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PHYLOGENY OF VASCULAR PLANTS

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ABSTRACT

Morphological and molecular analyses resolve many aspects of vascular plant phylogeny, though others remain uncertain. Vascular plants are nested within bryophytes; lycopsids and zosterophylls are one branch of crown-group vascular plants, and euphyllophytes (*Psilophyton*, sphenopsids, ferns, seed plants) are the other. In Filicales, Osmundaceae are basal; water ferns and Polypodiaceae sensu lato are both monophyletic. Seed plants are nested within progymnosperms, and coniferophytes are nested within platyspermic seed ferns. Morphology indicates that angiosperms and Gnetales are related, but detailed scenarios depend on uncertain relationships of fossils; molecular data are inconsistent but indicate that both groups are monophyletic. *Amborella*, Nymphaeales, *Austrobaileya*, and Illiciales appear basal in angiosperms. Groups with tricolpate pollen form a clade (eudicots), with ranunculids and lower hamamelids basal. Most eudicots belong to the rosid and asterid lines, with higher hamamelids in the rosid line and dilleniids scattered in both. Alismids, Arales, and *Acorus* are basal in monocots; palms are linked with Commelinidae.

INTRODUCTION

In the last two decades, unprecedented progress has been made in understanding the phylogeny of vascular plants, thanks to new methods and new data. First, cladistics (75), which uses shared derived character states (synapomorphies) to identify clades and the criterion of parsimony (minimizing character state changes) to decide among hypotheses, replaced subjective approaches to reconstructing phylogeny. Second, advances in molecular biology have allowed

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mass use of molecular characters in phylogenetic analysis. To some (e.g. 84), it may appear that molecular systematics has replaced cladistics, but in fact it simply applies cladistic methods to a new kind of data.

The relative value of morphological and molecular data is a topic of debate. Clearly, molecular data are not infallible. Molecular data sets often disagree, which implies that—like any sort of data—they can be misleading. In addition, molecular data are especially susceptible to long-branch attraction (58): When branches are of different lengths (i.e. the number of character state changes differs) because of different rates of evolution or extinction of side branches, some changes on the long branches will be at the same sites; of these, a third will be to the same new base. As a result, cladistic analysis may indicate that terminal taxa on long branches are related to each other rather than to their true relatives. The same factors can cause incorrect rooting (where a clade is connected to its outgroups), because changes on a long branch may be reversals to the outgroup state. These effects are especially severe in radiations that occurred rapidly a long time ago (40, 41). In cases where stem lineages to modern groups split over a short amount of time, and when a long amount of time elapsed before radiation occurred of the crown groups that include living members, there may be few molecular synapomorphies on the short internodes between lines, and these may be erased by later changes at the same sites or overwhelmed by long-branch attraction.

An advantage of molecular over morphological systematics is that it involves fewer subjective decisions about whether features are similar or different enough to be treated as the same or different states. Except when alignment is uncertain, no one will argue whether a base at a particular site is an A or a G, as they might argue whether layers around the ovule are the same. However, cladistic analysis based on morphology is still the only method for determining relationships between fossils and living organisms. Fossils can alter inferred relationships among living organisms in morphological studies (40), especially when they are stem relatives that retain states lost in the crown group. Finally, even if molecular data give correct relationships among living taxa, fossil intermediates may be needed to infer homologies and the course of character evolution on the long branches leading to modern groups.

In this review, I summarize advances in understanding the phylogeny of vascular plants, considering both morphological and molecular evidence. In many cases, phylogenetic analyses have resolved long-standing controversies (e.g. whether angiosperms are monophyletic). Many hypotheses discussed at length in introductory texts can be considered obsolete and are mentioned there only for historical interest. However, other relationships seem just as uncertain as ever, if not more so (e.g. among seed plant groups). These are areas that need more investigation. In some cases, genes are unanimous but

morphological analyses have given inconsistent results. This may seem to support the view that molecular evidence is more reliable, but in other cases the situation is reversed, apparently for the reasons just discussed. There is reason to hope that by combining different types of data (1, 48, 96, 117) such conflicts may be resolved: Even when the phylogenetic signal is overwhelmed by homoplasy in individual data sets, the patterns of homoplasy in different data sets should differ; the true signal, however, is presumably always the same.

The interest of phylogeny, especially for other areas of biology, lies not only in establishing branching relationships and thus providing the basis for a natural classification, but also in its implications for the evolution of structures and adaptations. Therefore, I note implications for character evolution in the origin of major groups and their relation to ecological factors. I discuss seed plants in the most detail; older groups are discussed by Bateman et al (9).

BASAL TRACHEOPHYTES

Morphological and molecular analyses indicate that vascular plants (tracheophytes) are a monophyletic subgroup of land plants (embryophytes), which in turn are nested within charophytes, fresh-water green algae that include Charales and *Coleochaete* (67). Within embryophytes, morphological analyses (95) indicate that bryophytes form a paraphyletic series of lines, with liverworts basal (the sister group of all other taxa) and anthocerotes and mosses closer to vascular plants. This implies that many key adaptations to the land arose in a stepwise fashion before vascular plants evolved: meiospores with a resistant exine, walled multicellular sporangia and gametangia (seen in liverworts); stomata (anthocerotes); and conducting tissue (mosses, with hydroids rather than tracheids). These results reaffirm the antithetic theory for origin of the land-plant life cycle: Land plants were derived from algae with a haploid life cycle (like charophytes), and the sporophyte was interpolated into the cycle by delay of meiosis and was progressively elaborated. The greatest advance of vascular plants themselves is the branched sporophyte. Studies of *rbc*L, 18S and 26S rDNA, and sperm morphology gave different results (64, 91, 96), but a combination of the last three data sets (96) reaffirmed the paraphyly of bryophytes and the monophyly of tracheophytes.

Because living "lower" vascular plants (pteridophytes) are separated by great morphological gaps, ideas about their early evolution have emphasized fossils, which include many remarkably preserved and reconstructed forms. The Early Devonian Rhynie Chert flora, dominated by rootless, leafless rhyniophytes with dichotomously branched stems and terminal sporangia, led to the telome theory of vascular plant morphology (141), which subsumed the classical theory that the sporophyte consists of stems, leaves, and roots by postulating that leaves

originated by overtopping, planation, and webbing of dichotomous branches. In the 1960s, the view emerged that rhyniophytes gave rise to two lines (8): one included Devonian zosterophylls and lycopsids, with exarch xylem and lateral sporangia; the other included Devonian trimerophytes such as *Psilophyton*, with terminal sporangia but overtopped branches, which led to all other groups.

Although early morphological analyses (20, 99) placed Psilotaceae at the base of living vascular plants, because they lack roots, present evidence indicates that lycopsids are basal. This evidence includes the fact that lycopsids and bryophytes lack a chloroplast inversion found in other vascular plants (104) and a broad morphological analysis of fossil and living taxa by Kenrick & Crane (83) (Figure 1). However, studies of gene sequences (91, 92, 139) give inconsistent and anomalous results (e.g. with lycopsids polyphyletic). Fossils on the stem lineage leading to living groups show a stepwise transition from bryophytic to tracheophytic construction. *Horneophyton* still had a columella in the sporangium and moss-like hydroids (without secondary wall thickenings) rather than tracheids, but it also had a branched sporophyte; *Aglaophyton* (*Rhynia major*) had hydroids but no more columella; *Rhynia* had tracheids with secondary wall thickenings but of a primitive S-type. Kenrick & Crane (83) restricted the name tracheophytes to *Rhynia* and living groups and called the larger clade—including forms with a branched sporophyte but hydroids—the polysporangiophytes.

Lycopsids

Reniform sporangia with transverse dehiscence link lycopsids and zosterophylls with *Cooksonia* and *Renalia*, which had sporangia on lateral dichotomous branchlets (83). This suggests that lateral sporangia arose by overtopping and reduction. The fact that some zosterophylls (e.g. *Sawdonia*) had nonvascularized enations has been considered evidence that the one-veined leaves (microphylls) of lycopsids were derived from enations. However, Kenrick & Crane (83) found that taxa with enations are nested within smooth-stemed zosterophylls, which led them to propose that microphylls are sterilized lateral sporangia. The basal lycopsid *Asteroxylon*, in which sporangia and leaves were intermixed, may support this scenario. Sporangia became associated with leaves (sporophylls) in the remaining groups. *Asteroxylon* also had leafless, dichotomous rhizomes that may be transitional to roots (not known in zosterophylls).

