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THE ORIGIN AND DIVERSIFICATION OF ANGIOSPERMS[1]

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The angiosperms, one of five groups of extant seed plants, are the largest group of land plants. Despite their relatively recent origin, this clade is extremely diverse morphologically and ecologically. However, angiosperms are clearly united by several synapomorphies. During the past 10 years, higher-level relationships of the angiosperms have been resolved. For example, most analyses are consistent in identifying *Amborella*, Nymphaeaceae, and Austrobaileyales as the basalmost branches of the angiosperm tree. Other basal lineages include Chloranthaceae, magnoliids, and monocots. Approximately three quarters of all angiosperm species belong to the eudicot clade, which is strongly supported by molecular data but united morphologically by a single synapomorphy—triaperturate pollen. Major clades of eudicots include Ranunculales, which are sister to all other eudicots, and a clade of core eudicots, the largest members of which are Saxifragales, Caryophyllales, rosids, and asterids. Despite rapid progress in resolving angiosperm relationships, several significant problems remain: (1) relationships among the monocots, Chloranthaceae, magnoliids, and eudicots, (2) branching order among basal eudicots, (3) relationships among the major clades of core eudicots, (4) relationships within rosids, (5) relationships of the many lineages of parasitic plants, and (6) integration of fossils with extant taxa into a comprehensive tree of angiosperm phylogeny.

Key words: *Amborella*; angiosperms; phylogeny.

The angiosperms, or flowering plants, one of the major clades of extant seed plants (see Burleigh and Mathews, 2004, in this issue), are the largest group of embryophytes, with at least 260 000 living species classified in 453 families (APG II, 2003). Angiosperms are amazingly diverse. They occupy every habitat on Earth except the highest mountaintops, the regions immediately surrounding the poles, and the deepest oceans, and they occur as epiphytes, floating and rooted aquatics in both freshwater and marine habitats, and terrestrial plants that vary tremendously in size, longevity, and overall form. Furthermore, the diversity in chemistry, reproductive morphology, and genome size and organization is unparalleled in the Plant Kingdom.

Despite their diversity, angiosperms are clearly united by a suite of synapomorphies (i.e., shared, derived features), including double fertilization and endosperm formation, the carpel, stamens with two pairs of pollen sacs, features of gametophyte structure and development, and phloem tissue composed of sieve tubes and companion cells (see Doyle and Donoghue, 1986; and P. Soltis et al., 2004, for further discussion). This evidence strongly negates hypotheses of polyphyletic origins of extant angiosperms.

The fossil record of the angiosperms extends back at least to the early Cretaceous, conservatively 130 million years ago (mya) (see Crane et al., 2004). Floral size, structure, and organization among early angiosperms varied tremendously, ranging from small (i.e., <1 cm in diameter) flowers of fossil Chloranthaceae and many other lineages (reviewed in Friis et al., 2000), both extant and extinct, to the large, *Magnolia*-like flowers of *Archaeanthus* (Dilcher and Crane, 1984). This floral diversity in the fossil record is consistent with an early radiation of angiosperms and associated diversification in floral form (e.g., Friis et al., 2000).

Large-scale collaborations among angiosperm systematists have greatly improved our understanding of angiosperm phylogeny. Strong support for many clades that correspond to traditionally recognized families provided early confidence that the molecular-based trees were producing reasonable reconstructions of phylogeny. However, some traditional families and many orders and higher groups have been shown to be nonmonophyletic, while many groups of previously uncertain placement have been placed with great confidence. The Angiosperm Phylogeny Group, an international consortium of systematists, recognized the need for a new classification that reflects current views of angiosperm phylogeny (APG, 1998; APG II, 2003). An abridged version of the classification is given in Appendix 1 (see Supplemental Data accompanying online version of this paper) and at the Deep Time website (http://flmnh.ufl.edu/deeptime).

In this paper, we provide a brief overview of angiosperm phylogeny as currently understood (Fig. 1) and examine patterns of angiosperm diversification. The monocot and eudicot clades will be considered in greater detail in the accompanying papers by Chase (2004) and Judd and Olmstead (2004), respectively.

ANGIOSPERM PHYLOGENY

The root of the tree—A mere decade ago, the possibility of identifying the basal nodes of the angiosperm clade seemed remote. However, most analyses of the past five years concur in placing the monotypic *Amborella* as the sister to all other extant angiosperms. *Amborella trichopoda*, endemic to cloud forests of New Caledonia, was described in the mid-nineteenth century (Baillon, 1869) and has since been classified with various groups of basal angiosperms, most often with Laurales (e.g., Cronquist, 1981). However, *Amborella* clearly differs from most Laurales in having spirally arranged floral organs (except perhaps the carpels; Buzgo et al., in press), rather than the whorled phyllotaxis typical of most Laurales (see studies of floral morphology and development by Endress and Igersheim, 2000b; Posluszny and Tomlinson, 2003; Buzgo et al., in press), and lacks those features considered to be synapomorphies for Laurales (Doyle and Endress, 2000; see Laurales later). *Amborella* has carpels that are closed only by secretion,

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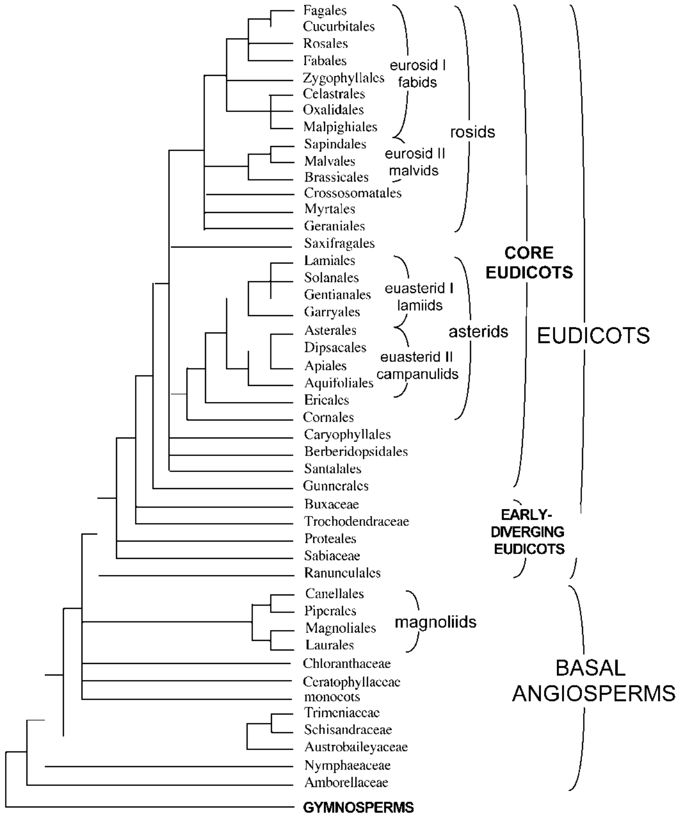

Fig. 1. Overview of angiosperm phylogenetic relationships, based on Qiu et al. (1999), P. Soltis et al. (1999), D. Soltis et al. (2000, 2003), Zanis et al. (2002), Hilu et al. (2003), Kim et al. (2004b).

rather than by fused tissue as in most angiosperms (Endress and Igersheim, 2000a)—a feature that may represent a plesiomorphy (i.e., ancestral feature) for the angiosperms. Vessels (Judd et al., 2002; but see Feild et al., 2000; Doyle and Endress, 2000) and pollen grains with a reticulate tectum (Doyle and Endress, 2001) appear to be synapomorphies for all extant angiosperms except *Amborella*. Ethereal oil cells—common throughout basal angiosperms—and columellate pollen grains with a perforate tectum are synapomorphies for all extant angiosperms except *Amborella* and Nymphaeaceae (Doyle and Endress, 2001).

