A survey of tricolpate (eudicot) phylogenetic relationships[1]

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The phylogenetic structure of the tricolpate clade (or eudicots) is presented through a survey of their major subclades, each of which is briefly characterized. The tricolpate clade was first recognized in 1989 and has received extensive phylogenetic study. Its major subclades, recognized at ordinal and familial ranks, are now apparent. Ordinal and many other suprafamilial clades are briefly diagnosed, i.e., the putative phenotypic synapomorphies for each major clade of tricolpates are listed, and the support for the monophyly of each clade is assessed, mainly through citation of the pertinent molecular phylogenetic literature. The classification of the Angiosperm Phylogeny Group (APG II) expresses the current state of our knowledge of phylogenetic relationships among tricolpates, and many of the major tricolpate clades can be diagnosed morphologically.

Key words: angiosperms; eudicots; tricolpates.

Angiosperms traditionally have been divided into two primary groups based on the presence of a single cotyledon (monocotyledons, monocots) or two cotyledons (dicotyledons, dicots). A series of additional diagnostic traits made this division useful and has accounted for the long recognition of these groups in flowering plant classifications. However phylogenetic analyses based on nuclear, plastid, and mitochondrial DNA sequences and morphology do not support this dichotomy (Donoghue and Doyle, 1989; Olmstead et al., 1992a; Chase et al., 1993; Doyle et al., 1994; Doyle, 1996, 1998; Mathews and Donoghue, 1999; Graham and Olmstead, 2000; Savolainen et al., 2000a; Soltis et al., 2000; Hilu et al., 2003; Zanis et al., 2003). In virtually all published cladistic analyses, the ''dicots'' form a paraphyletic complex and their diagnostic features are mainly plesiomorphic within angiosperms (see also Soltis and Soltis, 2004), although the monocots do constitute a clade (Chase, 2004).

Nonetheless, a large number of species previously considered ''dicots'' do constitute a well-supported clade: the tricolpates (Donoghue and Doyle, 1989) or eudicots (Doyle and Hotton, 1991). A synapomorphy of the tricolpate clade is pollen with three apertures (tricolpate/tricolporate pollen and derivatives thereof). The tricolpate clade is the largest group of angiosperms, containing perhaps 165 000 species in just over 300 families (ca. 64% of angiosperm diversity) and encompassing phenomenal variation in morphological, anatomical, and biochemical features. The clade also is characterized by cyclic flowers and the presence of differentiated outer and inner perianth members (i.e., a calyx and corolla) may be an additional, albeit homoplasious synapomorphy (Zanis et al., 2003). The staminal filaments are usually slender, bearing well-differentiated anthers, and most members have S-type plastids in their sieve elements. This clade was first recognized in the morphology-based phylogenetic analysis of Donoghue and Doyle (1989). Their monophyly was soon thereafter supported by numerous molecular analyses (Olmstead et al.,

1992a; Chase et al., 1993; Doyle et al., 1994; Soltis et al., 1997, 2000, 2003; Källersjö et al., 1998; Nandi et al., 1998; Hoot et al., 1999; Savolainen et al., 2000a, b; Hilu et al., 2003; Zanis et al., 2003; Kim et al., 2004). This clade was first called the ***tricolpates*** (Donoghue and Doyle, 1989), but the name ***eudicots*** (Doyle and Hotton, 1991) has gained wider usage. We prefer tricolpates because this name is both descriptive and avoids a connection with the nonmonophyletic assemblage ''Dicotyledoneae.'' Embryos having two (or more) cotyledons are not synapomorphic for this clade because they are also characteristic of Coniferales, Cycadales, Gnetales, and the basal grade of flowering plants from which monocots (which, as their name implies, share the synapomorphy of a single cotyledon) and tricolpates are derived.

During the past 15 years, our understanding of phylogenetic relationships within tricolpates has improved dramatically. This has been accomplished largely on the basis of phylogenetic analysis of molecular data, with many studies representing collaborations of several authors and combining several data sets (Chase et al., 1993; Chase and Cox, 1998; Soltis et al., 1998; Hilu et al., 2003). Thus, we now have an accurate outline (though incomplete in many details) of phylogenetic relationships within tricolpates (Fig. 1). The classifications of the Angiosperm Phylogeny Group (APG, 1998; APG II, 2003) have been based on these ongoing molecular analyses, leading to the recognition of a series of putatively monophyletic orders and families. Various secondary criteria, such as strength of support for monophyly, ease of recognition on the basis of phenotypic features, minimization of taxonomic redundancy, etc., also are used in ranking decisions (APG, 1998; Backlund and Bremer, 1998; Judd et al., 2002; APG II, 2003). The result is a classification that is phylogenetically accurate, to the extent we can presently determine, and that system is used with some slight modifications as the basis for the discussion of tricolpate diversity in this paper.