Within lycopsids, *Selaginella*, *Isoetes*, and Paleozoic arborescent forms (Lepidodendrales) are united by ligules and heterospory. The Devonian genus *Leclercqia* had a ligule but was homosporous, which implies that the ligule arose first. Lepidodendrales had secondary xylem (but no secondary phloem, reflecting the independent origin of secondary growth here and in seed plants),

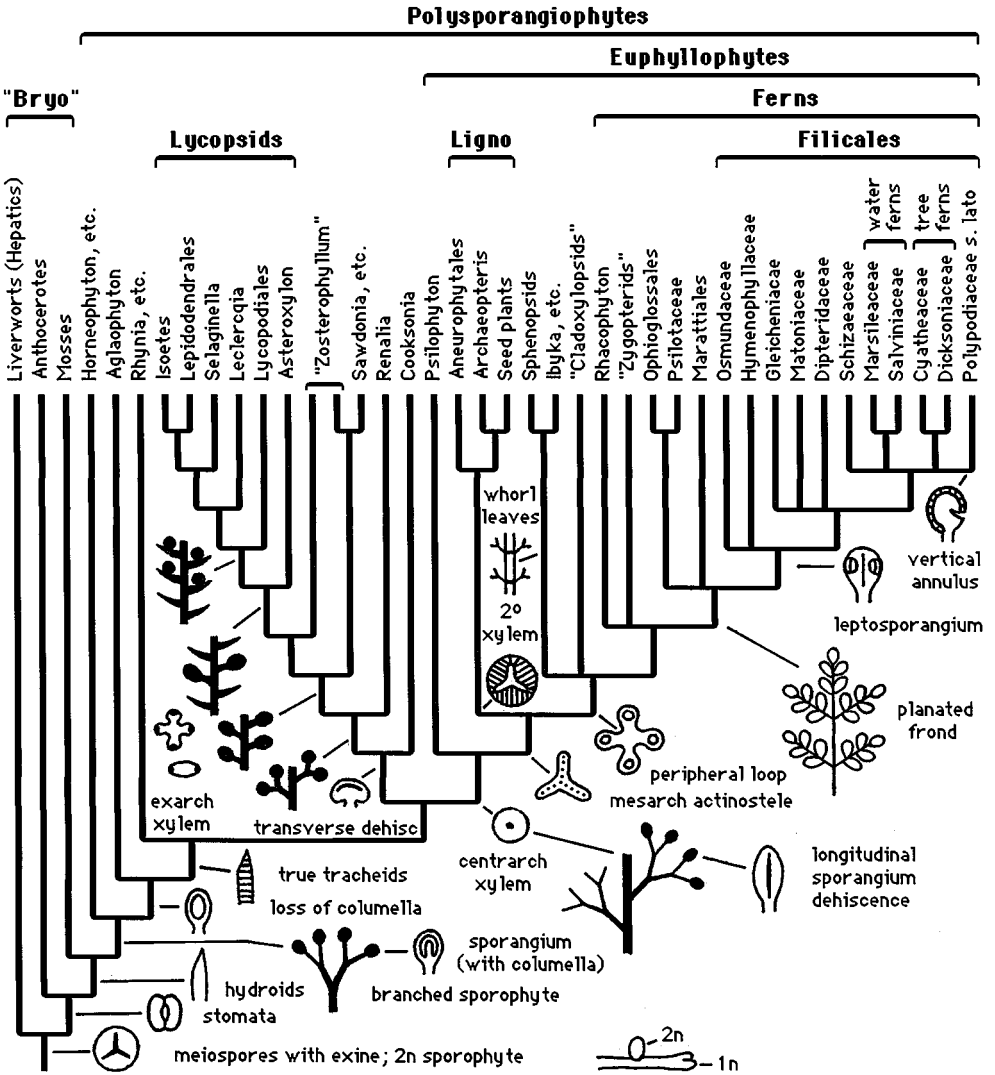

Figure 1 Synopsis of relationships among bryophytes and "lower" vascular plants found in morphological and molecular analyses [based primarily on the work of several others (83, 95, 102)], with sketches illustrating important synapomorphies in vegetative morphology, stem anatomy, and sporangia. "Bryo," bryophytes; Ligno, lignophytes.

periderm, and dichotomous "roots" (*Stigmaria*) covered with spirally arranged "rootlets;" developmentally and anatomically, the roots appear to be rhizomes and the rootlets modified leaves. The fact that *Isoetes* has anomalous cambial activity and hollow roots that resemble stigmarian rootlets, and the existence of the Triassic intermediate *Pleuromeia*, have suggested that *Isoetes* is reduced from Lepidodendrales. However, *Isoetes* and *Pleuromeia* appear to be related to smaller Carboniferous members of this clade (*Chaloneria*), not derived from large trees (11).

Euphyllophytes

Phylogenetic analyses also confirm the view that other vascular plants form a clade with trimerophytes, called euphyllophytes (83). Early Devonian members (*Psilophyton*) share such advances as longitudinal sporangial dehiscence, centrarch or mesarch xylem, and overtopped branches. Besides the chloroplast inversion mentioned (104), extant members are united by multiflagellate sperm (Lycopodiales and *Selaginella* are biflagellate, like bryophytes; the multiflagellate condition of *Isoetes* is presumably a convergence). Leaves in this group are often called megaphylls and are said to originate by overtopping, but this confuses different modes of origin and homologies of leaves. In some taxa (sphenopsids, progymnosperms), the leaf appears to represent a single overtopped branchlet; in others (ferns, seed plants), it is a branch system of several orders of overtopped axes that bear dichotomous branchlets. Roots apparently originated independently here and in lycopsids, where they are unusual in being dichotomous; roots are known in cladoxylopsids, *Rhacophyton*, and progymnosperms but not in *Psilophyton*.

Living euphyllophytes consist of three lines—sphenopsids, ferns, and seed plants—whose relationships are poorly resolved. Key fossil groups are the Devonian cladoxylopsids and progymnosperms. Both had lobed or dissected steles (actinosteles, polysteles), which may indicate they (and their derivatives) form a clade (83). In early progymnosperms (Aneurophytales), each lobe of the actinostele had several mesarch protoxylem points, whereas in cladoxylopsids, there was one parenchymatous protoxylem area near the tip of each lobe or stele segment, resulting in peripheral loops of metaxylem surrounding spongy protoxylem (83).

Sphenopsids

The oldest sphenopsids were long thought to be Devonian Hyeniales, which had highly overtopped branchlets that could be modified into the microphylls and sporangiophores of living *Equisetum*. This scenario is supported by the dichotomous leaves of *Sphenophyllum* and *Archaeocalamites*, the latter linked with *Equisetum* and Paleozoic trees (*Calamites*: Equisetales) by a hollow pith

surrounded by vascular bundles (eustele). This view fell out of favor with evidence that Hyeniales cannot be separated from cladoxylopsids, then considered primitive ferns, and that the supposed jointing of their stems was a preservational artifact. However, it is possible that both ferns and sphenopsids are derived from cladoxylopsids (115, 122): The equisetalian eustele could be derived from a polystele or actinostele by differentiation of the central tissue into pith and transformation of the spongy protoxylem into protoxylem canals, connected with internode elongation. Furthermore, some cladoxylopsids were more like sphenopsids than had been formerly believed: Appendages were whorled in *Ibyka* and *Cladoxylon dawsonii* (29, 122).

Stewart (125) suggested that Sphenophyllales—which had whorled, wedge-shaped leaves—were related to lycopsids rather than sphenopsids because they had exarch actinosteles rather than eusteles. However, this characteristic is overwhelmed by features that link Sphenophyllales with other sphenopsids (83, 122). Their stele might be derived from the actinostele of primitive cladoxylopsids by loss of the outer metaxylem.

Ferns

Living ferns are traditionally divided into two categories: eusporangiate ferns (Ophioglossales, Marattiales), which retain thick-walled sporangia like other vascular plants; and leptosporangiate ferns or Filicales, with small, delicate sporangia. Paleozoic coenopterids were thought to show stages in evolution of the fern frond: Some had three-dimensional branch systems rather than leaves, but others (now considered primitive Filicales) had planated fronds. Ophioglossales have files of tracheids sometimes interpreted as secondary xylem; it has been suggested, therefore, that they are closer to progymnosperms than to ferns (16), but similar tissue occurred in supposed Paleozoic ferns (*Rhacophyton*, *Zygopteris*, etc).

Kenrick & Crane (83) did not analyze ferns in detail, but they did link modern ferns with sphenopsids, cladoxylopsids, and the Devonian genus *Rhacophyton*, based on one protoxylem area per stele arm (and peripheral loops). *Rhacophyton* and Carboniferous zygopterids had quadriseriate fronds, with pinnae in pairs perpendicular to the rachis; pinnae themselves bore dichotomous pinnules in two rows. *Rhacophyton* shows all degrees of reduction of one pinna of each pair, which suggests that planated fronds arose by an unexpected process of suppression of half of each pair. The Carboniferous genus *Ankyropteris*, which had zygopterid-like H-shaped petiole traces but planated fronds, might be a link between zygopterids and Filicales. However, Rothwell (110) separated living ferns from *Rhacophyton* and zygopterids, which were linked with lignophytes, based on secondary growth, which would otherwise be lost between zygopterids and Filicales. This would mean that no Devonian members

of the line leading to modern ferns and no steps in origin of the fern frond are known.

Within extant ferns, analyses based on morphology (102), *rbc*L (73, 74), the two data sets combined (102), *cpITS* (98), and *atp*B (139) give more consistent results. They confirm that Filicales are a clade, united by leptosporangia and exposed antheridia. Marattiales and Ophioglossales are lower, but their exact relationships are poorly resolved.

Remarkably, four molecular data sets (74, 92, 98, 139) link Psilotaceae (*Psilotum*, *Tmesipteris*) with Ophioglossales. Because Psilotaceae have dichotomous stems and no roots, they have been considered living rhyniophytes, but they have also been linked with ferns based on their axial, subterranean gametophytes [as in Gleicheniaceae and Schizaeaceae (17)] and spore structure (89). They appear to be euphyllophytes because they have multiflagellate sperm and the chloroplast inversion cited above (83, 104). A relationship with Ophioglossales may seem preposterous because Psilotaceae have no roots, have highly branched stems, and have small appendages often considered enations rather than leaves, whereas Ophioglossales have thick roots, unbranched stems, and one large leaf at a time. However, they do share axial gametophytes and the unusual feature of sporangia borne on a structure attached to the adaxial side of an appendage. If this relationship is correct, the lack of roots in Psilotaceae is due to loss and is not primitive.

