratory*. Available: <http://www.ucmp.berkeley.edu/IB181/VPL/Osp/Osp1.html>. Last accessed 10 March 2003.
- Arens, N. C., C. Strömberg, and A. Thompson. 1998d. Lab VI—sphenopsids and ferns. In *Virtual paleobotany labora-*

- tory. Available: <http://www.ucmp.berkeley.edu/IB181/VPL/SpheFe/SpheFe4.html>. Last accessed 10 March 2003.
- Arens, N. C., C. Strömberg, and A. Thompson. 1998e. Lab VI—sphenopsids and ferns. In Virtual paleobotany laboratory. Available: <http://www.ucmp.berkeley.edu/IB181/VPL/SpheFe/SpheFe2.html>. Last accessed 10 March 2003.
- Arens, N. C., C. Strömberg, and A. Thompson. 1998f. Lab VII—the origin of seed plants. In Virtual paleobotany laboratory. Available: <http://www.ucmp.berkeley.edu/IB181/VPL/Osp/Osp2.html>. Last accessed 10 March 2003.
- Bailey, I. W. 1953. Evolution of the tracheary tissue of land plants. *Am. J. Bot.* 40:4–8.
- Banks, H. P. 1975. Reclassification of Psilophyta. *Taxon* 24:401–413.
- Banks, H. P. 1992. The classification of early land plants—revisited. *Geophytology* 22:49–64.
- Barkman, T. J., G. Chenery, J. R. McNeal, L. Lyons-Weiler, W. J. Ellisens, G. Moore, A. D. Wolfe, and C. W. dePamphilis. 2000. Independent and combined analyses of sequences from all three genomic compartments converge on the root of flowering plant phylogeny. *Proc. Natl. Acad. Sci. USA* 97:13166–13171.
- Bateman, R. M., P. R. Crane, W. A. DiMichele, P. Kenrick, N. P. Rowe, T. Speck, and W. E. Stein. 1998. Early evolution of land plants: phylogeny, physiology, and ecology of the primary terrestrial radiation. *Annu. Rev. Ecol. Syst.* 29:263–292.
- Bateman, R. M., and W. A. DiMichele. 1994. Heterospory: the most iterative key innovation in the evolutionary history of the plant kingdom. *Biol. Rev.* 69:345–417.
- Beerling, D. J., C. P. Osborne, and W. G. Chaloner. 2001. Evolution of leaf-form in land plants linked to atmospheric CO₂ decline in the Late Palaeozoic era. *Nature* 410:352–354.
- Berner, R. A. 2001. The effect of the rise of land plants on atmospheric CO₂ during the Paleozoic. Pp. 173–178 in *Plants invade the land: evolutionary and environmental perspectives* (P. G. Gensel and D. Edwards, eds.). Columbia University Press, Cambridge, MA.
- Berry, C. M., and M. Fairon-Demaret. 2001. The Middle Devonian flora revisited. Pp. 120–139 in *Plants invade the land: evolutionary and environmental perspective* (P. G. Gensel and D. Edwards, eds.). Columbia University Press, Cambridge, MA.
- Bierhorst, D. W. 1971. *Morphology of vascular plants*. Macmillan Press, New York.
- Blackwell, M. 2000. Terrestrial life—fungal from the start? *Science* 289:1884–1885.
- Boyce, C. K., and A. H. Knoll. 2002. Evolution of developmental potential and the multiple independent origins of leaves in Paleozoic vascular plants. *Paleobiology* 28:70–100.
- Brundrett, M. C. 2002. Coevolution of roots and mycorrhizas of land plants. *New Phytol.* 154:275–304.
- Cairney, J. W. G. 2000. Evolution of mycorrhiza systems. *Naturwissenschaften* 87:467–475.
- Carlquist, S. 1996. Wood, bark, and stem anatomy of Gnetales: a summary. *Int. J. Plant Sci.* 157(suppl.):S58–S76.
- Carroll, R. 2002. Early land vertebrates. *Nature* 418:35–36.
- Chaw, S.-M., C. L. Parkinson, Y. Cheng, T. M. Vincent, and J. D. Palmer. 2000. Seed plant phylogeny inferred from all three plant genomes: monophyly of extant gymnosperms and origin of Gnetales from conifers. *Proc. Natl. Acad. Sci. USA* 97:4086–4091.