Despite tremendous advances in understanding phylogenetic pattern, there is a need for more studies addressing the relationships between morphological characters and phylogenetic hypotheses based on DNA sequences (Endress et al., 2000). Studies, such as those of Nandi et al. (1998), Doyle and Endress (2000), and Zanis et al. (2003) represent an effort, either through combined analysis or by the mapping of morpholog-
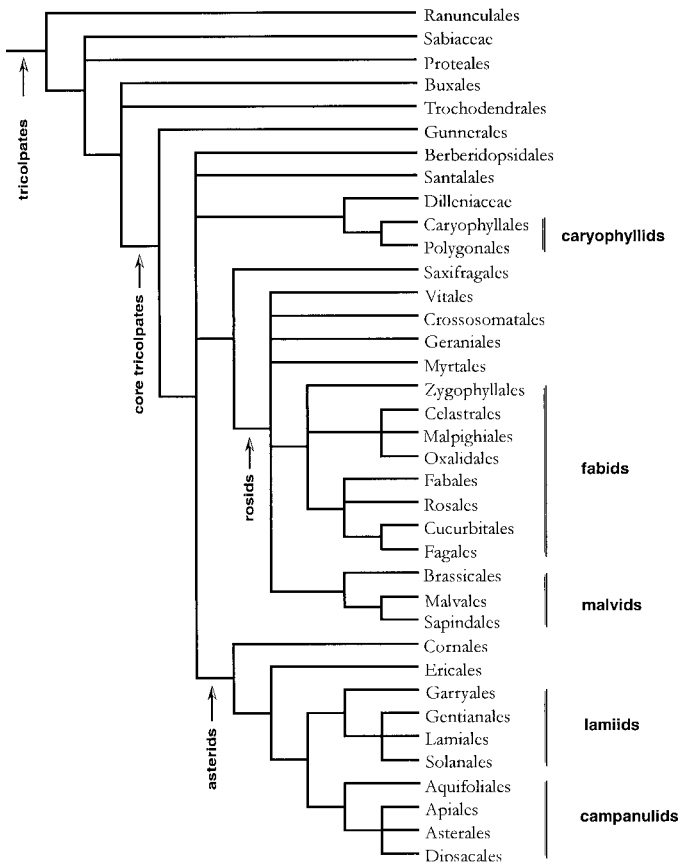
Fig. 1. Phylogenetic relationships of major groups of Tricolpates (Eudicots); modified from APG II (2003). The names lamiids (for euasterids I) and campanulids (for euasterids II) were suggested by Bremer et al. (2002). The names fabids (for eurosids I) and malvids (for eurosids II) are proposed here.

ical features on DNA-based topologies, towards integrating morphological and molecular characters. Without careful integration of morphological and molecular data, precise determination of the level of universality of particular morphological characters is often difficult, and this must be kept in mind in the following discussion of tricolpate diversity. At best, we hope to be able to identify diagnostic characters for many groups. Confirmation that these characters represent synapomorphies awaits further study in many cases. It is, of course, impossible to present the full diversity of tricolpates in a paper of this length, and readers are urged to consult APG II (2003) for a complete listing of the families comprising each of the orders discussed. Judd et al. (2002) and Stevens (2003) should also be consulted for more detailed information regarding morphological variation and phylogenetic relationships within most of these orders and families.

The overall evolutionary pattern seen in tricolpates is one of hierarchically nested clades, with those recognized as families or orders in the APG systems (1998, 2003) representing the "long branch" portions of the molecular-based phylogenetic trees, i.e., the well-supported clades that have been comparatively easy to "find" in DNA studies (Chase et al., 2000; Soltis et al., 2000). Most families, as circumscribed in APG II (2003), are also easily and accurately diagnosable on the basis of their morphological characters, and have a long history of taxonomic recognition. (There are some notable exceptions, e.g., Salicaceae s. l. and several families of Lamiales,

but by and large, the long-recognized families have been shown to be monophyletic, especially when obviously paraphyletic groups, such as the traditional Apocynaceae, Capparaceae, Caprifoliaceae, Ericaceae, Sapindaceae, and Tiliaceae/Sterculiaceae/Bombacaceae, are restructured.) It has been suggested that these familial clades are the result of the canalization of suites of traits within lineages over long periods of time (Chase et al., 2000; Soltis et al., 2000). The same pattern is evident among the clades recognized at ordinal rank, although fewer of these are morphologically diagnosable. Thus many of the ordinal groupings outlined here are of novel circumscription. Relationships among familial clades within these orders are frequently problematic because the branches are short and cannot be "found" even with several genes (see for example, Ericales, Malpighiales, Saxifragales, Lamiales, and others discussed later), indicating that diversification of major lineages within these ordinal clades occurred relatively rapidly. The ordinal synapomorphies likely have been obscured by subsequent radiations, which produced the clades now recognized as families, as a result of homoplasious morphological changes within a developmentally constrained pattern of morphological variation (Soltis et al., 2000).

The repeated pattern of longer branches to some clades, which, in turn, possess very short branches indicates that the history of tricolpates is characterized by periodic bursts of evolution, followed by a mosaic of lineage persistence and extinction, with subsequent additional periods of rapid evolutionary diversification (Chase et al., 2000; Davies et al., 2004). We think it likely that familial and ordinal clades showing numerous morphological synapomorphies have suffered more extinction of early divergent lineages than have those clades with fewer diagnostic features (see also discussion in Chase et al., 2000). It is unfortunate that we know so little regarding the potential phenotypic synapomorphies for many higher-level clades, which necessarily limits our ability to understand the reasons for these episodic evolutionary diversifications.