Within Filicales, Osmundaceae are basal in most trees, consistent with the fact that they have the least reduced leptosporangia (the exceptions are trees in which Hymenophyllaceae, which have extremely thin leaves, are one node lower). Subsequent branches, in uncertain order, are Gleicheniaceae, Dipteridaceae, and Matoniaceae, which have often been linked based on their round sori and seemingly dichotomous fronds, Schizaeaceae, and tree ferns (Cyatheaceae, Dicksoniaceae).

Marsileaceae and Salviniaceae, which are unusual in being both aquatic and heterosporous, have been thought to be derived from different terrestrial, homosporous ancestors (16, 19–19b), but both morphological and molecular analyses indicate they are a monophyletic group nested among Schizaeaceae, tree ferns, and more advanced ferns. Coincidentally, their monophyly has been confirmed by discovery of fossils intermediate between the two families (112).

Phylogenetic analyses have also refuted long-standing dogma concerning ferns with a vertical interrupted annulus—the majority of the group. These were once grouped as the huge family Polypodiaceae, but it has been argued (16, 19–19b) that they are polyphyletic—with different members related to Gleicheniaceae, Schizaeaceae, and tree ferns—based primarily on sporangial position and presence or absence of indusia rather than on structure of the

sporangia themselves. However, molecular analyses indicate that they form a clade, nested among Schizaeaceae, tree ferns, and water ferns.

SEED PLANTS (LIGNOPHYTES)

Phylogenetic analyses have radically affected ideas on relationships of seed plants (gymnosperms plus angiosperms), which differ from "lower" groups not only in having seeds but also in vegetative advances such as secondary growth and axillary branching. Formerly, it was widely believed that seed plants are diphyletic (5, 23), consisting of two lines that differ in vegetative and seed characters. Cycadophytes (cycadopsids), including modern cycads and Paleozoic seed ferns or pteridosperms (which had seeds but fern-like fronds), have unbranched or sparsely branched stems with diffuse (manoxylic) wood, pinnately compound leaves, and radial seed symmetry (radiospermic). Coniferophytes (coniferopsids)—including conifers, *Ginkgo*, and Paleozoic Cordaitales—have highly branched stems with dense (pycnoxylic) wood, simple leaves with one vein or dichotomous venation, and bilateral (more precisely biradial) seed symmetry (platyspermic). Cycadophytes were assumed to be derived from ferns via seed ferns, coniferophytes from some Devonian group with dichotomous branches that might be transformed into simple leaves. This would imply that the seed originated twice; its different symmetry in the two lines was taken as support for this view. Discovery of Early Carboniferous seeds with the megasporangium (nucellus) surrounded by lobes showing all degrees of fusion into an integument confirmed suggestions that the seed itself was derived from a dichotomous fertile branch.

New insights came from recognition of the progymnosperms, Devonian trees with coniferophyte-like secondary xylem, phloem, and periderm that reproduced by spores, which implies that secondary growth arose before the seed (a prime example of mosaic evolution). Beck (12, 13) argued that both seed plant lines were derived from progymnosperms, but different subgroups. He linked coniferophytes with *Archaeopteris*, which had distichous branch systems with spiral, wedge-shaped leaves, recalling the branch systems of early conifers and the compound strobili of cordaites. The leaves would be barely modified in *Ginkgo* and cordaites and reduced to one-veined needles in conifers. He derived cycadophytes from the older Aneurophytales, which still had three-dimensional branch systems, because they and early seed ferns had actinosteles whereas *Archaeopteris* already had a eustele. The compound leaf would be derived by planation of a whole branch system, with leaves converted to leaflets.

This hypothesis was challenged by Rothwell (109), based on coniferophytic features in the Late Carboniferous seed fern *Callistophyton*: platyspermic seeds, saccate pollen, and frequent axillary branching. Deriving coniferophytes

from a seed fern prototype would require a radical change in leaf morphology, which Rothwell proposed occurred not by reduction but by heterochrony. *Callistophyton* not only had fronds but also pointed cataphylls (bud scales), like seed plants in general; if fronds were suppressed and the plant continued to produce cataphylls its whole life, the result would be a coniferophytic morphology. Early conifers occurred in arid areas of the Euramerican tropical zone, which suggests that this shift adapted them to aridity.

Phylogenetic analyses largely confirm Rothwell's scenario. Although morphological analysis of modern plants (20) linked seed plants with ferns, they are nested within progymnosperms in analyses that include fossils (30, 46, 97, 111) (Figure 2). The combined clade has been called the lignophytes (46), because its most conspicuous synapomorphy is secondary wood. Several Late Devonian-Carboniferous seed ferns (lyginopterids, medullosans) form a basal paraphyletic series in seed plants, whereas coniferophytes are nested in a clade called platysperms (31) that includes *Callistophyton*, Permian-Mesozoic seed ferns (peltasperms, glossopterids, corystosperms, *Caytonia*), and some or all living taxa. This implies that the fronds of ferns and seed ferns arose from branch systems, but independently. Other seed plant innovations are a shift from pseudomonopodial to axillary branching, cataphylls (arrested frond primordia?), and fusion of microsporangia into synangia. Because it is heterosporous, *Archaeopteris* falls nearer seed plants than aneurophytes, but autapomorphies such as the eustele and grouped pitting imply that it is not ancestral. This shift to heterospory is the last of many iterative origins in vascular plants (10). The eustele apparently arose several times within seed plants, by formation of a pith at the center of an actinostele, leaving the lobes stranded as vascular bundles (13). The similarities between *Archaeopteris* and coniferophytes are convergences (eustele, branching pattern) or reversals (pycnoxylic wood, free microsporangia). Molecular data also support the monophyly of seed plants (1, 27, 66); this would not contradict belief that seed plants originate from two groups of progymnosperms, but it does rule out a separate relationship of cycadophytes and ferns.

These results clarify steps in the evolution of the seed (ovule) (Figure 2). Basal seed ferns had dichotomous cupules, shaped like two hands with seeds in the palms. These cupules may be derived from the fertile appendages of progymnosperms, the seeds from groups of sporangia, and the integument from sterilized outer sporangia (83). Successive taxa document steps from the original hydrasperman pollination mechanism (111), where pollen was captured by a drop secreted by the lagenostome (a nucellar beak with a pollen chamber formed by separation of the epidermis from a central column), to the modern condition, where a drop is exuded from the micropyle (made possible by fusion of the integument lobes—an example of transfer of function in the origin of

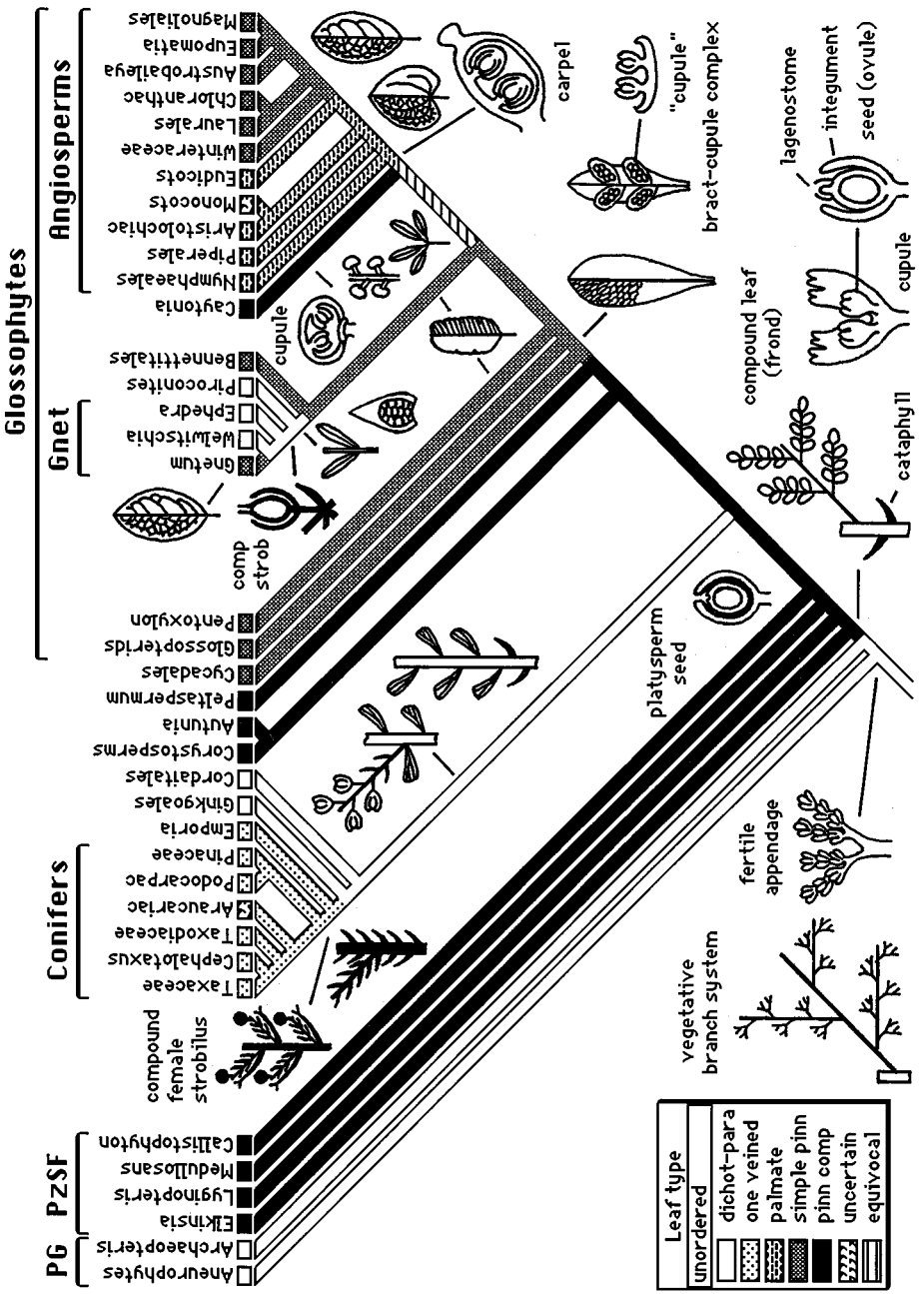

Figure 2 Representative cladogram of seed plants based on morphology (44) [progymnosperms added as by others (46, 111)], with branches shaded to indicate evolution of leaf type, and sketches of leaves, ovules, and ovule-bearing structures. PG, progymnosperms; PzSF, Paleozoic seed ferns; Gnet, Recent Gnetales.

new structures). Medullosans and primitive platysperms (including cycads and *Ginkgo*) still have a nucellar beak but have lost the central column. This is one synapomorphy of medullosans and platysperms; others are loss of the cupule, origin of a fleshy sarcotesta layer in the integument, and vascular tissue in the nucellus. It is possible that the cupule was not lost but is represented by the integument and that the original integument fused with the nucellus, leaving the nucellar vasculature as a vestige (136). Platysperms show additional steps in modernization of the seed: biradial symmetry and sealing of the micropyle after pollination.