The evidence for Amborella—Nearly all multigene analyses of basal angiosperms have identified *Amborella* as the sister to all other extant angiosperms (e.g., Mathews and Donoghue, 1999, 2000; Parkinson et al., 1999; Qiu et al., 1999; P. Soltis et al., 1999; Graham and Olmstead, 2000; Graham et al., 2000; D. Soltis et al., 2000; Magallón and Sanderson, 2001; Zanis et al., 2002; see also Nickerson and Drouin, 2004), with varying levels of support. The genes that support this position come from all three plant genomes and represent relatively ‘‘slowly evolving’’ protein-coding and ribosomal RNA genes. Furthermore, analyses of the ‘‘rapidly evolving’’ plastid gene *matK* (Hilu et al., 2003) and mostly noncoding *trnL-trnF* (Borsch et al., 2003) each showed these same results. In all of these studies, Nymphaeaceae and Austrobaileyales (both sensu the Angiosperm Phylogeny Group, APG II, 2003) ‘‘followed’’ *Amborella* as successive sisters to the remaining extant angiosperms. Furthermore, the structural organization of the floral MADS-box genes *Apetala3* and *Pistillata* also supported the position of *Amborella* and Nymphaeaceae as sisters to all other extant angiosperms, and analyses of nucleotide and amino acid sequences of these genes also placed *Amborella*, either alone or with Nymphaeaceae, in this position (Kim et al., in press).

Alternative views—Despite general support for the placement of *Amborella* as sister to the rest of the extant angiosperms, a few studies have found alternative rootings, using either different genes or different methods of analysis. For example, *Amborella* + Nymphaeaceae (e.g., Parkinson et al., 1999; Barkman et al., 2000; Mathews and Donoghue, 2000; Qiu et al., 2000; P. Soltis et al., 2000; Kim et al., in press) or Nymphaeaceae alone (e.g., Parkinson et al., 1999; Graham and Olmstead, 2000, with partial sampling of Nymphaeaceae; Mathews and Donoghue, 2000) have occasionally been reported as sister to all other angiosperms. However, statistical analyses of these alternative rootings using a data set of up to 11 genes generally favor the tree with *Amborella* as sister to the rest, although the *Amborella* + Nymphaeaceae tree could not always be rejected (Zanis et al., 2002). Nearly all of these studies are consistent in noting that conflicting topologies are not strongly supported. Furthermore, the difference among these three topologies is relatively minor and consists solely of the relative placement of *Amborella* and Nymphaeaceae.

A more dramatic alternative, based on a selection of 61 genes from the totally sequenced plastid genomes of 13 plant species, placed the monocots (represented only by three grasses—rice, maize, and wheat) as the sister to all other extant angiosperms (Goremykin et al., 2003). Whereas all molecular analyses of angiosperms with dense taxon sampling strongly supported monophyly of the monocots and most placed this clade among the basal nodes of the angiosperm tree, none has indicated that monocots are sister to all other extant angiosperms. In the analysis by Goremykin et al. (2003), *Amborella* was sister to *Calycanthus* of Laurales, a position consistent with the original description of *Amborella*, but clearly at odds with other aspects of morphology (see Laurales section). Goremykin et al. (2003) attributed their results to the increased character sampling (30 017 nucleotides in their aligned matrix) in their study relative to other analyses that included fewer genes but many more taxa. However, further analyses of a data set of three genes and nearly equivalent taxon sampling indicated that the ‘‘monocots basal’’ topology is an artifact of limited taxon sampling (Soltis and Soltis, 2004). When either *Nymphaea* or *Austrobaileya*, representing Nymphaeaceae and Austrobaileyales, respectively, was substituted for *Amborella*, each appeared as the sister to *Calycanthus*, in exactly the same position that *Amborella* had occupied, presumably because the data set, which was limited to a subset of those plant species for which entire plastid genome sequences are available, contained no other close relatives. Furthermore, representing monocots by taxa other than grasses, which reside at the end of a long branch (e.g., Gaut et al., 1992, 1996; Chase et al., 2000), broke up the long branch to the monocots and resulted in the ‘‘*Amborella* basal’’ topology. Likewise, broader sampling of the monocots beyond grasses (the sole monocots included by Goremykin et al., 2003) also severed the long monocot branch and yielded the ‘‘*Amborella* basal’’ tree. Finally, when plastid sequences of the monocot *Acorus* were added to the data set of Goremykin et al., also disrupting the long branch to the grasses, *Amborella* resumed its position as sister to the other angiosperms (S. Stefanovic et al., Indiana University, unpublished data). Although increasing the number of characters will generally lead to greater accuracy (Hillis, 1996) and support (e.g., Givnish and Sytsma, 1997; Soltis et al., 1998), the increase in characters cannot come at the expense of adequate taxon sampling (e.g., Chase et al., 1993; Sytsma and Baum, 1996; Zwickl and Hillis, 2002; Pollock et al., 2002; Soltis et al., in press-a). Limited taxon sampling, such as that dictated by the small number of organisms with complete genome sequences, may lead to artifacts, as apparently occurred in the analysis by Goremykin et al. (2003).

The fossil record—The fossil record does not clarify basal groups within the angiosperms. However, it clearly identifies a number of morphologically diverse lineages early in angiosperm evolution (e.g., Crane et al., 1995; Friis et al., 2000). Although some of these early fossils seem to belong to extant families, many do not fit easily into extant groups. For example, two species of *Archaefructus* (Sun et al., 1998, 2002) may be the sister to all other angiosperms (Sun et al., 2002), although a reanalysis of their data, with the inclusion of additional material, indicated alternative placements (Friis et al., 2003). Notably, with regard to the plastid topology of Goremykin et al. (2003), the monocots are not among the earliest angiosperm fossils, although both the fossil record (Gandolfo et al., 2002) and molecular clock estimates (K. Bremer, 2000; Wikström et al., 2001; Davies et al., 2004) have indicated that many lineages of monocots date back at least 80–100 mya. However, Nymphaeaceae are among the earliest angiosperm fossils: a water lily from approximately 125 mya (Friis et al., 2001) is consistent with the basal or near-basal position of the Nymphaeaceae branch in most molecular-based trees, and the floral features of *Microvictoria* (90 mya; Gandolfo et al., 2004) provide evidence of beetle entrapment pollination in early angiosperms. Likewise, the abundance of fossils of Chloranthaceae and Ceratophyllaceae from the early Cretaceous (e.g., Couper, 1958; Walker and Walker, 1984; Dilcher, 1989; Friis et al., 2000; see Endress, 2001, for review) is also consistent with the placement of these clades among extant angiosperms in molecular-based trees (Figs. 1, 2).