Currently, the major supraordinal clades within tricolpates (eudicots) for which we have relatively strong support are the core tricolpates, rosids (and within rosids, the fabids and malvids), and asterids (and within asterids, the lamiids and campanulids) (Fig. 1). The phylogenetic structure of these clades, as well as their ordinal subclades, is outlined here.

BASAL TRICOLPATE RELATIONSHIPS

A consensus on what constitute the major groups of tricolpates is emerging from among the numerous molecular phylogenetic studies of angiosperms cited earlier (Fig. 1). Apart from a few mostly minor clades, the vast majority of species form a large clade informally designated the "core tricolpates" (or "core eudicots"). Floral form and merosity in early-diverging tricolpate lineages is highly labile, whereas floral development in core tricolpates is more strongly canalized, and except for Gunnerales, these plants usually have pentamerous flowers with two differentiated perianth whorls (Endress, 1987; Drinnan et al., 1994; Soltis et al., 2003; Zanis et al., 2003).

Branching order at the base of the core tricolpates is poorly supported (Savolainen et al., 2000b; Soltis et al., 2000, 2003; Hilu et al., 2003; Kim et al., 2004), but three large groups emerge along with several smaller lineages. The three large groups, caryophyllids, rosids, and asterids, correspond to a

substantial degree with three of the major groups recognized at the rank of subclass in some late-20th century classifications (e.g., Cronquist 1981, 1988; Takhtajan, 1997), Caryophyllidae, Rosidae, and Asteridae. However, it should be noted that there are significant differences in circumscription between the informally named monophyletic groups recognized today and those subclasses as previously delimited (see also Soltis and Soltis, 2004). In addition, the two remaining dicot subclasses in the Cronquist/Takhtajan systems, Hamamelidae and Dilleniidae, leave only fractured remnants in the tricolpate phylogenetic tree, distributed among the early-branching lineages at the base of the tricolpates as well as the three large clades in the core tricolpates.

Ranunculales are well supported as sister to the remaining tricolpates, with Proteales and Sabiaceae the subsequent sisters to other tricolpates, although the branching order is unclear, and in some analyses Proteales and Sabiaceae instead form a clade sister to other tricolpates (Nandi et al., 1998; Hoot et al., 1999; Doyle and Endress, 2000; Savolainen et al., 2000b; Soltis et al., 2000, 2003; Hilu et al., 2003; Zanis et al., 2003; Kim et al., 2004). Monophyly of Ranunculales is supported by DNA sequence studies (Chase et al., 1993; Drinnan et al., 1994; Hoot and Crane, 1995; Soltis et al., 1997, 1998, 2000; Källersjö et al., 1998; Hoot et al., 1999; Savolainen et al., 2000a, b; Hilu et al., 2003) and morphology (Loconte et al., 1995), and synapomorphies may include presence of the alkaloid berberine and reduced fiber-pit borders. Ranunculales previously have been associated with woody magnoliids (e.g., Cronquist, 1981) because their flowers have free parts that are sometimes spirally arranged. Cronquist (1981) suggested that the connection to the woody magnoliids was via Illiciaceae (ANITA grade; Qiu et al., 1999) due to the presence of triaperturate pollen in both groups. Illiciaceae and the related Schisandraceae are now recognized as the sole exception to the exclusive presence of triaperturate pollen in the tricolpates and are not closely related to them.

Some analyses have recovered Papaveraceae (including Fumariaceae) sister to the remaining families of Ranunculales (Hoot and Crane, 1995; Hoot et al., 1999; Soltis et al., 2000), whereas others (Hilu et al., 2003; Kim et al., 2004) support Eupteleaceae (trees with reduced, wind-pollinated flowers) as sister to the rest, with Papaveraceae the next family to diverge. Ranunculaceae apparently are sister to Berberidaceae, although no morphological synapomorphy is evident (Hoot and Crane, 1995; Kim and Jansen, 1995; Hoot et al., 1999; Kim et al., 2004). In contrast to most Ranunculaceae, Berberidaceae have only a single carpel. Menispermaceae, a group of vines or lianas with imperfect flowers and drupaceous fruits, are probably sister to the Berberidaceae + Ranunculaceae clade. Lardizabalaceae, which apparently evolved the climbing habit independently, are sister to that more inclusive clade.

Proteales, with Nelumbonaceae sister to Proteaceae + Platanaceae, represent a novel grouping that had not been associated prior to the acquisition of molecular data (Olmstead et al., 1992a; Chase et al., 1993; Hoot et al., 1999; Soltis et al., 2000; Hilu et al., 2003), but gynoecia with one or two pendent ovules per carpel are putatively synapomorphic for these plants. Synonymy of Platanaceae under Proteaceae is recommended in APG II, because extant Platanaceae are monogeneric and, thus, their inclusion in an expanded Proteaceae would reduce taxonomic redundancy. However, other genera of Platanaceae are known as fossils and even the extant species of *Platanus* belong to two morphologically distinct subgenera.

Thus, the characterization of Platanaceae as "monogeneric" is misleading about their past diversity. In addition, an expanded Proteaceae would be difficult to diagnose morphologically.