- Coates, M. I. 2001. Origin of tetrapods. Pp. 74–79 in *Palaeobiology II* (D. E. G. Briggs and P. R. Crowther, eds.). Blackwell Science, London.
- Collinson, M. E. 1996. "What use are fossil ferns?" twenty years on: with a review of the fossil history of extant pteridophyte families and genera. Pp. 349–394 in *Pteridology in perspective* (J. M. Camus, M. Gibby, and R. J. Johns, eds.). Royal Botanic Gardens, Kew.
- Collinson, M. E. 2001. Cainozoic ferns and their distribution. *Brittonia* 53:173–235.
- Coulter, J. M., and C. J. Chamberlain. 1917. *Morphology of gymnosperms*. University of Chicago Press, Chicago.
- Crane, P. R. 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. *Ann. Mo. Bot. Gard.* 72:716–793.
- Crane, P. R. 1999. Major patterns in botanical diversity. Pp. 171–187 in *Evolution: investigating the evidence* (J. Scotchmoor and D. A. Springer, eds.). Palaeontological Society Special Publications 11.
- Crane, P. R., and P. Kenrick. 1997. Diverted development of reproductive organs: a source of morphological innovation in land plants. *Plant Syst. Evol.* 206:161–174.
- Cronk, Q. C. B. 2001. Plant evolution and development in a post-genomic context. *Nat. Rev. Genet.* 2:607–620.
- Cronk, Q. C. B., R. M. Bateman, and J. A. Hawkins (eds.). 2002. *Developmental genetics and plant evolution*. Taylor and Francis, London.
- Des Marais, D. L., K. M. Pryer, D. M. Britton, and A. R. Smith. 2003. Phylogenetic relationships and evolution of extant horsetails, *Equisetum*, based on chloroplast DNA sequence data (*rbcL* and *trnL-F*). *mt. J. Plant Sci.* 164:737–751.
- DiMichele, W. A., and T. L. Phillips. 2002. The ecology of Paleozoic ferns. *Rev. Palaeobot. Palynol.* 119:143–159.
- DiMichele, W. A., W. E. Stein, and R. M. Bateman. 2001. Ecological sorting of vascular plant classes during the Paleozoic evolutionary radiation. Pp. 285–335 in *Evolutionary paleoecology: the ecological context of macroevolutionary change* (W. D. Allmon and D. J. Botjtjer, eds.). Columbia University Press, New York.
- Donoghue, M. J. 2002. Plants. Pp. 911–918 in *Encyclopedia of evolution* (M. Pagel, ed.), vol. 2. Oxford University Press, Oxford.
- Donoghue, M. J., and J. A. Doyle. 2000. Seed plant phylogeny: demise of the anthophyte hypothesis? *Curr. Biol.* 10:R 106–R109.
- Doyle, J. A. 1998a. Molecules, morphology, fossils, and the relationships of angiosperms and Gnetales. *Mol. Phylogenet. Evol.* 9:448–462.
- Doyle, J. A. 1998b. Phylogeny of vascular plants. *Annu. Rev. Ecol. Syst.* 29:567–599.
- Doyle, J. A., and M. J. Donoghue. 1986. Seed plant phylogeny and the origin of angiosperms: an experimental cladistic approach. *Bot. Rev.* 52:321–431.
- Doyle, J. A., and M. J. Donoghue. 1987. The importance of fossils in elucidating seed plant phylogeny and macroevolution. *Rev. Palaeobot. Palynol.* 50:63–95.
- Driese, S. G., and C. I. Mora. 2001. Diversification of Siluro-Devonian plant traces in paleosols and influence on

- estimates of paleoatmospheric CO₂ levels. Pp. 237–253 in *Plants invade the land: evolutionary and environmental perspectives* (P. G. Gensel and D. Edwards, eds.). Columbia University Press, Cambridge, MA.
- Edwards, D., and C. Wellman. 2001. Embryophytes on land: the Ordovician to Lochkovian (Lower Devonian) record. Pp. 3–28 in *Plants invade the land: evolutionary and environmental perspectives* (P. G. Gensel and D. Edwards, eds.). Columbia University Press, Cambridge, MA.
- Fischer, D., T. Liu, E. Yip, and K. Yu. 1998. Localities of the Devonian: Rhynie Chert, Scotland. In *Virtual paleobotany, laboratory*. Available: <http://www.ucmp.berkeley.edu/devonian/rhynie.html>. Last accessed 10 March 2003.