Basal lineages—The positions of Amborellaceae and Nymphaeaceae as successive sisters to the rest of the angiosperms are followed in turn by Austrobaileyales. Although these first three nodes are well supported (e.g., Zanis et al., 2002; Hilu et al., 2003), resolution and support for relationships of the next few nodes are poor (Fig. 2). Ceratophyllaceae, monocots, Chloranthaceae, magnoliids, and eudicots are each well supported, and both the fossil record and molecular-based trees identify these lineages as ancient. However, their interrelationships remain unclear. It is clear, however, that angiosperms do not fall into two major groups that correspond to monocots (Liliopsida) and dicots (Magnoliopsida) of longstanding classification systems (such as Cronquist, 1981; Takhtajan, 1997, and their predecessors). Although monocots clearly form a strongly supported clade, dicots in the traditional sense do not: most are found in the eudicot clade, but the remaining nonmonocot basal branches (i.e., Amborellaceae, Nymphaeaceae, Austrobaileyales, Ceratophyllaceae, Chloranthaceae, magnoliids) were also ‘‘traditional’’ dicots. The nonmonophyly of the dicots has long been suspected, and the lack of monophyly precludes their recognition in current classifications (e.g., APG II, 2003). The concept of ‘‘dicot’’ should be abandoned in favor of eudicots, with recognition that considerable diversity exists outside the monocot and eudicot clades.

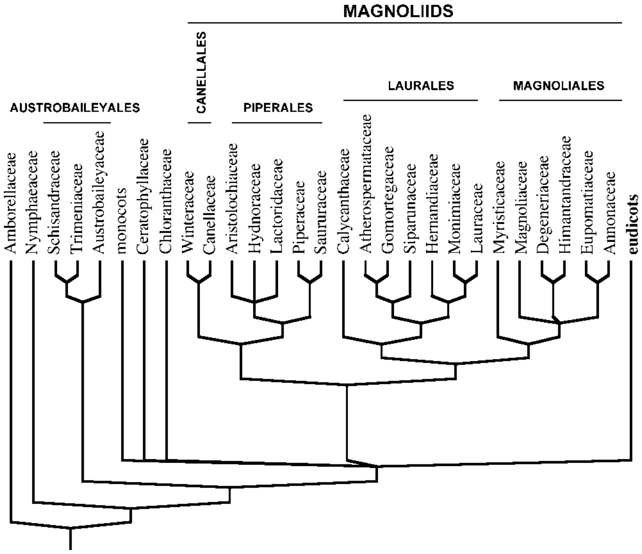

Fig. 2. Summary of phylogenetic relationships among clades of basal angiosperms, based primarily on Zanis et al. (2002).

Nymphaeaceae—The phylogenetic position of Nymphaeaceae as one of the two basalmost lineages of extant angiosperms is strongly supported by nearly all molecular analyses. This clade of eight genera has a worldwide distribution, consistent with both the ancient age of this lineage and aquatic habitats. Although all genera occupy aquatic habitats, these habitats range from temperate to tropical. Floral diversity among genera is extensive, ranging from the small, simple, trimerous, monocot-like flowers of *Cabomba* to the large, showy, elaborate flowers of *Nymphaea* and *Victoria*. Although the latter were considered ‘‘primitive’’ by most authors, Schneider (1979) suggested that the numerous floral organs of *Nymphaea* and *Victoria* resulted from secondary increase. Phylogenetic analyses (Les et al., 1999) and character reconstructions (Ronse DeCraene et al., 2003; Soltis et al., in press-b) supported Schneider’s (1979) hypothesis. Floral diversification in Nymphaeacae may be related to changes in pollination: proliferation of parts in response to beetle pollination in *Nymphaea* and *Victoria* and a reduction in number of parts associated with a shift to cleistogamy in *Euryale* (Gottsberger, 1977, 1978; Williams and Schneider, 1993; Lipok et al., 2000).

Austrobaileyales—This small clade comprises Austrobaileyaceae (*Austrobaileya*) and Trimeniaceae (*Trimenia*) from Australasia plus Schisandraceae sensu APG II (2003), i.e., Schisandraceae (*Schisandra* and *Kadsura*) and Illiciaceae (*Illicium*) of most other recent classifications (Qiu et al., 1999; Renner, 1999; Savolainen et al., 2000a, b; P. Soltis et al., 1999; D. Soltis et al., 2000). Although the traditional Illiciaceae and Schisandraceae have typically been united in Illiciales, a relationship between these taxa and *Austrobaileya* and *Trimenia* had not been suspected. No morphological synapomorphies have been identified for this clade, despite the strong molecular support for its monophyly.

Ceratophyllaceae—Ceratophyllaceae (*Ceratophyllum*) had the distinction of appearing as the sister to all other angiosperms in the first large molecular phylogenetic analysis based on *rbcL* (Chase et al., 1993). The aquatic habit and simple flowers seemed at odds with most hypotheses about the earliest angiosperms, although *Ceratophyllum* has a long fossil record, going back at least 125 mya (Dilcher, 1989). Subsequent analyses demonstrated that this placement was unique to the *rbcL* data set, but the position of *Ceratophyllum*, based on evidence from many other genes, is still not clear. It appears as the sister to monocots in some analyses (e.g., Zanis et al., 2002; Davies et al., 2004), but further work is needed to identify its proper position.

Monocots—Among extant angiosperms, monocotyledons represent the earliest-appearing major clade. Using a molecular clock, K. Bremer (2000) dated the origin of the monocot clade to be 134 mya, older than the oldest angiosperm fossils. Although their exact age is unclear from the fossil record (but see Gandolfo et al., 2002), monocots clearly represent an early lineage of angiosperms. There are approximately 52 000 species of monocots (Mabberley, 1993), representing 22% of all angiosperms. Half of the monocots can be found in the two largest families, Orchidaceae and Poaceae, which comprise 34% and 17%, respectively, of all monocots.

Phylogenetic studies of nonmolecular data (Donoghue and Doyle, 1989; Loconte and Stevenson, 1991; Doyle and Donoghue, 1992) have identified 13 putative synapomorphies for the monocots, including, among others, a single cotyledon, parallel-veined leaves, sieve cell plastids with several cuneate protein crystals, scattered vascular bundles in the stem, and an adventitious root system. An often-overlooked synapomorphy for monocots is their sympodial growth; although there are other angiosperms with sympodial growth, monocots are nearly exclusively so. These synapomorphies are covered in detail in the paper by Chase in this issue (2004; see also Judd et al., 2002; Soltis et al., in press-b).