Early seed plants, including not only lyginopterids and medullosans but also cordaites and Paleozoic conifers (101), had prepollen with a proximal tetrad scar, like the spores of lower vascular plants, rather than a distal sulcus, where the pollen tube germinates in modern groups. The pollen tube anchors the pollen and absorbs nutrients in cycads and *Ginkgo*, which still have motile sperm (zooidogamy), but it transfers nonmotile sperm to the egg in conifers, Gnetales, and angiosperms (siphonogamy). *Callistophyton* had a sulcus, and it is even known to have had a pollen tube, though the sperm type is unknown. Phylogenetic results indicate that the sulcus either originated more than once or was lost in cordaites and early conifers, which would be surprising considering that they are the oldest known platysperms. The first scenario would suggest that the pollen tube also arose several times, unless it originated before the exine was modified for its exit. Platysperms are united by a change from spongy-alveolar exine structure, as in progymnosperms, to honeycomb-alveolar structure, as in conifers and cycads. In some trees, saccate pollen originated at the same point, which implies that the nonsaccate monosulcate pollen of cycads, *Ginkgo*, and other groups arose later by loss of sacs. Other trees reverse this scenario; however, all known Carboniferous platysperms are saccate, and nonsaccate monosulcate pollen is rare until the Mesozoic. These uncertain relationships among platysperm lines are largely a function of incomplete information on Permian and Mesozoic fossils.

Cycads

Many early researchers derived cycads from medullosans, based on large ovules with a sarcotesta and nucellar vasculature and manoxylic stems with mucilage canals and numerous leaf traces, although cycads lack the internal secondary xylem of medullosans. In contrast, phylogenetic analyses that include fossils (30, 46, 47, 97, 111) place cycads either between medullosans and platysperms or nested in platysperms, with peltasperms and/or *Ginkgo* (a connection also found in molecular analyses, discussed below). This is because cycads and platysperms share many advances over medullosans, such as endarch primary xylem, abaxial microsporangia, linear megaspore tetrad, sulcate pollen,

honeycomb-alveolar exine, and sealed micropyle. Cycads are basal in morphological analyses of living seed plants (47, 87), which suggests that their lack of axillary branching is primitive. However, in analyses that include fossils, cycads are nested among taxa with axillary branching, which implies that this feature was lost. Cycads do branch dichotomously (87), but this differs from the progymnosperm state, which is pseudomonopodial (47).

It would be ironic if cycads, often used as the type example of radiospermic seeds, were platysperms. *Cycas* has biradial ovules, however, and possible Permian cycad precursors with *Taeniopteris* leaves apparently did also (90). Present trees confirm that the motile sperm of cycads is primitive, but it is uncertain whether their monosulcate pollen is primitively or secondarily nonsaccate.

Relationships within cycads are better resolved. *Cycas* has been considered primitive in having leaflike megasporophylls with several ovules along the rachis, rather than peltate sporophylls with two ovules and likewise *Stangeria* (87) in having fern-like leaflets with a midrib and secondary veins rather than one vein (*Cycas*) or several parallel-dichotomous veins (*Zamia*, etc). Permian plants with simple, pinnately veined *Taeniopteris* leaves and sporophylls with numerous ovules support the primitive status of *Cycas* sporophylls but suggest the unexpected possibility that *Cycas* and *Zamia* leaves were derived by dissection of a simple blade into segments of different widths (90). Morphological and molecular analyses (25, 27, 123) indicate that *Cycas* is the sister group of other genera, which confirms the standard scenario for sporophyll evolution and is consistent with the *Taeniopteris* hypothesis for leaf evolution.

Conifers

Since the work of Florin on Paleozoic fossils (60), conifers have been associated with Paleozoic cordaites, which had strap-shaped leaves, compound male and female strobili, platyspermic seeds, and saccate pollen. Paleozoic conifers had compound female strobili made up of bracts and axillary fertile short shoots, apparently transformed into the cone scales of modern forms. However, there is reason to doubt that conifers were directly derived from cordaites because they have simple male strobili on normal branch systems, a condition that appears more primitive. Thus, compound female strobili may have arisen independently by grouping of simple strobili. Some Podocarpaceae have grouped male cones that have been compared with compound strobili of cordaites (138), but Paleozoic conifers had solitary male cones.

In all morphological analyses, conifers and cordaites are nested among platysperms. However, in some trees they are linked with each other (and ginkgos) whereas in others they are separate lines, which implies a parallel origin of coniferophyte from cycadophyte features. Rothwell & Serbet (111) contradict Florin's scheme in separating modern conifers from Paleozoic conifers

(*Emporia*) and cordaites (which are still linked with each other) and placing them between cycads and anthophytes. This is because of characteristics in which modern conifers are more advanced than *Emporia* and cordaites, such as siphonogamy and loss of the lagenostome. However, it may also be a result of including only Pinaceae, Podocarpaceae, and Taxaceae, the last of which lack features—such as saccate pollen and compound strobili—that other conifers share with *Emporia* and cordaites. In analyses including all extant groups, modern conifers are linked with cordaites and ginkgos (44, 97) (Figure 2).

Because *Ginkgo*, cordaites, and early conifers have or are suspected to have had motile sperm (101), siphonogamy presumably originated between *Emporia* and modern conifers; this would coincide with loss of the lagenostome. An advance that occurred between cordaites or *Ginkgo* and *Emporia* is loss of the sarcotesta. Modern conifers and *Ginkgo* are derived over other seed plants (except Gnetales) in lacking scalariform pitting in the metaxylem (7, 16), but *Emporia* had scalariform metaxylem, which suggests that scalariform pitting was lost independently in the two groups.

Within conifers, morphological and molecular analyses (25, 27, 71, 121) have resolved several persistent problems. According to analyses of *rbc*L (25), conifers are not a clade but two adjacent lines (Pinaceae and other families). However, they are monophyletic in other studies. All analyses confirm the view (53) that Cupressaceae are a subgroup of Taxodiaceae that changed from helical to opposite phyllotaxy. These studies refute the concept (60) that Taxaceae are not conifers, based on the fact that they have simple female shoots with one terminal ovule rather than compound strobili with ovules on axillary cone scales. This view was questioned based on comparisons with *Cephalotaxus*, which is like Taxaceae in vegetative morphology and anatomy (tertiary spiral thickenings in the tracheids) and has cones that are highly reduced but still bear ovules on axillary structures; further reduction and a shift of the ovule to the apex could result in the taxaceous condition (70). All analyses link Taxaceae with *Cephalotaxus* and Taxodiaceae, confirming this scenario.

Morphological analyses give inconsistent basal relationships in living conifers, but molecular analyses agree that Pinaceae are the sister group of other families. Podocarpaceae and Araucariaceae form a clade; a possible synapomorphy is one ovule per cone scale, although the two ovules of supposed Triassic Podocarpaceae (131) pose a problem. Pinaceae and Podocarpaceae are the only living conifers with saccate pollen. Molecular trees are consistent with the view that this is a primitive feature retained from cordaites and Paleozoic conifers, and that the nonsaccate pollen of other conifers arose by loss of sacs and a shift from alveolar to granular exine structure—probably independently in Araucariaceae, which have large pollen, and the Taxodiaceae-Taxaceae clade, where the pollen is smaller.

Ginkgos

Ginkgo and its fossil relatives have been considered coniferophytes because they have simple, dichotomously veined leaves, simple strobili in the axils of leaves, and platyspermic seeds. Florin (59) proposed the Permian genus *Trichopitys* as a link because it had axillary female short shoots like those of Paleozoic conifers. *Karkenia* and *Baiera* had strobili bearing many ovules (4, 140), supporting the view that the biovulate stalk of *Ginkgo* is a reduced strobilus. However, this interpretation was questioned by Meyen (94), who argued that the short shoots of *Trichopitys* were actually pinnate structures. He associated ginkgos with Permian-Triassic peltasperms, which were also platyspermic, showed transitions from pinnate to dichotomous leaves, and sometimes had ginkgo-like nonsaccate monosulcate pollen. Mesozoic Czekanowskiales had ginkgo-like leaves and short shoots but female strobili of "capsules" composed of two valves with seeds on their facing surfaces; if these are related to ginkgos, they could be a link with peltasperms, which had seeds on paddle-like sporophylls. Other possible relatives are the Paleozoic Rufloriaceae of Siberia, which had cordaite-like strap-shaped leaves but simple male and female strobili (94).