- Friis, E. M., K. R. Pedersen, and P. R. Crane. 2001a. Fossil evidence of water lilies (Nymphaeales) in the Early Cretaceous. *Nature* 410:357–360.
- Friis, E. M., K. R. Pedersen, and P. R. Crane. 2001b. Origin and radiation of angiosperms. Pp. 97–102 in *Palaeobiology II* (D. E. G. Briggs and P. R. Crowther, eds.). Blackwell Science, London.
- Frohlich, M. W., and D. S. Parker. 2000. The mostly male theory of flower evolutionary origins: from genes to fossils. *Syst. Bot.* 25:155–170.
- Gaunt, M. W., and M. A. Miles. 2002. An insect molecular clock dates the origin of the insects and accords with palaeontological and biogeographic landmarks. *Mol. Biol. Evol.* 19:748–761.
- Gensel, P. G., and C. M. Berry. 2001. Early lycophyte evolution. *Am. Fern J.* 91:74–98.
- Gensel, P. G., M. E. Kotyk, and J. F. Basinger. 2001. Morphology of above- and below-ground structures in Early Devonian (Pragian-Emsian) plants. Pp. 83–102 in *Plants invade the land: evolutionary and environmental perspectives* (P. G. Gensel and D. Edwards, eds.). Columbia University Press, New York.
- Geological Society of America. 1999. Geologic time scale. Product code CTS004. (A. R. Palmer and J. Geissman, comps.).
- Gifford, E. M., and A. S. Foster. 1989. *Morphology and evolution of vascular plants*. 3rd ed. Freeman, New York.
- Goremykin, V., V. Bobrova, J. Pahnke, A. Troitsky, A. Antonov, and W. Martin. 1997. Noncoding sequences from the slowly evolving chloroplast inverted repeat in addition to *rbcL* data do not support Gnetales affinities of angiosperms. *Mol. Biol. Evol.* 13:383–396.
- Graham, S. W., and R. G. Olmstead. 2000. Utility of 17 chloroplast genes for inferring the phylogeny of the basal angiosperms. *Am. J. Bot.* 87:1712–1730.
- Gugerli, F., C. Sperisen, U. Büchler, I. Brunner, S. Brodbeck, J. D. Palmer, and Y.-L. Qiu. 2001. The evolutionary split of Pinaceae from other conifers: evidence from an intron loss and a multigene phylogeny. *Mol. Phylogenet. Evol.* 21:167–175.
- Hasebe, M., P. G. Wolf, K. M. Pryer, K. Ueda, M. Ito, R. Sano, G. J. Gastony, J. Yokoyama, J. R. Manhart, N. Murakami, E. H. Crane, C. H. Haufler, and W. D. Hauk. 1995. Fern phylogeny based on *rbcL* nucleotide sequences. *Am. Fern J.* 85:134–181.
- Hibbett, D. S., L.-B. Gilbert, and M. J. Donoghue. 2000. Evolutionary instability of ectomycorrhizal symbioses in basidiomycetes. *Nature* 407:506–508.
- Hill, C. R., and J. M. Camus. 1986. Evolutionary cladistics of marattialean ferns. *Bull. Br. Mus. Nat. Hist. (Bot.)* 14:219–300.
- Judd, W. S., C. S. Campbell, E. A. Kellogg, P. F. Stevens, and M. J. Donoghue. 2002. *Plant systematics: a phylogenetic approach*. 2nd ed. Sinauer, Sunderland, MA.
- Karol, K. G., R. M. McCourt, M. T. Cimino, and C. F. Delwiche. 2001. The closest living relatives of land plants. *Science* 294:2351–2353.
- Kearney, M. 2002. Fragmentary taxa, missing data, and ambiguity: mistaken assumptions and conclusions. *Syst. Biol.* 51:369–381.
- Kenrick, P. 1994. Alternation of generations in land plants: new phylogenetic and morphological evidence. *Biol. Rev.* 69:293–330.
- Kenrick, P. 2000. The relationships of vascular plants. *Philos. Trans. R. Soc. Lond. B* 355:847–855.
- Kenrick, P. 2002a. The origin of roots. Pp. 1–13 in *Plant roots: the hidden half*. 3rd ed. (Y. Waisel, A. Eshel, and U. Kafkafi, eds.). Dekker, New York.