Recognition of the monocots as a distinct group within the angiosperms dates from Ray (1703) and was largely based on their possession of a single cotyledon relative to the two cotyledons typical of the dicotyledons or ‘‘dicots.’’ As reviewed earlier, the latter group is now known to be nonmonophyletic, and the term ‘‘dicot’’ should be abandoned. There is, however, a great diversity of form in monocot seedlings (Tillich, 1995) and not all possess an obvious single cotyledon.

Another major, distinctive trait of the monocots is their vascular system, which is characterized by vascular bundles that are scattered throughout the medulla and cortex and are closed (i.e., do not contain an active cambium; reviewed in Tomlinson, 1995). In contrast, basal angiosperms formerly considered dicots (e.g., members of the magnoliid clade) and eudicots possess open vascular bundles arranged in a ring.

Another widely cited character of the monocots is their particular form of sieve cell plastids (Behnke, 1969), which are triangular with cuneate proteinaceous inclusions. Similar sieve cell plastids are found in Aristolochiaceae (Dahlgren et al., 1985). This similarity between monocots and Aristolochiaceae apparently represents convergence, not shared ancestry, because phylogenetic studies of DNA sequences from all three genomes (Qiu et al., 1999; Zanis et al., 2002, 2003) have demonstrated a strongly supported relationship of Aristolochiaceae to other Piperales within the magnoliid clade.

Other traits characteristic of the monocots include parallel venation without free vein-endings (vs. reticulate venation with free vein-endings), intercalary meristem, adventitious roots, and roots without secondary growth. Adventitious roots are found elsewhere in the angiosperms, in both Piperaceae and Nymphaeaceae.

Trimerous flowers have long been considered a uniting feature of the monocots, but it is not an exclusive one because there are many other basal angiosperms, including Nymphaeaceae and magnoliids, that also exhibit trimery. In fact, character-state reconstructions of the angiosperms indicate that trimery arose early in the angiosperms; it may be ancestral for all angiosperms except *Amborella* (Ronse De Craene et al., 2003; Zanis et al., 2003; Soltis et al., in press-b), or perhaps all angiosperms, if the shift away from trimery in *Amborella* occurred along the lineage leading to *Amborella*. Trimery appears, therefore, to be a symplesiomorphic feature for monocots and other angiosperms and is not a ‘‘monocot character.’’

Our understanding of monocot phylogenetics has greatly improved over the past decade, aided greatly by the foci provided by the international monocot symposia held in 1993, 1998, and 2003. These meetings have focused attention both on what was known and, more importantly, on which groups needed additional research. As a result, we now know more about monocots than any other group of angiosperms of comparable size, a situation that is remarkable given the paucity of information available in 1985 (Dahlgren et al., 1985). This model should be adopted for the other large groups of angiosperms (e.g., rosids, asterids) so that attention is likewise focused on integration of research programs and gaps in the database.

There have been several recent analyses of relationships among the monocots, including the three-gene analyses of Chase et al. (2000) and D. Soltis et al. (2000) and the seven-gene analysis of Chase et al. (in press). The first two studies are based on the same three genes (*rbcL*, *atpB*, 18S rDNA); however, Chase et al. (2000) focused only on the monocots and employed a larger number of taxa than used in D. Soltis et al. (2000). The analysis by Chase et al. (2004) included those three genes, plus partial nuclear 26S rDNA, plastid *matK* and *ndhF*, and mitochondrial *atpA*. The paper in this issue by Chase (2004) provides greater detail on monocot phylogeny, and our coverage will therefore be brief.

All but two molecular phylogenetic analyses of monocots have placed *Acorus* alone as sister to all other monocots. The first exception to this statement was the 18S rDNA analysis of Bharathan and Zimmer (1995), in which *Acorus* was placed outside of the monocots altogether, a result that has to be considered spurious. Combination of 18S rDNA sequence data with sequences from *rbcL* and *atpB* (Chase et al., 2000; D. Soltis et al., 2000) resulted in strong support for the monophyly of monocots, as well as strong support for the monophyly of all monocots excluding *Acorus*. A recent analysis of two of the seven genes used in Chase et al. (in press), *rbcL* and *atpA* (Davis et al., in press), retrieved an alismatid clade that included *Acorus*. This deviating result is perplexing because neither *rbcL* (Chase et al., 1993; Duvall et al., 1993) nor *atpA* (Davis et al., 1998) analyzed alone produced such a position for *Acorus*. In contrast, studies of basal angiosperm relationships that have employed more genes (six to 11) have consistently found *Acorus* sister to the remaining monocots with strong support (e.g., Qiu et al., 1999, 2000; Zanis et al., 2002, 2003). A recent angiosperm-wide analysis of *matK* sequence data (Hilu et al., 2003), an analysis of *ndhF* in monocots (Givnish et al., in press), and a seven-gene analysis of monocots (Chase et al., in press) found moderate to strong support for the placement of *Acorus* as sister to other monocots. Hence, most analyses agree on the placement of *Acorus* as sister to all other monocots.

Following *Acorus*, the monophyly of the remaining monocots is strongly supported. Alismatales are sister to the remaining monocots, which themselves are strongly supported. Within this remaining large clade are several component subclades: commelinids, Dioscoreales, Petrosaviaceae, Pandanales, Liliales, and Asparagales. Although many of these component subclades receive moderate to strong support, relationships among these subclades have been generally poorly resolved. In the strict consensus of Chase et al. (2000), the branching order above Alismatales is Dioscoreales, Pandanales, Liliales, and Asparagales + commelinids. The seven-gene analysis of Chase et al. (in press) is consistent with this pattern, except that Dioscoreales and Pandanales are sister taxa, and most of these relationships received at least moderate bootstrap support.

Chloranthaceae—Chloranthaceae, with their small, simple flowers, have an extensive fossil record, dating back 125 my (e.g., Couper, 1958; Walker and Walker, 1984; Friis et al., 2000). Chloranthaceae are clearly an isolated lineage separate from the magnoliid clade (Fig. 2), but their phylogenetic position remains uncertain. In some analyses (e.g., Zanis et al., 2002; Davies et al., 2004), they are sister to a clade of magnoliids + eudicots. Relationships and patterns of evolution within Chloranthaceae have been addressed by Kong et al. (2002), Doyle et al. (2003), Zhang and Renner (2003), and Eklund et al. (2004).

Magnoliids—The magnoliid clade comprises most of those lineages typically referred to as ''primitive angiosperms'' in earlier works (e.g., Stebbins, 1974; Cronquist, 1981, 1988; Takhtajan, 1997). Although the component families of the magnoliid clade were loosely associated in previous classifications, for example, as Cronquist's (1981) subclass Magnoliidae, relationships among the families and orders were not clear. In addition, Magnoliidae contained groups that are not part of the magnoliid clade as recognized by phylogenetic analyses. Reconstructing relationships within this clade, and even recognition of the clade itself, is challenging, given the age of this clade (some putative members, such as *Archaeanthus*, Dilcher and Crane, 1984, date to the early Cretaceous) and presumably high levels of extinction. Although the major lineages of the magnoliid clade were identified as well-supported clades in earlier studies (e.g., Soltis et al., 1999), composition and interrelationships of the magnoliid clade did not become clear until data sets of at least five genes for a broad sample of taxa were assembled to address these problems (e.g., Qiu et al., 1999, 2000; Zanis et al., 2002). Within the magnoliids, Magnoliales and Laurales are sisters, and Piperales and Canellales are sisters (Fig. 2).