Proteales, Sabiaceae, Buxaceae, Didymelaceae, and Trochodendraceae (*Trochodendron* and *Tetracentron*) form a grade (Soltis et al., 2000, 2003; Hilu et al., 2003; Kim et al., 2004) sister to the core tricolpates. Trochodendraceae are united by their distinctive flattened seeds and laterally connate carpels that are nectiferous and protrude abaxially forming follicle-like fruits. Buxaceae and Didymelaceae (now both optionally included in Buxaceae in APG II, but treated here together as Buxales) are united by encyclocytic stomata and racemose inflorescences of small, imperfect flowers with a biseriate perianth of tepals. Their stigmas are decurrent, extending the entire length of the style. Recent evidence indicates that Buxaceae + Didymelaceae may be sister to core tricolpates (Hilu et al., 2003).

CORE TRICOLPATES

Gunnerales are well supported as sister to all other core tricolpates (Hilu et al., 2003; Soltis et al., 2003). Gunnerales are dioecious, have reduced, two-merous flowers, and have either bisporic or tetrasporic megagametophyte development. In contrast, the remaining core tricolpates, consisting of Berberidopsidales, Santalales, Dilleniaceae, caryophyllids, Saxifragales, rosids, and asterids, usually have pentamerous (or less commonly, tetramerous) flowers, and predominantly show the *Polygonum*-type megagametophyte development.

It is noteworthy that phylogenetic analyses of angiosperm MADS-box genes show two gene clades within the core tricolpates, i.e., eu*AP1* (including *Arabidopsis APETALA1* and *Antirrhinum SQUAMOSA*) and eu*FUL* (including *Arabidopsis FRUITFULL*), whereas non-core tricolpate clades have only sequences similar to eu*FUL* genes (Litt and Irish, 2003). This indicates that a duplication event occurred in these floral genes in the common ancestor of the core tricolpates. The eu*AP1* gene clade includes key regulators of floral development, which have been implicated in the specification of perianth identity. The presence of eu*AP1* genes only in core tricolpates indicates that there may have been changes in developmental mechanisms that are correlated with the fixation of floral structures seen in this clade (Litt and Irish, 2003). In addition, the core tricolpates have evolved a divergent *APETALATA3* C-terminal domain, which is correlated with the acquisition of a role in specifying perianth structures (Lamb and Irish, 2003).

Relationships among the core tricolpate clades are still unclear (Hoot et al., 1999; Savolainen et al., 2000b; Soltis et al., 2000, 2003; Hilu et al., 2003; Kim et al., 2004), as illustrated in the uncertainties regarding the phylogenetic position of the small Southern Hemisphere clade, Berberidopsidales.

Berberidopsidales (Fig. 1), comprising Aextoxicaceae and Berberidopsidaceae, are a well-supported clade (Soltis et al., 2000, 2003; Kim et al., 2004); they were not recognized by APG II (2003) because their relationships are still unclear. These two families are distinctive: Aextoxicaceae are dioecious and have opposite leaves that, along with the ovary, are covered with peltate scales; Berberidopsidaceae have bisexual flowers, a scrambling habit with alternate, often spinose-serrate leaves, and flowers with parietal placentation. They share the possible apomorphies of stout filaments and presence of a ring of vascular bundles in the petiole. The order may be sister to the rosids plus Saxifragales and Vitales (Soltis et al., 2000),

caryophyllids (Savolainen et al., 2000b), asterids plus Santalales (Soltis et al., 2003; Kim et al., 2004), asterids plus caryophyllids and Santalales (Hilu et al., 2003), or just asterids (Kim et al., 2004).

Dilleniaceae, another isolated clade, may be the sister group of the caryophyllids (Soltis et al., 2000, 2003; APG II, 2003) or Vitales (Hilu et al., 2003). They are distinctive in that their often showy, pentamerous flowers have the petals crumpled in the bud, numerous stamens (a secondary increase), and separate carpels. Like many caryophyllids, the sepals are persistent, and often accrescent. Santalales are another clade of uncertain position. Placements indicated by molecular studies include sister to caryophyllids (Soltis et al., 2000) or caryophyllids plus asterids (Hilu et al., 2003). Monophyly of Santalales is based on molecular studies (Nickrent and Soltis, 1995; Källersjö et al., 1998; Savolainen et al., 2000b; Soltis et al., 2000, 2003; Hilu et al., 2003) and the presence of polyacetylenes, roots lacking root hairs, one-seeded, indehiscent fruits, and seeds with the coat reduced/crushed. The parasitic habit (with conventional roots replaced by developmentally complex haustoria, which connect the parasite to the host) is present in most, and it certainly evolved early in the history of the clade, but is nonetheless derived. Santalales also lack mycorrhizal associations, and the stamens are typically opposite the petals. Delimitations of families within this clade are problematic, with both "Olacaceae" and "Santalaceae," as previously circumscribed, being paraphyletic: the rest of the order is embedded in "Olacaceae," whereas Viscaceae are part of the "Santalaceae." For this reason, Viscaceae, despite their phenetic distinctiveness (e.g., twig epiphytism), are sometimes placed within an expanded Santalaceae (APG II, 2003; but compare with Nickrent, 2003).