Phylogenetic analyses have not resolved these issues. Some studies associate ginkgos with coniferophytes (30, 44, 46, 97), but others place them elsewhere in platysperms, sometimes with peltasperms and/or cycads (47, 111). Neither Czekanowskiales nor Rufloriaceae have been included in these studies because so many of their characteristics are unknown. Some molecular analyses link *Ginkgo* and cycads (27, 66); this could mean that both groups are peltasperm derivatives. Chaw et al (27) listed several morphological features—such as haustorial pollen tube, motile sperm, and free-nuclear megagametophyte and embryo development—as support for a *Ginkgo*-cycad relationship, but these are basic seed plant states that do not favor any relationship. However, nonsaccate monosulcate pollen could be a synapomorphy of *Ginkgo*, cycads, and some peltasperms.

Angiosperms and Gnetales

The most controversial topic in seed plant phylogeny is the relationship of angiosperms and Gnetales. The englerian theory (137) held that angiosperms were derived from Gnetales, homologizing the compound strobili of Gnetales, which consist of simple, unisexual, flower-like units in the axils of bracts, with the inflorescences of Amentiferae, which are also made up of simple flowers. This view lost favor with increasing evidence that Magnoliidae (which usually have complex, bisexual flowers) are primitive in angiosperms. Arber & Parkin (2, 3) also thought angiosperms and Gnetales were related, but they linked them with Mesozoic Bennettitales, which had large, often bisexual flowers, implying that the flowers of Gnetales and Amentiferae are reduced. Angiosperms have

also been associated with Permian and Mesozoic seed ferns such as *Caytonia* (42, 65, 120) or glossopterids (106, 120). *Caytonia* had reflexed seed-bearing "cupules" borne in two rows on a rachis; glossopterids had one or more cupules or sporophylls on top of a leaflike bract (bract-sporophyll or bract-cupule complex). This would explain the morphology of most angiosperm ovules, which are bitegmic (with two integuments) and anatropous (reflexed): If the ovules in a *Caytonia* cupule were reduced to one, the cupule wall would provide a homolog for the outer integument, and the whole structure would be reflexed. The carpel might be derived by widening and folding of the *Caytonia* rachis, or by folding of the glossopterid bract. As for Gnetales, Eames (52) linked *Ephedra* with coniferophytes and *Welwitschia* and *Gnetum* with Bennettitales, whereas others (7, 16, 42) associated all three genera with coniferophytes, based on their compound stobili, lack of scalariform pitting in the primary xylem, and linear leaves (in *Ephedra* and *Welwitschia*).

Morphological analyses of seed plants have produced conflicting updated versions of these views, although they have resolved some issues. In particular, they all indicate that Gnetales are the closest living relatives of angiosperms, along with Bennettitales and the Cretaceous genus *Pentoxylon*. They also agree on the arrangement of the three genera of Gnetales, with *Welwitschia* and *Gnetum* linked by complex leaf venation, reduction of the male gametophyte, and tetrasporic development and incomplete cellularization of the female gametophyte, with free nuclei functioning as eggs. This implies that Gnetales originally had pollen of the striate ephedroid type seen in *Ephedra* and *Welwitschia*, which was reduced to spiny and inaperturate in *Gnetum*.

The first analyses (30, 46, 47) linked angiosperms, Gnetales, and Bennettitales, called anthophytes, with *Caytonia*, glossopterids, and Triassic corystosperms. This implies (*a*) that flowers (short axes with closely aggregated sporophylls) originated not in angiosperms but in their common ancestor with Gnetales and Bennettitales, before the ovules were enclosed in a carpel, and were reduced and grouped into compound strobili in Gnetales (a convergence with coniferophytes) and (*b*) that angiosperm ovules were derived from cupules of a *Caytonia* or glossopterid type. Crane (30) directly linked angiosperms with Gnetales, but Doyle & Donoghue (46, 47) placed angiosperms basal in anthophytes. Trees of the latter type imply that the vessels of angiosperms and Gnetales are convergent because Bennettitales and *Pentoxylon* were vesselless. Although both groups have two integuments, the outer integument of Gnetales corresponds to the perianth of the male flowers and of Bennettitales. The real synapomorphies of the two groups are more cryptic: a tunica in the apical meristem, lignin chemistry (Mäule reaction), loss of sacs and shift to granular exine in the pollen, and reduction of the megaspore wall (shared with Bennettitales and *Caytonia*). The most interesting synapomorphy is double

fertilization, presumably of the type documented in Gnetales (22, 61), where both sperm produced by the male gametophyte fuse with nuclei in the female gametophyte but the second fusion produces an extra zygote rather than triploid endosperm. This implies that endosperm originated later on the angiosperm line, probably from the extra embryo (62).

These analyses treated angiosperms as a single taxon, which required questionable assumptions about basic states. One attempt to correct this problem (44) included 11 angiosperms and *Piroconites*, a Jurassic gnetalian relative with opposite, linear leaves and ephedroid pollen but glossopterid-like fertile structures (133). This gave generally similar trees, but with *Caytonia* on the line to angiosperms and glossopterids at or near the base (Figure 2). According to these trees, typical flowers arose independently in angiosperms, Bennettitales, and Gnetales. The whole clade originally had *Glossopteris*-like simple leaves with simple-reticulate venation and cupules attached to a bract, hence the name glossophytes. The bract-cupule complex was retained up to *Piroconites* on the line to Gnetales; cupules became anatropous on the *Caytonia*-angiosperm line only. In Gnetales, the bract-cupule complex was reduced to one ovule and shifted to the apex of an axillary branch; a possible intermediate is *Dechellyia* (6), a Triassic plant with opposite leaves and winged seeds (if the wing is derived from the bract). The original leaf became palmately compound in *Caytonia* (with four leaflets that resemble *Glossopteris* leaves), complex-reticulate by interpolation of finer veins in angiosperms, simple or pinnately dissected with secondarily open venation in Bennettitales and *Pentoxylon*, linear and opposite in *Piroconites* and Gnetales, and angiosperm-like in *Gnetum* (another convergence).

This scheme specifies a sequence of origin of angiosperm features: simple leaves, reticulate venation, loss of the lagenostome, and a carpel prototype below glossopterids; reduced megaspore wall, nonsaccate pollen, and granular exine above glossopterids; anatropous cupule/ovule and flat stomata below *Caytonia*; complex venation, flower, simple stamen with two pairs of microsporangia, and carpel closure in angiosperms. Features of angiosperms and Gnetales that are unknown in fossils—such as tunica, Mäule reaction, and double fertilization—could have arisen as far back as glossopterids. Unfossilizable features known only in angiosperms—such as companion cells in the phloem, three-nucleate male gametophyte, eight-nucleate female gametophyte, and endosperm—originated later, above or below *Caytonia*. By reducing the number of features that have no homologs in other groups, this scheme would reduce the mystery of the origin of angiosperms.

Other analyses have found very different trees, some of which are only slightly less parsimonious in terms of the data sets just discussed. Most notable are neo-englerian trees, in which anthophytes are linked with coniferophytes

rather than *Caytonia* and glossopterids. This would mean that the simple flowers of Gnetales are primitive and derived from axillary short shoots of coniferophytes, whereas complex flowers in angiosperms originated by aggregation or elaboration of parts (43). The outer integument might be derived from the perianth of Gnetales and, ultimately, the sterile appendages of a short shoot; the carpel might be derived from the subtending bract. Somewhat similar trees were found by Rothwell & Serbet (111). Analyses of modern plants only (47, 87) also link angiosperms and Gnetales with conifers, although this would not exclude inserting glossopterids and *Caytonia* between them. A potential conifer-anthophyte synapomorphy is siphonogamy, which originates twice on previous trees; however, this is not so if *Emporia* is related to conifers and had no pollen tube (101). In trees of Nixon et al (97), who included 18 angiosperms, angiosperms are nested within Gnetales and linked with *Welwitschia* and *Gnetum* on leaf and embryological features, so that Gnetales are paraphyletic and angiosperms are derived from a gnetalian prototype.

Molecular studies appear to resolve some of these issues, but they introduce new conflicts (Figure 3). They do not directly address the position of fossils, which is essential in order to formulate and test hypotheses on the origin of flowers, carpels, and bitegmic ovules. However, except for early analyses with few taxa, they all indicate that both angiosperms and Gnetales are monophyletic, supported by high bootstrap values (1, 18, 27, 48, 66, 69, 72). They therefore refute trees in which Gnetales are paraphyletic (97), as does closer examination of the characters that link angiosperms, *Welwitschia*, and *Gnetum* (44). Most also confirm the basal position of *Ephedra* in Gnetales. However, in most molecular studies, angiosperms and Gnetales are not related at all. They are sister groups in some analyses of partial rRNA sequences (69), whereas cycads, *Ginkgo*, and conifers form a clade at the base of seed plants. However, with different taxon sampling or method of analysis, angiosperms are linked with cycads, *Ginkgo*, and conifers, and Gnetales are basal, a result also found with *rbc*L (1). With other *rbc*L data (72) and 28S rDNA (121), angiosperms are basal and Gnetales are linked with cycads, *Ginkgo*, and conifers. These variations are a function of rooting, which could be incorrect because living outgroups are so distant—angiosperms and Gnetales would be related if seed plants were rerooted among cycads, *Ginkgo*, and conifers, as in morphological trees. However, this is not true of trees based on *cpITS* (66), 18S (27), and *coxI* (18), in which angiosperms are basal but Gnetales are linked with conifers. If such trees are correct, we are farther from understanding the origin of angiosperms than we thought because there is no modern seed plant group that shares special homologies with angiosperms.