Magnoliales. This clade comprises six families (Myristicaceae, Degeneriaceae, Himantandraceae, Magnoliaceae, Eupomatiaceae, and Annonaceae), relationships among which are now clear (e.g., Sauquet et al., 2003; Fig. 2). This same clade emerged in the nonmolecular analysis of Doyle and Endress (2000). Apparent synapomorphies for the clade include reduced fiber pit borders, stratified phloem, an adaxial plate of vascular tissue in the petiole, palisade parenchyma, astrosclereids in the leaf mesophyll, continuous tectum in the pollen, and multiplicative testa in the seed (Doyle and Endress, 2000). Furthermore, all members of this clade examined to date have a characteristic deletion in their *Apetala3* gene (Kim et al., in press).

Laurales. Laurales, as currently circumscribed (APG II, 2003; see Renner, 1999), comprise seven families: Calycanthaceae (including Idiospermaceae), Monimiaceae, Gomortegaceae, Atherospermataceae, Lauraceae, Sipurunaceae, and Hernandiaceae. Amborellaceae and Trimeniaceae have also occasionally been placed in Laurales (e.g., Cronquist, 1981, 1988); in fact, both *Amborella* and *Trimenia* have even been considered part of Monimiaceae (Perkins, 1925). Chloranthaceae have also occasionally been placed in Laurales (e.g., Thorne, 1974; Takhtajan, 1987, 1997). Laurales are united by a perigynous flower in which the gynoecium is frequently deeply embedded in a fleshy receptacle (Endress and Igersheim, 1997; Renner, 1999). Other apparent synapomorphies include the presence of inner staminodia, ascendant ovules, and tracheidal endotesta (Doyle and Endress, 2000).

Piperales. Previous circumscriptions of Piperales have varied (e.g., Dahlgren, 1980; Cronquist, 1981, 1988; Takhtajan, 1987, 1997; Thorne, 1992; Heywood, 1993), but molecular studies clearly united Aristolochiaceae, Lactoridaceae, Piperaceae, and Saururaceae (e.g., Qiu et al., 1999; Soltis et al., 1999; Barkman et al., 2000; D. Soltis et al., 2000; Zanis et al., 2002). In addition, recent studies have placed Hydnoraceae, a family of parasitic plants often placed in Rosidae (e.g., Cronquist, 1981; Heywood, 1993), within Piperales, although the exact position is not certain (Nickrent et al., 2002). Although not recognized as a group prior to molecular analyses, a number of morphological synapomorphies have been identified: distichous phyllotaxis, a single prophyll, and oil cells (Doyle and Endress, 2000).

Canellales. The sister group of Canellaceae and Winteraceae has been strongly supported in all multigene analyses (e.g., Qiu et al., 1999; Soltis et al., 1999; D. Soltis et al., 2000; Zanis et al., 2002, 2003), and the clade was obtained in Doyle and Endress's (2000) nonmolecular analysis as well. However, these two families have not typically been considered closely related to each other, and neither was suspected of being related to any members of Piperales. For example, Winteraceae have often been considered a close relative of Magnoliaceae (e.g., Cronquist, 1981, 1988; Heywood, 1993), with Canellaceae close to Myristicaceae (e.g., Wilson, 1966; Cronquist, 1981, 1988). Furthermore, Winteraceae have often been regarded as perhaps the ''most primitive'' extant family of angiosperms (Cronquist, 1981; Endress, 1986). The phylogenetic position of Winteraceae clearly indicates that the vesselless xylem and plicate carpels found in members of the family are secondarily derived (see also Young, 1981). Possible synapomorphies for Canellales are a well-differentiated pollen tube transmitting tissue, an outer integument with only two to four cell layers, and seeds with a palisade exotesta (Doyle and Endress, 2000). Additional synapomorphies may include an irregular ''first-rank'' leaf venation (Hickey and Wolf, 1975; Doyle and Endress, 2000), stelar and nodal structure (Keating, 2000), and vascularization of the seeds (Deroin, 2000).

Eudicots—Eudicots comprise approximately 75% of all angiosperm species (Drinnan et al., 1994) and are strongly sup-

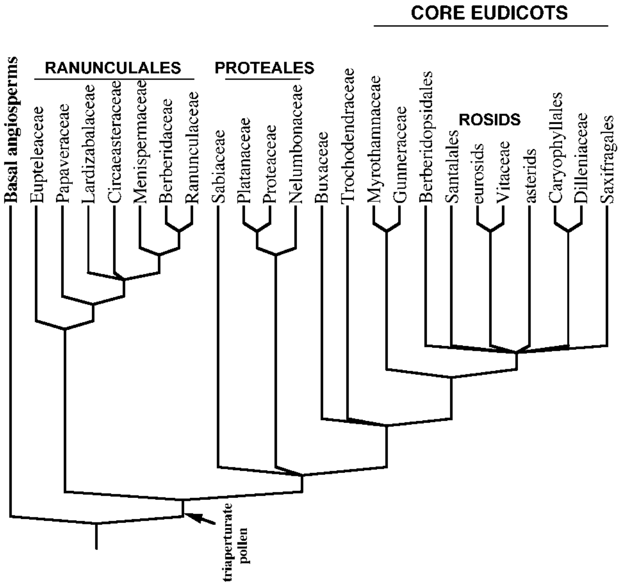

Fig. 3. Summary of phylogenetic relationships among clades of eudicots, based on Hoot et al. (1999), D. Soltis et al. (2000, 2003), and Kim et al. (2004).

ported by molecular data. However, only a single morphological synapomorphy—triaperturate pollen—has been identified. This pollen type is clearly distinct from the uniaperturate pollen of basal angiosperms, monocots, and all other seed plants, allowing easy assignment of fossil pollen to the eudicots. The fossil pollen record indicates that the eudicots appeared 125 mya, shortly after the origin of the angiosperms themselves. The extensive fossil pollen collections worldwide, coupled with solid dates, make it unlikely that the eudicots arose much before this time. Although triaperturate pollen is a synapomorphy for this clade, not all eudicots have triaperturate pollen due to subsequent changes in pollen structure. The eudicots (referred to instead as tricolpates) are covered in greater detail by Judd and Olmstead (2004).

Basal lineages—A basal grade of five lineages (Ranunculales, Proteales, Sabiaceae, Trochodendraceae, and Buxaceae) subtends the large clade of core eudicots (Hoot et al., 1999; D. Soltis et al., 2000; Kim et al., 2004; Fig. 3). Although Ranunculales are supported as the sister to all other eudicots, the relative placements of the remaining four lineages of basal eudicots are not clear and require additional study.