Caryophyllids are treated as Caryophyllales by APG II (2003), whereas this clade is divided into two orders, i.e., Caryophyllales and Polygonales, in Judd et al. (2002). The monophyly of caryophyllids is supported by molecular data (Soltis et al., 2000, 2003; Hilu et al., 2003) and possibly by anther wall development and simple, nonbordered perforation plates (but the latter may be a synapomorphy of a more inclusive group including Santalales). There are also similarities in the type of sieve-element plastids (Behnke, 1999). The lack of clear morphological support for this clade leads us to prefer its division into two orders: Caryophyllales sensu stricto and Polygonales (see also Hilu et al., 2003).

Caryophyllales s. s. largely correspond to previous circumscriptions of this order (Cronquist, 1981; Takhtajan, 1997; Thorne, 2001), with the small families Simmondsiaceae, and Asteropeiaceae plus Physenaceae, as successive sister groups of the core members. The monophyly of Caryophyllales s. s. is moderately to strongly supported on the basis of DNA sequences (Soltis et al., 2000, 2003; Cuénoud et al., 2002; Hilu et al., 2003) as well as morphology. Successive cambia and unilacunar nodes are synapomorphic for the order, with core Caryophyllales (i.e., all families except Simmondsiaceae, Asteropeiaceae, and Physenaceae) diagnosed by numerous additional derived characters, including P-type plastids with a ring of proteinaceous filaments and a central angular crystal, betalains, a single whorl of tepals, free-central/basal placentation, pollen with spinulose and tubuliferous/punctate ektexine, and seeds with perisperm and curved embryo (Mabry, 1973; Behnke, 1976, 1994; Eckardt, 1976; Cronquist, 1981; Rodman et al., 1984; Rodman, 1990, 1994; Bittrich, 1993). These families also typically have separate styles or well-developed style branches. Within core Caryophyllales, phylogenetic relationships and family circumscriptions are not clear and circumscriptions of some commonly recognized families have been altered (Judd et al., 2002; APG II, 2003; Stevens, 2003). Amaranthaceae now include Chenopodiaceae; both share the loss of the central protein crystal in their sieve element plastids. Phytolaccaceae, as traditionally circumscribed, may not be monophyletic, but are likely closely related to Sarcobataceae and Nyctaginaceae, a group characterized by raphides. Portulacaceae (Judd et al., 2002) are blatantly paraphyletic, having given rise to Cactaceae, Didiereaceae, and possibly Basellaceae. Portulacaceae, Cactaceae, and Didiereaceae are nearly all succulents with crassulacean acid metabolism (CAM) metabolism. The monophyly of Cactaceae is supported by numerous characters, including their conspicuous differentiated shoots, with the leaves of the short shoots forming spines (Judd et al., 2002). Betalains apparently have been lost (and anthocyanins re-acquired) more than once in the order, because Caryophyllaceae and Molluginaceae, which have anthocyanins, are not closely related (Soltis et al., 2000).

Polygonales are here defined broadly, including Plumbaginaceae, Polygonaceae, Droseraceae, Nepenthaceae, and relatives. The monophyly of the order is supported by the putative apomorphies of plumbagin (a naphthoquinone) and related compounds, vascularized glandular hairs, starchy endosperm, and possibly basal placentation (Williams et al., 1994; Soltis et al., 2000, 2003; Hilu et al., 2003). These families comprise two major subclades. The first includes Polygonaceae, Plumbaginaceae, Tamaricaceae, and Frankeniaceae and is supported by sulphinated flavonols and vessels with minute lateral wall pits. The second includes Droseraceae, Nepenthaceae, Drosophyllaceae, Dioncophyllaceae, and Ancistrocladaceae and is supported by carnivorous habit, coiled leaves, and corolla contorted in bud (Meimberg et al., 2000; Soltis et al., 2000, 2003; Cuénoud et al., 2002; Hilu et al., 2003). The carnivorous habit evidently has been lost in Ancistrocladaceae and two of the three genera of Dioncophyllaceae, to which the former is clearly sister, and the two share the lianous habit, sclerenchyma bundles in their petioles, actinocyclic stomata, and the loss of cortical vascular bundles in the stems.

The remaining species of core tricolpates belong to the rosid clade, asterid clade, or Saxifragales (Fig. 1). Saxifragales are possibly sister to the rosids (Soltis et al., 2000; Savolainen et al., 2000a); however, Saxifragales were found to be sister to the caryophyllids based on the data set of Soltis et al. (2003) and Kim et al. (2004) or in a polytomy with rosids, Vitales, Dilleniaceae, Berberidopsidales, Santalales, caryophyllids, and asterids by Hilu et al. (2003). Saxifragales are a grouping not appreciated until the advent of recent molecular phylogenetic analyses (Chase et al., 1993; Morgan and Soltis, 1993; Soltis and Soltis, 1997; Soltis et al., 1997, 2000, 2003; Hoot et al., 1999; Savolainen et al., 2000b; Hilu et al., 2003; Davis and Chase, 2004). The group is morphologically heterogeneous, and its members were placed by Cronquist (1981) into three different subclasses. Lack of resolution within the order makes determination of morphological synapomorphies especially difficult, but the group is characterized by having the floral apex concave early in development (Soltis and Hufford, 2002; Fishbein et al., in press) and carpels that are free, at least apically (Stevens, 2003). Paeoniaceae, Peridiscaceae, Hamamelidaceae, Altingiaceae, and Cercidophyllaceae are isolated and of unclear relationships to the other families of the order. Saxifragaceae, themselves, may be most closely related to