The lack of a molecular signal linking angiosperms and Gnetales may seem to be a major conflict between morphological and molecular data, but the

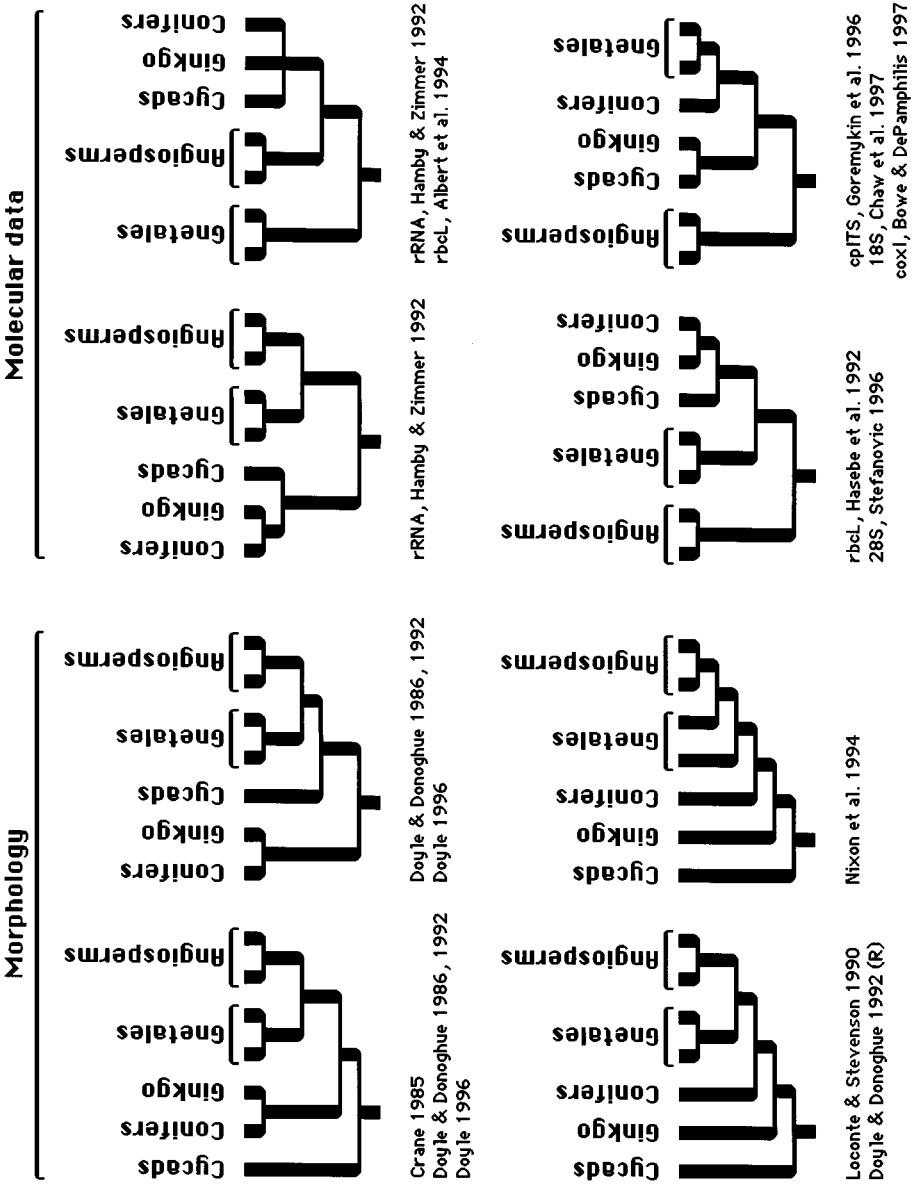

Figure 3 Relationships among living groups of seed plants found in different analyses of morphological and molecular data.

variations among molecular trees raise doubts about the ability of molecular data to resolve relationships at this level. In addition, the bootstrap support for arrangements that separate the two groups is low. The lack of resolution could be due to problems expected in rapid ancient radiations (41)—too few molecular synapomorphies and too much time for homoplasy on the long branches leading to modern taxa. Conifers, cycads, *Ginkgo*, and glossopterids diverged in the Late Carboniferous, all being known in that epoch or the Permian, and earlier seed plants being more primitive. Furthermore, the number of morphological characteristics that contradict the molecular arrangements is high. With the data set of Doyle (44), when angiosperms or Gnetales are forced to the base of living seed plants (45), the resulting trees are at least four to five steps longer than the shortest trees. They may be nine to ten steps longer because they assume that five states of angiosperms and Gnetales that are unknown in fossils (e.g. tunica, double fertilization) are primitive in seed plants whereas, other data suggest they are derived. These trees also conflict with the stratigraphic record (45): The oldest groups branch off first (Devonian-Carboniferous seed ferns), then the two youngest lines (angiosperms, Gnetales, and their fossil relatives), and finally taxa of intermediate age (cycads, ginkgos, conifers).

ANGIOSPERMS

Because of the vast diversity of angiosperms, there have been no morphological analyses of the whole group, although there have been studies of basal relationships and many subgroups. These have been overshadowed by molecular analyses of three genes in several hundred taxa: *rbc*L (25, 107), 18S (118), and *atp*B (114). These analyses give broadly consistent results (Figure 4), which in many cases conflict with earlier classifications but in hindsight make sense in terms of morphology. In particular, they break up many of the widely used subclasses of Takhtajan (127, 128) and Cronquist (34, 35). However, positions of many "floater" taxa vary among analyses. Combination of the three data sets promises to resolve many of the conflicts (117), but sampling of the same taxa is not yet complete.

Basal Relationships

Traditionally, much discussion focused on which living angiosperms are most primitive, a problem closely related to that of rooting (which taxa are basal). Most authors agreed that the most primitive angiosperms are in the subclass Magnoliidae (34, 35, 127, 128), a paraphyletic grade united by retention of monosulcate pollen and other gymnosperm features. However, this permits a wide range of hypotheses because magnoliids vary in habit from woody to herbaceous and in flowers from showy and bisexual to extremely simple.

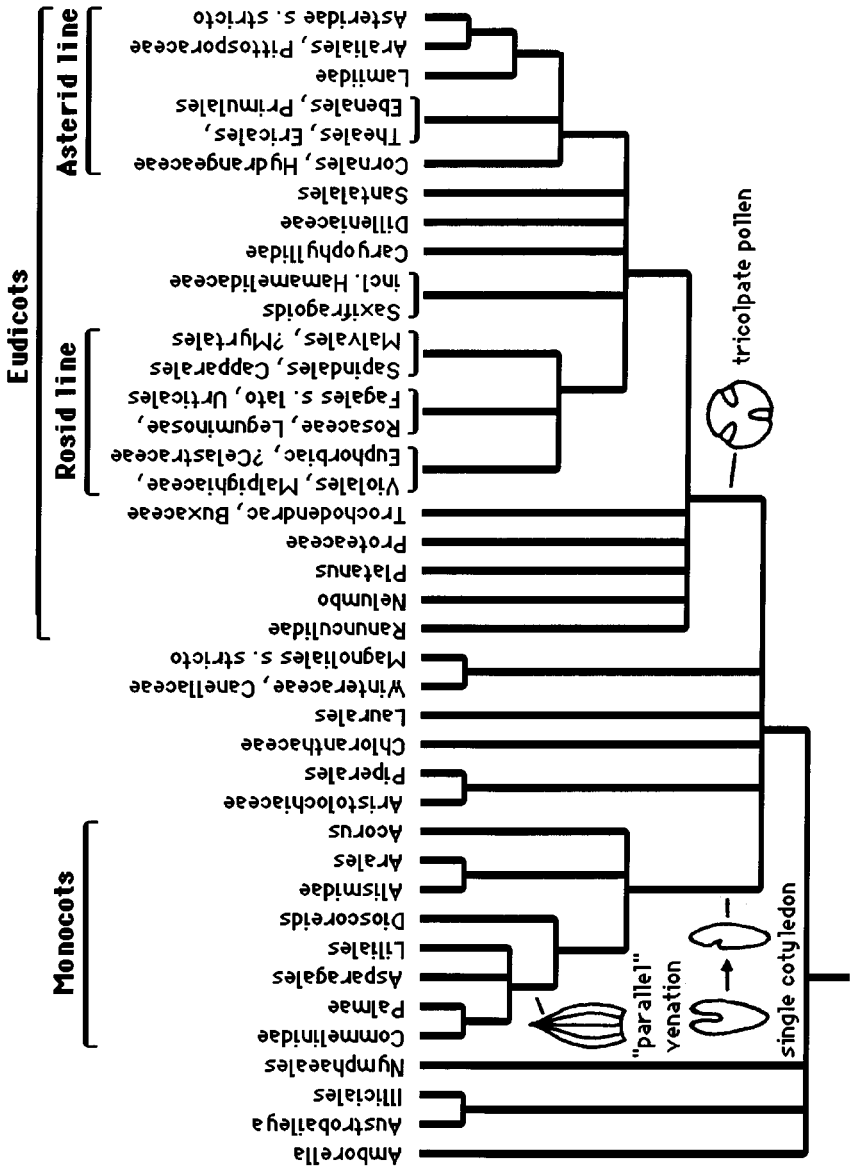

Figure 4 Synopsis of relationships within angiosperms based on analyses of *rbcL*, 18S rDNA, and *atp*B sequences (25, 107, 114, 118).