Core eudicots—The core eudicots comprise the vast majority of eudicot species. Seven major clades (Gunnerales, ‘‘Berberidopsidales,’’ Saxifragales, Santalales, Caryophyllales, rosids, and asterids) have been recognized, but the relationships among these clades are not clear (Figs. 1, 3; D. Soltis et al., 2000). The topology indicates a rapid radiation, but additional data are needed to evaluate this hypothesis. Recent studies have identified Gunnerales as the sister to all other core eudicots (Hilu et al., 2003; Soltis et al., 2003). Several important changes in floral genes appear to coincide with the origin of core eudicots, including duplication of *AP3* yielding the *euAP3* lineage (Kramer et al., 1998) and the origin of *Apetala1* (Litt and Irish, 2003).

Gunnerales. Gunnerales comprise two small families, Gunneraceae (*Gunnera* with approximately 40 species) and Myrothamnaceae (*Myrothamnus* with two species) (or Gunneraceae s.l. sensu APG II, 2003). This relationship had not previously been suggested on the basis of morphology because the two genera differ substantially, although molecular support for their relationship is very strong. Gunneraceae have a dimerous perianth (Drinnan et al., 1994), as do many of the basal eudicot lineages; dimery probably typifies Buxaceae, Trochodendraceae, and Proteaceae (but perhaps not the *Platanus* lineage) and is common and perhaps ancestral in Ranunculales (van Tieghem, 1897; Drinnan et al., 1994; Douglas and Tucker, 1996). The placement of Gunnerales as sister to the rest of the core eudicots implies that the pentamerous perianth typical of most core eudicots was derived from dimerous ancestors (Ronse De Craene et al., 2003; Soltis et al., 2003).

‘‘Berberidopsidales’’. Like Gunnerales, ‘‘Berberidopsidales’’ comprise two small and morphologically disparate families: Berberidopsidaceae (*Berberidopsis* and *Streptothamnus*, which is sometimes included in *Berberidopsis*) and Aextoxicaceae (*Aextoxicon*, one species). Although this clade has not been recognized at the ordinal level by APG (hence the quotation marks), it is strongly supported by molecular data and is isolated from all other clades. Furthermore, both families have encyclocytic stomata, a rare character and an apparent synapomorphy for this clade (Soltis et al., in press-b).

Saxifragales. Saxifragales are a morphologically eclectic clade of annual and perennial herbs, succulents, aquatics, shrubs, vines, and large trees. Prior to molecular phylogenetics (Morgan and Soltis, 1993; Fishbein et al., 2001), members of this clade were classified in three of Cronquist’s (1981) six subclasses of dicots (see also Takhtajan, 1997). Possible synapomorphies for this clade include a partially fused bicarpellate gynoecium, a hypanthium, and glandular leaf teeth (Judd et al., 2002); aspects of leaf venation and wood anatomy are similar in the woody members of the clade. The best known of the 13 families in this clade are Saxifragaceae, Crassulaceae, Grossulariaceae, Paeoniaceae, and Hamamelidaceae. Molecular studies continue to reveal new, unexpected members of this clade, such as Peridiscaceae (Davis and Chase, 2004), a family placed in Malpighiales in APG II (2003).

Monophyly of Saxifragales is strongly supported, but the position of this clade relative to other core eudicots remains uncertain. Some analyses have placed it as sister to the rosids, although with weak support (e.g., D. Soltis et al., 2000). The simple, pentamerous flowers have long been thought to indicate a relationship with Rosaceae and other rosids, but whether these floral features are synapomorphies for Saxifragales + rosids or symplesiomorphies (i.e., shared ancestral features) is unclear. Despite the fairly constant general floral structure of Saxifragales, certain aspects of floral evolution within this clade appear to be quite labile, especially ovary position (e.g., Kuzoff et al., 2001). Additional research is needed to resolve the relationship of Saxifragales within the core eudicots.

Santalales. The seven families of Santalales are united by molecular characters and aspects of their parasitic habit and are a strongly supported clade of core eudicots. However, relationships of Santalales to other core eudicots are not clear, although they occasionally appear near the asterids in at least some shortest trees. Furthermore, relationships within this clade have not yet been resolved, and the monophyly of some of the currently recognized families has not been supported by molecular evidence. The lack of resolution within Santalales may be explained in part by apparently rapid rates of molecular evolution in all three plant genomes (e.g., Nickrent and Starr, 1994; Nickrent et al., 1998). Aerial hemiparasites (mistletoes) have evolved multiple times in Santalales.

Caryophyllales. The core of Caryophyllales sensu APG II (2003) was considered a closely related group of families as long ago as the mid-nineteenth century (e.g., Braun, 1864; Eichler, 1876) and was formally recognized as the Centrospermae by Harms (1934) based on morphological and embryological characters. Recent molecular studies have identified a larger clade (Caryophyllales sensu APG II) that includes the Caryophyllidae of Cronquist (1981; i.e., Caryophyllales, Polygonales, and Plumbaginales) plus a number of families previously considered distantly related to Caryophyllales, including the carnivorous sundews and Venus' flytrap (Droseraceae) and Old World pitcher plants (Nepenthaceae).

Relationships of Caryophyllales to other core eudicots are not clear, although Dilleniaceae are sister to Caryophyllales in some analyses, although with low support (e.g., Chase and Albert, 1998; D. Soltis et al., 2000; Fig. 3), and some shortest trees have indicated a possible relationship with the asterids. Within Caryophyllales, there are two large clades, core and noncore Caryophyllales (Cuénoud et al., 2002), that correspond to Caryophyllales and Polygonales sensu Judd et al. (2002). The core Caryophyllales clade generally corresponds to Caryophyllales of recent classifications (e.g., Cronquist, 1981; Takhtajan, 1997) and comprises 19 families, although some currently recognized families (e.g., Portulacaceae, Phytolaccaceae) are poly- or paraphyletic and require recircumscription (Cuénoud et al., 2002). Synapomorphies for this clade include unilacunar nodes, stems with concentric rings of xylem and phloem, phloem sieve tubes with plastids with a peripheral ring of proteinaceous filaments and a central protein crystal, betalains (rather than anthocyanins), loss of the intron in the plastid gene *rpl2*, a single perianth whorl, free central to basal placentation, an embryo curved around the seed, and presence of perisperm with little or no endosperm (Judd et al., 2002 and references therein). The noncore clade has been identified on the basis of molecular data and comprises families classified in Cronquist's (1981) Rosidae and Dilleniidae. Most surprising is the inclusion in this clade of the carnivorous Droseraceae and Nepenthaceae. Synapomorphies for the noncore clade are scattered secretory cells containing plumbagin, an indumentum of stalked, gland-headed hairs, basal placentation, and starchy endosperm (Judd et al., 2002).

Many Caryophyllales are adapted to harsh environments, such as high-alkaline soils, high-salt conditions, extreme aridity, and nutrient-poor soils (see descriptions of component families in Heywood, 1993; Judd et al., 2002). Various adaptations, such as Crassulacean acid metabolism and C_4 photosynthesis, succulence, carnivory, and salt secretion, have evolved multiple times (e.g., Juniper et al., 1989; Meimberg et al., 2000; Pyankov et al., 2001; Cameron et al., 2002) and have allowed Caryophyllales to exploit these habitats.