- Kenrick, P. 2002b. The telome theory. Pp. 365–387 in *Developmental genetics and plant evolution* (Q. C. B. Cronk, R. M. Bateman, and J. A. Hawkins, eds.). Taylor and Francis, London.
- Kenrick, P., and P. R. Crane. 1997a. The origin and early diversification of land plants: a cladistic study. Smithsonian Institution Press, Washington, DC.
- Kenrick, P., and P. R. Crane. 1997b. The origin and early evolution of plants on land. *Nature* 389:33–39.
- Labandeira, C. C. 2001. The rise and diversification of insects. Pp. 82–88 in *Palaeobiology II* (D. E. G. Briggs and P. R. Crowther, eds.). Blackwell Science, London.
- Langdale, J. A., R. W. Scotland, and S. B. Corley. 2002. A developmental perspective on the evolution of leaves. Pp. 388–394 in *Developmental genetics and plant evolution* (Q. C. B. Cronk, R. M. Bateman, and J. A. Hawkins, eds.). Taylor and Francis, London.
- Liu, Z.-H., J. Hilton, and C.-S. Li. 2000. Review on the origin, evolution and phylogeny of Marattiales. *Chin. Bull. Bot.* 17:39–52.
- Long, A. G. 1960. "*Stamnostoma huttonense*" gen. et sp. nov.—pteridosperm seed and cupule from the calciferous sandstone series of Berwickshire. *Trans. R. Soc. Edinb.* 64:201–215.
- Looy, C. V., R. J. Twitchett, D. L. Dilcher, J. H. A. Van Konijnenburg-Van Cittert, and H. Visscher. 2001. Life in the end-Permian dead zone. *Proc. Natl Acad. Sci. USA* 98:7879–7883.
- Mable, B. K., and S. P. Otto. 1998. The evolution of life cycles with haploid and diploid phases. *Bioessays* 20:453–462.
- Magallón, S., and M. J. Sanderson. 2002. Relationships among seed plants according to highly conserved genes: sorting conflicting phylogenetic signals among ancient lineages. *Am. J. Bot.* 89:1991–2006.
- McElwain, J. C., D. J. Beerling, and F. I. Woodward. 1999. Fossil plants and global warming at the Triassic-Jurassic boundary. *Science* 285:1386–1390.
- Meyer-Berthaud, B., and P. Gerrienne. 2001. *Aarabia*, a new Early Devonian vascular plant from Africa (Morocco). *Rev. Palaeobot. Palynol.* 116:39–53.

- Meyer-Berthaud, B., S. E. Scheckler, and J. Wendt. 1999. *Archaeopteris* is the earliest known modern tree. *Nature* 398:700–701.
- Nickrent, D. L., C. L. Parkinson, J. D. Palmer, and R. J. Duff. 2000. Multigene phylogeny of land plants with special reference to bryophytes and earliest land plants. *Mol. Biol. Evol.* 17:1885–1895.
- Niklas, K. J., B. H. Tiffney, and A. H. Knoll. 1985. Patterns in vascular land plant diversification: an analysis at the species level. Pp. 97–128 in *Phanerozoic diversity patterns: profiles in macroevolution* (J. W. Valentine, ed.). Princeton University Press, Princeton University Press, Princeton, NJ.
- Nixon, K. C. 1996. Paleobotany in cladistics and cladistics in paleobotany: enlightenment and uncertainty. *Rev. Palaeobot. Palynol.* 90:361–373.
- Nixon, K. C., W. L. Crepet, D. Stevenson, and E. M. Friis. 1994. A reevaluation of seed plant phylogeny. *Ann. Mo. Bot. Gard.* 81:484–533.
- O'Leary, M. A. 2000. Operational obstacles to total evidence analyses considering that 99% of life is extinct. *J. Vert. Paleontol.* 20(suppl.):61A.
- Parenti, L. R. 1980. A phylogenetic analysis of the land plants. *Biol. J. Linn. Soc.* 13:225–242.
- Pataki, D. E. 2002. Atmospheric CO₂, climate and evolution—lessons from the past. *New Phytol.* 154:1–14.
- Pigg, K. B. 2001. Isoetalean lycopod evolution: from the Devonian to the present. *Am. Fern J.* 91:99–114.