Morphological analyses have given several rootings, depending in part on choice of outgroups. Using Bennettitales, Gnetales, and *Caytonia* to polarize characters, Donoghue & Doyle (39) found that the basal branch was Magnoliales, which have granular monosulcate pollen (like Bennettitales and Gnetales), followed by other woody magnoliids (Laurales, Winteraceae, Illiciales). This implies that woody habit, pinnately veined leaves, showy bisexual flowers, and laminar stamens are primitive. Herbaceous magnoliids (Nymphaeales, Piperales, Aristolochiaceae) and monocots formed a clade called paleoherbs, showing a shift to herbaceous habit, palmately veined leaves, and stamens with a well-differentiated filament. These results generally agree with traditional ideas on polarity, except in implying that the lack of vessels in Winteraceae and other groups is due to loss because they are nested among taxa with vessels. However, trees rooted among paleoherbs were only one step longer, and these were favored in later seed plant analyses (44) (Figure 2). This implies that herbaceous habit, palmate venation, and differentiated stamens were primitive; flowers would still be bisexual, with a perianth, but trimerous. Loconte & Stevenson (88), who used Gnetales as the outgroup, found the basal line to be Calycanthales, a woody group usually placed in Laurales. Taylor & Hickey (129) and Nixon et al (97) nested angiosperms in Gnetales, and the basal line was Chloranthaceae (reduced Laurales in 39), which resemble Gnetales in having opposite leaves, simple flowers, and orthotropous ovules.

Analyses of partial rRNA sequences (48, 69) and *cpITS* (66) also rooted angiosperms among paleoherbs, with aquatic Nymphaeales basal. The first large analysis, of *rbc*L (25), placed the reduced aquatic genus *Ceratophyllum* at the base, whereas the remaining angiosperms split into (*a*) other magnoliids and monocots and (*b*) eudicots. However, judging from various experiments and other molecular results, this is probably a long-branch effect (38, 103). Both 18S (118) and *atp*B (114) place Nymphaeales near the base but variously associated with three woody taxa: *Amborella*, a vesselless shrub, and *Austrobaileya*, a liana, both often placed in Laurales, and Illiciales, which are small trees and lianas. When these data are combined with *rbc*L, the same result is found (117). Based on these trees, it cannot be inferred whether the first angiosperms were woody magnoliids or paleoherbs. However, the basal taxa do share one primitive-looking feature (56, 78): In most angiosperms the carpel margins are closed by postgenital fusion of the epidermal layers, but here they are sealed by a secretion.

Among magnoliids, molecular data imply that Magnoliales (purged of Winteraceae, *Austrobaileya*, and *Lactoris*) form a clade; apparently their granular exine structure is secondary, not primitive. Morphological analyses (39, 88) linked Winteraceae with Illiciales, but molecular data associate them with Canellaceae (the next-closest group in some morphological trees), which have

fused stamens and carpels but winteraceous leaves. Although molecular data move some former Laurales to the base of the angiosperms, the rest (Calycanthaceae, Monimiaceae s. lat., Lauraceae) form a clade united by nodal anatomy, hypanthium, and reduction in ovule number (105). The position of Chloranthaceae—which have been (*a*) linked with Piperales because they have no perianth and orthotropous ovules, (*b*) considered basal, and (*c*) interpreted as reduced Laurales—seems isolated and unresolved and may remain so until Trimeniaceae, which have similar but less reduced flowers (39, 55), are included. Among paleoherbs, molecular data confirm morphological indications (39) that Piperales and Aristolochiales form a clade and the controversial genus *Lactoris* belongs with Aristolochiaceae.

Eudicots

Phylogenetic analyses indicate that all non-magnoliid dicots, which make up six to nine subclasses recognized by Takhtajan (127, 128) and Cronquist (34, 35), form a monophyletic group named eudicots (49). Their most obvious morphological synapomorphy is tricolpate (and derived) pollen; another is loss of the oil cells typical of most magnoliids. An apparent exception is Illiciales, described as having three fused colpi, but these colpi are oriented—not like those of eudicots—but like the arms of a branched sulcus (77). Takhtajan and Cronquist assumed that tricolpate pollen arose several times, but they gave little evidence for links between eudicots and different magnoliids. Morphological analyses (39, 88) unite herbaceous Ranunculidae (kept in Magnoliidae by Cronquist) and "lower" Hamamelidae, wind-pollinated trees with reduced flowers, such as Hamamelidaceae, *Platanus*, and Trochodendraceae (*Trochodendron*, *Tetracentron*). Eudicots are monophyletic in *rbc*L and *atp*B trees; with 18S, a few eudicots are inserted among magnoliids and vice versa, but the identity and position of these vary among shortest trees. In general, 18S shows more anomalous relationships than *rbc*L and *atp*B, an impression confirmed by tests of congruence among data sets (117). Outgroup relations of the eudicots are unresolved; in morphological analyses (39, 88) they are earlier linked with paleoherbs based on palmate leaf venation and differentiated stamens, but in molecular trees they occupy various positions among magnoliids.

Molecular data agree remarkably on which groups are near the base of the eudicots, although their exact order is unresolved. These are ranunculids (including Papaverales and, surprisingly, the woody genus *Euptelea*, considered a hamamelid), the aquatic *Nelumbo* [often placed in Nymphaeales, but anomalous in having tricolpate pollen and earlier linked with ranunculids (39)], several lower hamamelids (*Platanus*, Trochodendraceae), and some unexpected groups. One of the latter is Proteaceae, placed in Rosidae but suspected of being lower (80); consistent with this, Proteaceae have triporate pollen with

simple pores, whereas most triporate rosids have compound pores. Another unexpected group is Buxaceae, often associated with Euphorbiaceae, which may be related to Trochodendraceae; both groups have striate-reticulate pollen. Many of these taxa have dimerous (or seemingly tetramerous) flowers, with parts in alternating pairs (Papaverales, Proteaceae, *Tetracentron*, Buxaceae). This suggests that a shift from trimerous or spiral-chaotic to dimerous floral phyllotaxy, later modified to pentamerous, is another synapomorphy of eudicots (51). Most Early Cretaceous eudicots are related to these lines [*Nelumbites*, platanoid leaves and inflorescences, buxaceous flowers (33, 50, 132)].

These results support a modified version of a scenario for floral and pollination evolution proposed by Walker & Walker (135) and Ehrendorfer (54): that the transition from magnoliids to lower hamamelids was associated with floral reduction and loss of petals, as a result of spread into cooler areas where reversion from insect to wind pollination was favored, followed in the evolution of rosids and dilleniids by reorigination of petals from stamens to attract more advanced insects. However, more of the intermediate lines (ranunculids, *Nelumbo*) have petals than was thought, and the hypothesis that petals originated from stamens needs closer scrutiny in a phylogenetic and developmental context.

Above the lower eudicots, all three molecular data sets show a split into two huge clades, called Rosidae and Asteridae (25, 114, 118) but representing these groups only in a highly modified sense. I call these the rosid line and the asterid line. These results break up the Dilleniidae, which were distinguished from Rosidae on the direction of stamen initiation when stamens are numerous: centripetal in Rosidae (the normal acropetal order of appendage formation), centrifugal in Dilleniidae, often grouped into fascicles derived from five primordia. The specific partitioning of dilleniids was anticipated by Hickey & Wolfe (76), based on leaf venation: Their palmate dilleniids belong to the rosid line, pinnate dilleniids to the asterid line. Centrifugal stamens apparently originated several times, probably as part of a widespread tendency for increase in stamen number (secondary polyandry) among more advanced insect-pollinated groups, which in other cases followed the centripetal route (54, 85). Both lines have basically tricolporate pollen (with compound apertures), an advance over the tricolpate type of lower eudicots.

Several smaller groups are not consistently associated with one line or the other. Many have primitive features such as tricolpate pollen, which suggests they belong below the rosid-asterid split. One is Caryophyllidae, known for their peculiar anatomy, embryology, and betalain pigments; it includes Polygonaceae, Plumbaginaceae, and more unexpectedly the insectivorous Droseraceae and Nepenthaceae. Contrary to some suggestions, these have no direct connection with Ranunculaceae. The saxifragoids (116) include woody

Hamamelidaceae and *Cercidiphyllum*, put in Hamamelidae because of their reduced flowers, and mostly herbaceous Saxifragaceae, Crassulaceae (Rosidae), and *Paeonia* (Dilleniidae). This suggests a trend from wind-pollinated trees to insect-pollinated herbs. These groups often have palmately lobed leaves, two carpels, and a hypanthium. Many Saxifragaceae in the older sense, including most woody members, are scattered among rosids and asterids (25, 116). Three other lines are Dilleniaceae, which show no molecular relationship to other dilleniids and have more primitive tricolpate pollen and free carpels; Vitaceae, which like saxifragoids have two carpels and palmately lobed leaves; and Santalales, which show trends for parasitism and ovule reduction.

Molecular analyses have consistently revealed three major clades in the rosid line, plus several lines of more uncertain position.