Rosids. The rosid clade is broader than the traditional subclass Rosidae (Cronquist, 1981; Takhtajan, 1980, 1997), also encompassing many families formerly classified in the polyphyletic subclasses Magnoliidae, Dilleniidae, and Hamamelidae. The rosids comprise 140 families and close to one-third of all angiosperm species. Clear synapomorphies for the rosids have not been identified, although most rosids share several morphological and anatomical features, such as nuclear endosperm development, reticulate pollen exine, generally simple perforations of vessel end-walls, alternate intervessel pitting, mucilaginous leaf epidermis, and two or more whorls of stamens, plus ellagic acid (Hufford, 1992; Nandi et al., 1998).

Relationships within rosids are not clearly resolved. Vitaceae may be sister to the rosids, but this relationship is not strongly supported (Fig. 3; Savolainen et al., 2000a, b; D. Soltis et al., 2000), and Saxifragales may be sister to the Vitaceae + rosids clade, but this relationship is not strongly supported either (D. Soltis et al., 2000). Two large subclades of rosids, eurosids I (fabids) and II (malvids), have been identified through molecular analyses (e.g., Chase et al., 1993; Savolainen et al., 2000a, b; D. Soltis et al., 2000; Fig. 1). However, some orders and families (e.g., Crossosomatales, Geraniales, Myrtales) do not fit into either eurosid I or eurosid II. The eurosid I clade comprises Celastrales, Cucurbitales, Fabales, Fagales, Zygophyllales, Malpighiales, Oxalidales, and Rosales. Of these, Cucurbitales, Fabales, Fagales, and Rosales form the ''nitrogen-fixing clade,'' a clade that contains all angiosperms known to have symbiotic relationships with nodulating nitrogen-fixing bacteria (see D. Soltis et al., 1995, 1997, 2000). The placements in previous classifications of the species that exhibit this symbiosis indicated that symbiotic relationships with nodulating bacteria must have occurred multiple times. Current phylogenetic evidence instead indicates a single origin of the predisposition for symbiosis, with perhaps both gains and losses of the symbiotic relationship within the nitrogen-fixing clade itself (Soltis et al., 1995; Swensen, 1996). Multiple gains of this association may be more parsimonious than a single gain followed by multiple losses (Swensen, 1996). The smaller eurosid II clade is composed of Brassicales, Malvales, Sapindales, and Tapisciaceae. Brassicales include all angiosperms known to produce glucosinolates, a form of chemical defense, except *Drypetes* and *Putranjiva* of the distantly related rosid family Putranjivaceae of Malpighiales (e.g., Rodman, 1991; Rodman et al., 1993, 1998). Previous classifications led to the conclusion that glucosinolate production had evolved several times in the angiosperms; current phylogenetic evidence indicates instead only two such origins. In addition to the large eurosid I and II clades, additional smaller clades have been recognized (Crossosomatales, Myrtales, Geraniales, and Picramniaceae), but their relationships to each other and to eurosids I and II are not clear. Furthermore, relationships within eurosids I and II are not fully resolved, and much additional work is needed to reconstruct relationships within the rosid clade. In fact, the rosids represent the largest remaining problematic group of angiosperms.

Several factors may have contributed to the lack of resolution of relationships within the rosids. The clade is old, dating at least to the late Santonian to Turonian (approximately 84–89.5 mya; Crepet and Nixon, 1998; Magallón et al., 1999), and possibly to 94 mya, based on an unnamed apparently rosid flower from the Dakota Formation in Nebraska (Basinger and Dilcher, 1984). Furthermore, molecular-based age estimates of Myrtales using penalized likelihood (Sanderson, 2002) placed the crown radiation of Myrtales at approximately 110 mya (Sytsma et al., in press), implying an even older age for the rosids. The age of the rosid clade is therefore sufficient to have allowed substantial morphological and molecular diversification and speciation, although the similar age of the monocots has not similarly obscured relationships within that clade. The rosid clade may have diversified via a series of radiations (P. Soltis et al., 2004), resulting in a pattern of polytomies (see Remaining Problems and Future Prospects). Furthermore, subtle nonmolecular features that could potentially unite large groups of families within the rosids have not generally been identified because, until the results of molecular analyses, many families of rosids were not suspected of being closely related, having been placed in four subclasses of dicots (Magnoliidae, Hamamelidae, Dilleniidae, and Rosidae), and were therefore not included together in most previous analyses and treatments. Gaps in morphological data sets across the rosids have likewise made it difficult to identify synapomorphies for groups of families.

Asterids. Like rosids, asterids are a large clade, encompassing nearly one-third of all angiosperm species (80 000 species) and classified in 114 families (Albach et al., 2001b). However, unlike the rosids, a group of families corresponding closely to the asterids has been recognized on morphological grounds for over 200 years (de Jussieu, 1789; Reichenbach, 1828; Warming, 1879), and several morphological and chemical features appear to unite all or most asterids. Most notable are iridoid chemical compounds (e.g., Jensen, 1992), sympetalous corollas, unitegmic and tenuinucellate ovules, and cellular endosperm development; however, it is still unclear which of these features are actually synapomorphies for asterids (cf. Albach et al., 2001a; Judd et al., 2002). The asterid clade is broader than Asteridae of recent classifications (e.g., Cronquist, 1981; Takhtajan, 1980, 1997) and includes also members of the polyphyletic subclasses Hamamelidae, Dilleniidae, and Rosidae (Olmstead et al., 1992, 1993, 2000; Chase et al., 1993; D. Soltis et al., 1997, 2000; Soltis et al., 1999; Savolainen et al., 2000a, b).

Many relationships within asterids were resolved by angiosperm-wide analyses, but asterids have also been analyzed in greater detail with extensive taxon sampling and data from four (Albach et al., 2001b) and six (Bremer et al., 2002) loci. These studies confirmed earlier results of four major clades within asterids (Fig. 1): Cornales are sister to all other asterids, with Ericales sister to a clade of euasterids I + euasterids II. The families of Cornales and Ericales were not considered closely related to those of Asteridae in previous classifications and were placed instead mostly in Rosidae and Dilleniidae, respectively. Euasterids are mostly united by flowers with epipetalous stamens that equal the number of corolla lobes and a gynoecium of two fused carpels.

Within the euasterids, the euasterid I (or lamiid, Bremer et al., 2002) and euasterid II (or campanulid, Bremer et al., 2002) clades are sisters and can be distinguished both morphologically and molecularly (Albach et al., 2001b; Bremer et al., 2001; Bremer et al., 2002). Most members of euasterids I have opposite leaves, entire leaf margins, hypogynous flowers, ‘‘early sympetaly’’ with a ring-shaped primordium, fusion of stamen filaments to the corolla tube, and capsular fruits (Bremer et al., 2001). The euasterid I clade comprises Garryales, Gentianales, Solanales, and Lamiales, plus Boraginaceae, Vahliaceae, and Oncothecaceae + Icacinaceae (APG II, 2003). Most taxa of euasterids II have alternate leaves, serrate-dentate leaf margins, epigynous flowers, ‘‘late sympetaly’’ with distinct petal primordia, free stamen filaments, and indehiscent fruits (Bremer et al., 2001). It is unclear which of the characters that distinguish euasterids I and II are truly synapomorphies for these clades and which are symplesiomorphies; both reversals and parallelisms have contributed to complex patterns of morphological evolution in the asterids (Albach et al., 2001a; Bremer et al., 2001). The euasterid II clade is composed of Dipsacales, Aquifoliales, Apiales, and Asterales, plus Bruniaceae + Columelliaceae, a small clade of Tribelaceae, Polyosmaceae, Escalloniaceae, and Eremosynaceae, and possibly Paracryphiaceae. The euasterid II clade includes families previously classified in Asteridae and Rosidae (Cronquist, 1981, 1988).