Grossulariaceae, Iteaceae, and Pterostemonaceae (Fishbein et al., 2001), all of which have been included in Saxifragaceae s. l. in the past. These plants all have flowers with variously developed hypanthia, although a hypanthium may have evolved independently in a few other members of the order. A second clear clade within this order includes Crassulaceae (succulents) and the small families Haloragaceae, Penthoraceae, Tetracarpaeaceae, and Aphanopetalaceae (Fishbein et al., 2001). Members of this clade lack stipules and have unilacunar nodes. Penthoraceae, Tetracarpaeaceae, and Aphanopetalaceae are each monogeneric, and in APG II (2003) are optionally included in Haloragaceae, but such a broadly defined Haloragaceae are not now known to be morphologically diagnosable.

ROSIDS

Rosids comprise a heterogeneous grouping of orders supported by DNA-based phylogenetic analyses (Soltis et al., 2000, 2003; Hilu et al., 2003). Most members of this group belong to one of two major subclades (Fig. 1), which are called fabids (Zygophyllales, Celastrales, Malpighiales, Oxalidales, Fabales, Rosales, Cucurbitales, and Fagales) and malvids (Brassicales, Malvales, and Sapindales; Fig. 1). These names were first suggested by J. Reveal at too late a date to be included in APG II to replace eurosids I and eurosids II, respectively. The position of Vitaceae (including *Leea*, sometimes placed in a separate family, Leeaceae) is unclear. The family is possibly sister to the rest of the rosids (Soltis et al., 2000; Kim et al., 2004), but may belong elsewhere nearby in the poorly resolved nexus at the base of the core tricolpates (e.g., Soltis et al., 2003; Hilu et al., 2003). Thus placement of Vitaceae in the rosids in APG II (2003) may not hold up. Other groups belonging to rosids, but not placed in the two large clades fabids and malvids, include several small families (Aphloiaceae, Geissolomataceae, Ixerbaceae, Picramniaceae, Strasburgeriaceae) and Crossosomatales, Geraniales, and Myrtales.

Crossosomatales, as defined in APG II (2003), contain Crossosomataceae, Stachyuraceae, and Staphyleaceae, and are characterized by a distinctive seed coat, in which the cell walls of the many-layered testa are more or less all lignified. The order possibly could be expanded to include Geossolomataceae, Ixerbaceae, and Strasburgeriaceae, which have a similar testa anatomy (APG II, 2003; Stevens, 2003). Geraniales include Geraniaceae and a few small families (APG II, 2003) having leaf margins with glandular teeth, vessels with simple perforations, obdiplostemonous flowers with a persistent calyx, and nectaries positioned on the outside of the androecium (Stevens, 2003). All of the families of Geraniales sensu Cronquist (1981), except Geraniaceae, are placed elsewhere in APG II (2003).

Myrtales were placed in malvids (eurosids II) in APG (1998), but they were left unplaced within the rosids in APG II (2003). Myrtales, along with Geraniales, are weakly associated with malvids in some studies (e.g., Savolainen et al., 2000b; Soltis et al., 2003; Hilu et al., 2003), or with fabids in others (e.g., Soltis et al., 2000). Monophyly of Myrtales is indicated by their vessel elements with vestured pits, stems with internal phloem, stipules absent or present only as small lateral or axillary structures, flowers with a short to elongate hypanthium, stamens incurved in bud, and a single style (the carpels being nearly completely connate) and receives strong

molecular support (Conti et al., 1996, 1997; Savolainen et al., 2000b; Soltis et al., 2000). Vochysiaceae are sister to Myrtaceae, a family characterized by pellucid dots (with aromatic terpenoids). Lythraceae and Onagraceae are sister, sharing a valvate calyx and grouped vessels in the wood, and Combretaceae are sister to them (Johnson and Briggs, 1984; Conti et al., 1996, 1997; Savolainen et al., 2000b; Soltis et al., 2000, 2003). Melastomataceae are sister to Memecylaceae (Clausing and Renner, 2001), and both have unusual anthers: those of Melastomataceae usually opening by pores and often bearing various appendages and those of Memecylaceae with a resin-secreting gland on the connective. The small families Rhynchocalycaceae, Oliniaceae, Penaeaceae, Alzateaceae, and Crypteroniaceae constitute a clade (Conti et al., 1999), the members of which have square stems with more or less swollen nodes, stamens equal in number to and opposite the petals, exotestal cells periclinally elongated, and a nonfibrous endotegmen. Stevens (2003) has suggested that these could be combined.