One clade includes Rosaceae, Leguminosae, Rhamnaceae (Rosidae), and Cucurbitales (Dilleniidae). Most important, it also includes the wind-pollinated Amentiferae, or "higher" Hamamelidae, thought to represent the culmination of a trend to wind pollination begun in lower Hamamelidae. These consist of two separate lines, Urticales and Fagales s. lat. (93), including Fagaceae, Betulaceae, Juglandaceae, and Myricaceae. These results continue the dismemberment of the Hamamelidae. The idea that lower and higher hamamelids are unrelated was anticipated by palynology (134): Lower hamamelids have tricolpate pollen, whereas Urticales and most Fagales (except Fagaceae) have triporate pollen with compound pores, apparently derived from rosid-type tricolporate pollen via the triangular Normapolles of the Late Cretaceous (63). These groups thus represent independent later reversions from insect to wind pollination. Some data link Fagales with Cucurbitales; this may seem absurd, but both groups do have basically three carpels and an inferior ovary. Urticales are consistently linked with Rhamnaceae; this suggests that their four to five tepals, usually assumed to be sepals, are really petals because they are opposite the stamens, like the petals in Rhamnaceae. Legumes are always linked with Polygalaceae—an irony because polygalaceous flowers are superficially legume-like, but the similar-looking parts are not morphologically equivalent. A possible morphological synapomorphy of this whole clade is loss of endosperm in the seed.

The second clade includes Sapindales, many with pinnately compound leaves, and the dilleniid orders Capparales and Malvales (including Theales such as Dipterocarpaceae). Capparales are greatly expanded from older concepts (centered on Cruciferae and Capparaceae) to include almost all groups (except *Drypetes*) with glucosinolates (mustard oils), such as Caricaceae, Tropaeolaceae, and Limnanthaceae, formerly scattered among several orders (108). In this case, molecular data show that secondary compounds are of greater systematic value than was recognized. The connection of Capparales and Sapindales

is not surprising because several glucosinolate groups were formerly placed in Sapindales. Two lines more equivocally linked with this clade are Myrtales [including Vochysiaceae, which have only one stamen but myrtalian anatomy (28)] and Geraniales in a narrow sense.

The third clade includes Euphorbiaceae, Malpighiaceae, Linales, and many Violales. Interestingly, it has been debated whether Euphorbiaceae are rosids or dilleniids. These results imply that stamen fascicles are less significant than was thought, but the fact that many of these taxa have three carpels may be more significant. Two less securely associated lines are Celastrales (in a restricted sense) and Oxalidales, including Cunoniaceae, often considered a link between lower hamamelids and rosids.

The asterid line contains Asteridae in the original sense, with a sympetalous corolla and epipetalous stamens, plus Cornales (Rosidae) and the remaining Dilleniidae, including Ericales, some Theales, Primulales, and Ebenales. Many of the latter groups were once associated with asterids as Sympetalae, whereas Takhtajan (127, 128) considered Cornales a link between Rosidae and Asteridae. Philipson (100) anticipated the whole group based on unitegmic-tenuinucellate ovules and chemistry (iridoid substances), another example of the value of chemical characters, although exceptions to the ovule characters in lower groups imply that they originated in parallel or were easily reversed. Hydrangeaceae, considered woody Saxifragaceae, are strongly linked with Cornales (116). These results imply that the numerous stamens of Theaceae are an example of secondary increase, not primitive. The dilleniid groups vary between free and fused petals; better resolution is needed to judge whether sympetaly is homologous here and in higher asterids but was often reversed or whether it arose many times.

Molecular analyses confirm Takhtajan's (128) separation of Lamiidae from Asteridae. The two groups are also supported by a shift from trilacunar to unilacunar nodes in Lamiidae and from superior to inferior ovary in Asteridae. Small groups near the base of the two lines include Aquifoliaceae, *Escallonia* (formerly Saxifragaceae), and a clade consisting of *Garrya*, *Aucuba* (Cornales), and *Eucommia* (misplaced in Hamamelidae because of its reduced flowers). Within Lamiidae, Labiatae and Verbenaceae are not linked with Boraginaceae (34, 35) but instead are nested within Scrophulariales, which implies that the gynobasic styles and four nutlets of Boraginaceae and Labiatae are purely convergent.

Molecular data link two former rosid groups, Araliales (Apiales) and Pittosporaceae, with each other and with Asteridae, a relationship supported by chemical features such as polyacetylenes. Araliales differ from typical asterids in having free petals, but in ontogeny the petals arise from a ring-like primordium. This suggests that they had sympetalous ancestors (57). Molecular data refute the hypothesis (34, 35) that Compositae are related to Rubiaceae

(Gentianales, Lamiidae); instead, they are nested in Campanulales, which like Compositae have inulin as a storage product and a "plunger" pollen presentation mechanism. Within Compositae, both a chloroplast inversion and restriction site data support the basal position of Barnadesiinae, with bilabiate florets, and the derived status of Asteroideae, with disk and ray florets (79).

Monocots

Monocots are clearly nested among magnoliids, consistent with the fact that they retain monosulcate pollen, but their closest outgroups are still uncertain. Some morphological analyses (39, 48, 88) support the classic concept that monocots are related to Nymphaeales, based on loss of secondary growth and aquatic habit (as in alismids). This suggests that monocot advances such as linear leaves, scattered bundles, and one cotyledon arose in aquatic habitats. Other analyses of morphology (44) and partial rRNA and 18S sequences (15, 48) link them with Aristolochiaceae, the only outgroup with monocot-like PII sieve tube plastids. However, *rbc*L, the large 18S data set, and *atp*B (25, 114, 118) place them in inconsistent positions among paleoherbs and woody magnoliids.

Within monocots, molecular data confirm many suggestions of Dahlgren et al (36) and more recent morphological analyses (15, 124). Alismidae have often been considered primitive, based on free carpels, aquatic habit, and laminar placentation (as in Nymphaeales), but they have several advances over other monocots, such as trinucleate pollen and loss of endosperm. Instead, Dahlgren et al (36) linked alismids with Arales [placed in Arecidae by others (34, 35, 127)], based on extrorse anthers and amoeboid tapetum, and argued that the most primitive monocots are dioscoreids (Liliidae), which are lianas with palmately veined, dicot-like leaves, recalling Aristolochiaceae. Dioscoreids form a basal paraphyletic grade in morphological analyses (15, 124), but most molecular analyses (15, 25, 26, 37) place alismids and aroids together just below dioscoreids. An unexpectedly important taxon is *Acorus*, which was placed in Araceae because it has a spadix but differs in having equitant, unifacial leaves and magnoliid-like oil cells (68). *Acorus* is the sister group of all other monocots (25), linked with *Ceratophyllum* (114) or the primitive aroid *Gymnostachys* (37) in the same position, or dissociated from monocots entirely, near Piperales (15, 118). *rbc*L and fossil intermediates (126) confirm that the highly reduced, aquatic Lemnaceae are nested in Araceae, with the floating aquatic *Pistia*.

These results have important implications for monocot leaf evolution. In dicots, the blade develops from the upper zone of the leaf primordium, whereas in monocots, it usually develops from the lower leaf zone while the upper leaf zone becomes the apical "Vorläuferspitze" (14, 81). This led to suggestions that monocots went through a stage in which the blade was lost. This might

seem less likely if the dicot-like leaves of dioscoreids were primitive. Although molecular trees indicate that dioscoreids are not basal, they still challenge the leaf reduction scenario because the blade develops from the upper leaf zone in *Acorus*, alismids, and aroids. This implies that the typical monocot pattern arose within the group (14). Contrary to usual assumptions, molecular data also imply that free carpels in monocots are secondarily derived from fused carpels (as in Aristolochiaceae) because apocarps (alismids, Melanthiaceae, some palms) are nested among syncarps.

As proposed by Dahlgren et al (36), *rbc*L data (24–26) group most Liliidae into two lines, Liliales and Asparagales. Derived features of Liliales include bulbs, spotted tepals, and tepalar nectaries. Asparagales, which include several secondarily woody lines, have capsules containing seeds with a black phytomelan crust or berries. Dahlgren et al (36) linked Iridaceae and Orchidaceae with Liliales, but *rbc*L places both taxa near Asparagales, with orchids linked with Hypoxidaceae.

Continuing the breakup of Arecidae, *rbc*L and restriction site data (25, 26, 37, 86) confirm the view of Dahlgren et al (36) that palms are the sister group of Commelinidae, based on fluorescent epidermal cell walls (cell-wall bound ferulic acids). Two other arecid groups, Cyclanthaceae and Pandanaceae, belong near Liliales. Commelinids themselves appear to be monophyletic, united by a shift to starchy endosperm (as in cereal grasses). Dahlgren et al (36) admitted one exception to the cell wall character in commelinids, Velloziaceae, but *rbc*L places this family near Liliales (26).

Petaloid taxa (Zingiberales, Bromeliaceae, etc) occupy poorly resolved positions near the base of commelinids, whereas Gramineae and Cyperaceae are the culmination of two lines that show floral reduction for wind pollination. Molecular data (25, 37, 86) confirm that Juncaceae and Cyperaceae are related, as inferred from their diffuse centromeres, the tetrad pollen of Juncaceae, and the pseudomonads (tetrads in which three nuclei abort) of Cyperaceae. Typhales belong near here rather than being wind-pollinated aroids (130). Gramineae are linked with Restionaceae and, more closely, with *Joinvillea* (37, 82), which resembles grasses in having long and short epidermal cells.

CONCLUSIONS

Judging from increasing congruence of results based on different kinds of data, phylogenetic analyses are approaching definitive answers to many of the most vexing questions of vascular plant phylogeny (relationships at the base of tracheophytes, within ferns, between cycadophytes and coniferophytes, and within eudicots and monocots). Other problems (rooting of angiosperms) may be resolved by addition of taxa and/or a combination of more molecular data sets.

However, some problems (relationship of angiosperms and Gnetales) may remain controversial for some time, requiring massive combination of molecular data, advances in analytical methods, or discovery of fossils on the stem lineages leading to modern groups. Even if molecular data resolve the relationships of modern groups, fossil taxa, integrated into phylogenies via morphology, will be needed to understand the evolution of many characters of modern plants.

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