- Pryer, K. M., H. Schneider, A. R. Smith, R. Cranfill, P. G. Wolf, J. S. Hunt, and S. D. Sipes. 2001. Horsetails and ferns are a monophyletic group and the closest living relatives to seed plants. *Nature* 409:618–622.
- Pryer, K. M., A. R. Smith, and J. E. Skog. 1995. Phylogenetic relationships of extant ferns based on evidence from morphology and *rbcL* sequences. *Am. Fern J.* 85:205–282.
- Qiu, Y.-L., J. Lee, F. Berasconi-Quadroni, D. E. Soltis, P. S. Soltis, M. Zanis, E. A. Zimmer, Z. Chen, V. Savolainen, and M. W. Chase. 1999. The earliest angiosperms. *Nature* 402:404–407.
- Qiu, Y.-L., J. Lee, F. Berasconi-Quadroni, D. E. Soltis, P. S. Soltis, M. Zanis, E. A. Zimmer, Z. Chen, V. Savolainen, and M. W. Chase. 2000. Phylogeny of basal angiosperms: analyses of five genes from three genomes. *Int. J. Plant Sci.* 161(suppl.):S3–S27.
- Raubeson, L. A., and R. K. Jansen. 1992a. Chloroplast DNA evidence on the ancient evolutionary split in vascular plants. *Science* 255:1697–1699.
- Raubeson, L. A., and R. K. Jansen. 1992b. A rare chloroplast-DNA structural mutation is shared by all conifers. *Biochem. Syst. Ecol.* 20:17–24.
- Raven, J. A., and D. Edwards. 2001. Roots: evolutionary origin and biogeochemical significance. *J. Exp. Bot.* 22:381–401.
- Redecker, D., R. Kodner, and L. E. Graham. 2000. Glomalean fungi from the Ordovician. *Science* 289:1920–1921.
- Renzaglia, K. S., R. J. Duff, D. L. Nickrent, and D. J. Garbary. 2000. Vegetative and reproductive innovations of early land plants: implications for a unified phylogeny. *Philos. Trans. R. Soc. Lond. B* 355:768–793.
- Rothwell, G. W. 1996. Phylogenetic relationships of ferns: a paleobotanical perspective. Pp. 395–404 in *Pteridology in perspective* (J. M. Camus, M. Gibby, and R. J. Johns, eds.). Royal Botanic Gardens, Kew.
- Rothwell, G. W. 1999. Fossils and ferns in the resolution of land plant phylogeny. *Bot. Rev.* 65:188–218.
- Rothwell, G. W., and R. Serbet. 1994. Lignophyte phylogeny and the evolution of spermatophytes. *Syst. Bot.* 19:443–482.
- Rydin, C., and M. Källersjö. 2002. Taxon sampling and seed plant phylogeny. *Cladistics* 18:485–513.
- Rydin, C., M. Källersjö, and E. M. Friis. 2002. Seed plant relationships and the systematic position of Gnetales based on nuclear and chloroplast DNA: conflicting data, rooting problems, and the monophyly of conifers. *Int. J. Plant Sci.* 163:197–214.
- Sanderson, M. J., M. F. Wojciechowski, J.-M. Hu, T. Ser Khan, and S. G. O'Brady. 2000. Error, bias, and long-branch attraction in data for two chloroplast photosystem genes in seed plants. *Mol. Biol. Evol.* 17:782–797.
- Schneider, H. 1996. *Vergleichende Wurzelanatomie der Farnpflanzen*. Shaker, Aachen.
- Schneider, H., K. M. Pryer, R. Cranfill, A. R. Smith, and P. G. Wolf. 2002. Evolution of vascular plant body plans: a phylogenetic perspective. Pp. 330–363 in *Developmental genetics and plant evolution* (Q. C. B. Croak, R. M. Bateman, and J. A. Hawkins, eds.). Taylor and Francis, London.
- Shear, W. A., and P. A. Selden. 2001. Rustling in the undergrowth: animals in early terrestrial ecosystems. Pp. 29–51 in *Plants invade the land: evolutionary and environmental perspectives* (P. G. Gensel and D. Edwards, eds.). Columbia University Press, New York.
- Shougang, H., C. B. Beck, and W. Deming. 2003. Structure of the earliest leaves: adaptations to high concentrations of atmospheric CO₂. *Int. J. Plant Sci.* 164:71–75.