Fabids (eurosids I)—The APG II (2003) circumscription of fabids includes seven orders (Celastrales, Cucurbitales, Fabales, Fagales, Malpighiales, Oxalidales, and Rosales) and two families unassigned to the order. The fabids were first recognized as "rosids I" by Chase et al. (1993), but with Myrtales and part of Geraniales included, and later renamed "eurosids I" with the present circumscription (APG, 1998; APG II, 2003). One of the unassigned families is Zygophyllaceae, including the hemiparasitic *Krameria*. These are sister groups and may be retained as separate families, together forming Zygophyllales (Soltis et al., 2000). It does not seem desirable to treat *Krameria* within an expanded Zygophyllaceae, because the expanded family would have no clear morphological apomorphies. Huaceae are the other unassigned family; they are placed consistently near Celastrales (Savolainen et al., 2000b; Soltis et al., 2000), but with weak support. Celastrales, Malpighiales, and Oxalidales may form a clade, as do Fabales, Cucurbitales, Rosales, and Fagales (Soltis et al., 1995; APG II, 2003; Hilu et al., 2003). It is noteworthy that the latter clade has some members of each order having nitrogen-fixing nodules on their roots (APG II, 2003).

Celastrales, as defined on the basis of molecular data (APG II, 2003), now comprise Celastraceae, Lepidobotryaceae, and Parnassiaeae (optionally including *Lepuropetalon*; Savolainen et al., 2000a; Soltis et al., 2000). Like Zygophyllales, the group is difficult to characterize morphologically. Oxalidales, including Brunelliaceae, Cephalotaceae, Connaraceae, Cunoniaceae, Elaeocarpaceae, and Oxalidaceae, are another order that has a novel circumscription based on recent phylogenetic analyses and are difficult to diagnose. Stevens (2003) noted that these plants have epitropous ovules with a multiplicative outer integument and seeds with a fibrous/tracheidal exotegmen and a crystalliferous and palisade endotesta.

The grouping of ca. 37 families currently recognized as Malpighiales (APG II, 2003) was not apparent prior to DNA-based phylogenetic analyses (Chase et al., 1993, 2002; Savolainen et al., 2000b; Soltis et al., 2000; Hilu et al., 2003), although members of the clade often have toothed leaves, with the teeth having a single vein running into a congested and often deciduous apex (i.e., teeth violoid, salicoid, or theoid; see Hickey and Wolfe, 1975; Judd et al., 2002). Relationships within this large clade are poorly resolved. However, several small monophyletic groups of families can be inferred. Pas-

sifloraceae, Malesherbiaceae, Turneraceae (optionally a single family, Passifloraceae, in APG II, 2003), and possibly also Achariaceae, form a clade supported by the presence of cyclopentenoid cyanogenic glucosides (or cyclopentenyl fatty acids), with the first three likely to be linked by the apomorphies of a hypanthium that does not involve the androecium, and a corona, the latter especially well developed in Passifloraceae. Turneraceae and Malesherbiaceae have similar reticulate seeds. Rhizophoraceae and Erythroxylaceae share tropane and pyrrolidin alkaloids, terminal buds protected by stipules, colleters, and green embryos and were optionally considered one family, Rhizophoraceae, in APG II (2003). Clusiaceae s. l. (Guttiferae; probably including Bonnetiaceae and Hypericaceae, although these are maintained in APG II, 2003) and the distinctive aquatic Podostemaceae share secretory canals and xanthone pigments. Podostemaceae may be nested within Clusiaceae s. l. (Gustafsson et al., 2002; Chase et al., 2002). Ochnaceae, Medusagynaceae, and Quiinaceae have vestured pits, tenuinucellate ovules, and lack floral nectaries; medullary bundles occur in both Ochnaceae and Medusagynaceae. These three families were optionally also proposed by APG II as the single family Ochnaceae. Malpighiaceae are sister to Elatinaceae, and both have glandular hairs on their opposite or whorled leaves and a base chromosome number of six (Davis and Chase, 2004). Finally, Chrysobalanaceae, Euphroniaceae, Dichapetalaceae, Trigoniaceae, and Balanopaceae form a strongly supported clade (Soltis et al., 2000). These plants have only two ovules per carpel and, except for Balanopaceae, which is sister to the rest, vestured pits, paracytic stomata, usually zygomorphic flowers, and tenuinucellate ovules (Stevens, 2003). All of these relationships receive molecular support (Litt and Chase, 1999; Savolainen et al., 2000a; Soltis et al., 2000; Chase et al., 2002; Davis and Chase, 2004). These same analyses indicate that Flacourtiaceae and Euphorbiaceae, as previously circumscribed, are not monophyletic. The cyanogenic members of "Flacourtiaceae" are now treated as Achariaceae. A major change, especially for temperate-zone botanists, is the transfer of the non-cyanogenic taxa (i.e., those with salicoid teeth) to Salicaceae (Judd, 1997; Chase et al., 2002; Boucher et al., 2003), thus dramatically expanding this otherwise homogeneous family. Salicoid teeth have a single vein entering the tooth, expanding at the apex, which is associated with a spherical, glandular structure (Nandi et al., 1998; Judd et al., 2002).