The supertree approach—The relationships described in this paper are all based on analyses that use the ‘‘supermatrix’’ approach, that is, a taxon-by-character data matrix is assembled and analyzed, directly producing a tree or set of trees. A problem with this approach is that comprehensive data sets become extremely large, and analyses become increasingly computationally complex and time-consuming. In addition, different gene sets have not always sampled the same taxa, requiring assumptions of generic or familial monophyly in the formation of ‘‘mosaic’’ taxa and/or leading to large amounts of missing data. An alternative to the supermatrix approach is the supertree approach (e.g., Baum, 1992; Ragan, 1992; Purvis, 1995; Ronquist, 1996; Bininda-Emonds and Bryant, 1998; Sanderson et al., 1998), in which trees that overlap in at least a single taxon may be joined together algorithmically. Although less satisfying than the supermatrix approach in relating support or conflict for a topology to specific characters, the supertree approach is a viable alternative when multiple data sets overlap in only a small fraction of the taxa or when the number of taxa to be analyzed is very large. Furthermore, the two approaches seem to give similar results (e.g., Salamin et al., 2002).

The supertree approach has not been applied extensively to angiosperms, but it offers an opportunity for representation of greater numbers of taxa than the supermatrix analyses conducted to date. A recent supertree analysis combined trees that included all angiosperm families and produced the first comprehensive family-level phylogenetic tree for angiosperms (Davies et al., 2004). The basic framework of the angiosperm supertree is largely consistent with the results of large, multigene analyses of exemplar taxa (e.g., D. Soltis et al., 2000) on which it was based. *Amborella* is sister to all other angiosperms, followed by Nymphaeaceae, Austrabaileyales, a clade of monocots + Ceratophyllaceae, Chloranthaceae, and a clade of magnoliids + eudicots. Relationships within monocots, magnoliids, and eudicots are also mostly consistent with the results of the supermatrix analyses. This congruence indicates that the placement of those taxa not included in the supermatrix analyses may be correct, inasmuch as the data set can convey. Furthermore, some clades that have been difficult to place appear in resolved locations. For example, Caryophyllales are sister to the asterids, and Saxifragales are sister to the rosids, positions they occupy in some of the shortest trees obtained in other analyses but not in the strict consensus trees (e.g., D. Soltis et al., 2000). Although the best methods of supertree construction remain under debate, supertree approaches seem a viable alternative to supermatrix analyses as data sets continue to grow.

REMAINING PROBLEMS AND FUTURE PROSPECTS

Despite tremendous progress in angiosperm phylogenetics during the past 10 years, several difficult problems remain. Most prominent are (1) relationships among monocots, Chloranthaceae, magnoliids, and eudicots, (2) branching order among basal eudicots, (3) relationships among the major clades of core eudicots, (4) relationships within rosids, (5) relationships of the many lineages of parasitic plants (although this problem has been addressed recently by Barkman et al., 2004), and (6) integration of fossils with extant taxa into a comprehensive tree of angiosperm phylogeny. Solving these problems will require coordinated efforts among angiosperm systematists and paleobotanists and a large amount of molecular (and other, where appropriate) data.

At least some of those nodes that remain poorly resolved (e.g., basal eudicots, core eudicots, rosids) may be the results of rapid radiations (see P. Soltis et al., 2004). If so, increased sampling of molecular characters coupled with inclusion of additional taxa (if a clade has not yet been thoroughly sampled) may help to resolve at least some of the remaining polytomies. For example, the addition of 26S rDNA sequences to the three-gene data set of D. Soltis et al. (2000) for a subset of eudicots provided evidence for Gunnerales as the sister to the remaining lineages of core eudicots (D. Soltis et al., 2003), and increased character sampling for data sets of more than 100 taxa improved relationships among basal angiosperms (Zanis et al., 2002) and within monocots (e.g., Chase et al., in press). However, if the lack of resolution is due to a true radiation, it may not be possible to resolve these nodes. Likewise, if poor resolution has resulted from other factors, such as extinction, inadequate sampling of extant lineages, ancient reticulation, horizontal gene transfer, or unequal evolutionary rates among lineages, then the prospects for resolution, using currently available data and methods of analysis, are also poor.

Estimates of the age of the angiosperms and the timing of important divergences based on molecular data do not generally agree with each other (ranging from ~125 to >400 mya) or with dates determined from the fossil record (see e.g., Sanderson and Doyle, 2001; P. Soltis et al., 2002; Sanderson et al., 2004). Although most molecular-based ages for angiosperms, and other groups of organisms (e.g., Heckman et al., 2001), are much older than the fossil record suggests, many recent estimates based on methods that do not assume equal rates of evolutionary change among lineages are similar to, if slightly older than, dates inferred from the fossil record (Sanderson et al., 2004). Furthermore, estimated ages for specific angiosperm clades are generally older than inferences from the fossil record (e.g., Wikström et al., 2001, compared with Magallón et al., 1999), but these discrepancies are much smaller than those reported for the age of the angiosperms. However, room for further reconciliation of age estimates inferred from fossils and molecular data remains. For example, given the numerous diverse fossils reported from as early as 115–125 mya, perhaps the earliest angiosperms were older than the conservative estimate of ~130 mya. Conversely, molecular methods tend to overestimate ages (Rodríguez-Trelles et al., 2002), so refinement of dating approaches is needed to compensate for this bias.

Many of the large clades identified through analysis of molecular data are not easily recognized morphologically. Although possible synapomorphies for many clades have been proposed by Doyle and Endress (2000) and Judd et al. (2002), the identification of nonmolecular synapomorphies is still needed for many clades. This task will require new morphological and molecular data for many groups, including both a search for new characters and filling in data for many families. Finally, all of this new information—sequences, trees, morphological data—will need to be managed in such a way as to make it easily accessible to all who are interested via public databases. The development and maintenance of informatics tools and resources are therefore also major challenges that lie ahead for angiosperm systematics. Informatics issues may become particularly important as new methods are needed to analyze large amounts of sequence data for more taxa than have yet been analyzed together and to develop algorithms and methods for constructing supertrees to link new trees with those that have been archived.

The phylogenetic information currently available for angiosperms, and that to come, is fundamentally important for organizing all that is known about the angiosperm branch of the tree of life. However, this phylogenetic information is also a prerequisite for addressing basic questions in a number of other fields, ranging from genomics to ecology.

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