- Singer, S. R. 1997. Plant life cycles and angiosperm development. Pp. 493–513 in *Embryology: constructing the organism* (S. F. Gilbert and A. M. Raunio, eds.). Sinauer Associates, Sunderland, MA.
- Skog, J. E. 2001. Biogeography of Mesozoic leptosporangiate ferns related to extant ferns. *Brittonia* 53:236–269.
- Smith, A. B. 1994. *Systematics and the fossil record: documenting evolutionary patterns*. Blackwell, London.
- Smith, A. R. 1995. Non-molecular phylogenetic hypotheses for ferns. *Am. Fern J.* 85:104–122.
- Soltis, D. E., P. S. Soltis, M. W. Chase, M. E. Mort, D. C. Albach, M. Zanis, V. Savolainen, W. H. Hahn, S. B. Hoot, M. F. Fay, M. Axtell, S. M. Swensen, L. M. Prince, W. J. Kress, K. C. Nixon, and J. S. Farris. 2000. Angiosperm phylogeny inferred from 18S rDNA, *rbcL*, and *atpB* sequences. *Bot. J. Linn. Soc.* 133:381–461.
- Soltis, D. E., P. S. Soltis, and M. J. Zanis. 2002. Phylogeny of seed plants based on evidence from eight genes. *Am. J. Bot.* 89:1670–1681.
- Soltis, P. S., and D. E. Soltis. 2000. Contributions of plant molecular systematics to studies of molecular evolution. *Plant Mol. Biol.* 24:45–75.
- Soltis, P. S., D. E. Soltis, and M. W. Chase. 1999. Angiosperm phylogeny inferred from multiple genes as a tool for comparative biology. *Nature* 402:402–404.

- Stein, W. E. 1993. Modelling the evolution of the stellar architecture in vascular plants. *Int. J. Plant Sci.* 154:229–263.
- Sues, H.-D., and R. R. Reisz. 1998. Origins and early evolution of herbivory in tetrapods. *Trends Ecol. Evol.* 13:141–145.
- Sun, G., D. L. Dilcher, S. Zheng, K. C. Nixon, and X. Wang. 2002. *Archaeofractaceae*, a new basal angiosperm family. *Science* 296:899–904.
- Sun, G., D. L. Dilcher, S. Zheng, and Z. Zhou. 1998. In search of the first flower: a Jurassic angiosperm, *Archaeofructus*, from northeast China. *Science* 282:1692–1695.
- Taylor, T. N., W. Remy, H. Haas, and H. Kerp. 1995. Fossil arbuscular mycorrhizae from the early Devonian. *Mycologia* 87:560–573.
- Theissen, G. A. Becker, K.-U. Winter, T. Münster, C. Kirchner, and H. Saedler. 2002. How the land plants learned their floral ABCs: the role of MADS-box genes in the evolutionary origin of flowers. Pp. 173–205 in *Developmental genetics and plant evolution* (Q. C. B. Cronk, R. M. Bateman, and J. A. Hawkins, eds.). Taylor and Francis, London.
- Tiffney, B. H., and S. R. Manchester. 2001. The use of geological and paleontological evidence in evaluating plant phylogenetic hypotheses in the northern hemisphere Tertiary. *Int. J. Plant Sci.* 162(suppl.):S3–S17.
- Wiens, J. J. 1998. Does adding characters with missing data increase or decrease phylogenetic accuracy? *Syst. Biol.* 47:625–640.
- Wikström, N., and P. Kenrick. 2001. Evolution of Lycopodiaceae (Lycopsidea): estimating divergence times from *rbcL* gene sequences by use of nonparametric rate smoothing. *Mol. Phylogenet. Evol.* 19:177–186.
- Wilkinson, M. 1995. Coping with abundant missing entries in phylogenetic inference using parsimony. *Syst. Biol.* 44:501–514.
- Willis, K. J., and J. C. McElwain. 2002. *The evolution of plants*. Oxford University Press, New York.
- Wolf, P. G., K. M. Pryer, A. R. Smith, and M. Hasebe. 1998. Phylogenetic studies of extant pteridophytes. Pp. 541–556 in *Molecular systematics of plants II. DNA sequencing* (D. E. Soltis, P. S. Soltis, and J. J. Doyle, eds.). Kluwer, Boston.