The subfamilies of Euphorbiaceae s. l. with two ovules per locule have been segregated (Savolainen et al., 2000a; Chase et al., 2002) as Picrodendraceae (spiny pollen), Phyllanthaceae (divided styles, schizocarps, often with dimorphic branches), and Putranjivaceae (mustard oils). This has resulted in a monophyletic and more homogeneous Euphorbiaceae s. s. (APG II, 2003; see also Judd et al., 2002; Stevens, 2003) having gynoecia with only one ovule per locule and, except for Acalyphoideae, laticifers with colored or milky latex. Imperfect flowers, divided styles, and trilobed, schizocarpic fruits apparently evolved independently in Euphorbiaceae and Phyllanthaceae or were lost in the putatively related families (which at present are not clear).

The core of Cucurbitales (Cucurbitaceae, Tetramelaceae, Datiscaceae, and Begoniaceae) represent a close-knit group recognized in previous classifications (e.g., Cronquist, 1981) and share similarities of stems with separate vascular bundles, cucurbitacins (oxidized triterpenes), palmate leaves with more or less cucurbitoid teeth, and imperfect flowers with an inferior ovary and often intruded parietal placentation (Judd et al., 2002; Stevens, 2003). In both Cucurbitaceae and Begoniaceae, the androecium and gynoecium converge in appearance, the yellow, twisted stigmas of Begoniaceae resembling the stamens and the contorted and usually connate anthers of Cucurbitaceae likely mimicking the stigma (Judd et al., 2002). Recent molecular studies (Savolainen et al., 2000a; Soltis et al., 2000; Hilu et al., 2003) have reinforced the monophyly of this group and inclusion in Cucurbitales (APG II, 2003) of Anisophylleaceae, Coriariaceae, and Corynocarpaceae.

Quillajaceae, Surianaceae, Polygalaceae, and Fabaceae comprise Fabales, another order that was not recognized until the advent of molecular data (Chase et al., 1993; Savolainen et al., 2000b; Soltis et al., 2000; Kajita et al., 2001). Morphological synapomorphies are unclear, but these plants have green embryos. Some also have fluorescing wood. Phylogenetic relationships within this order are still unclear. The zygomorphic flowers of Polygalaceae are superficially like those of Fabaceae subfamily Faboideae, but in detail they are different (Judd et al., 2002). Fabaceae (or Leguminosae) are monophyletic (Chappill, 1994; Doyle, 1994; Doyle et al., 1997; Kajita et al., 2001) and nitrogen fixation occurs in most species, but is lacking in many early-diverging lineages; it is homoplasious, and not synapomorphic for the family. Three subgroups are usually recognized within Fabaceae: "Caesalpinioideae," Mimosoideae, and Faboideae (= Papilionoideae). In most classifications (e.g., Pohill et al., 1981), these are considered subfamilies. Phylogenetic analyses of both morphological (Chappill, 1994; Tucker and Douglas, 1994) and molecular data (Doyle, 1987; Doyle et al., 1997; Bruneau et al., 2001; Kajita et al., 2001; Doyle and Luckow, 2003) have indicated that "Caesalpinioideae" are paraphyletic; *Cercis* and its immediate relatives, including *Bauhinia*, probably are sister to the rest of the family.

Fagales represent the core of the "Englerian" Amentiferae (Stern, 1973; Hamamelidae of Cronquist, 1981) and are monophyletic and easily recognized (Chase et al., 1993; Manos et al., 1993; Källersjö et al., 1998; Savolainen et al., 2000b; Soltis et al., 2000; Hilu et al., 2003). Their flowers are unisexual, typically in spikes or catkins, have a reduced or missing perianth and inferior ovaries, and the plants have gland-headed and/or stellate hairs (Hufford, 1992; Judd et al., 2002). *Nothofagus* (Nothofagaceae) is distinct from Fagaceae and sister to the remaining families of Fagales, with Fagaceae sister to the rest (Manos et al., 1993; Manos and Steele, 1997; Hilu et al., 2003). The remaining families (Betulaceae, Casuarinaceae, Juglandaceae, Myricaceae, Rhoipteleaceae, and Ticodendraceae) are united by their triporoporate pollen and represent the extant members of the fossil Normapolles complex (Kedves, 1989). Juglandaceae and Rhoipteleaceae (the latter an optional synonym of the former; APG II, 2003) are sisters, forming a clade diagnosed by pinnately compound leaves; these two, along with Myricaceae, may form a clade on the basis of their aromatic glandular hairs and gynoecia with a single orthotropous ovule (Savolainen et al., 2000a; Judd et al., 2002). Betulaceae are sister to Ticodendraceae, and both have two-ranked leaves and clusters of sclerids in the bark; this clade is then sister to Casuarinaceae (Manos and Steele, 1997; Savolainen et al., 2000a; Soltis et al., 2000), which share pollen grains with the exine having tiny spines in rows. The cupules of *Nothofagus* are unlikely to be homologous with those of Fagaceae, and doubly serrate leaves and horizontal lenticels

apparently have evolved independently in Nothofagaceae and Betulaceae.

Monophyly of Rosales has received strong support from analyses of DNA sequences (Chase et al., 1993; Källersjö et al., 1998; Savolainen et al., 2000b; Soltis et al., 2000; Sytsma et al., 2002; Hilu et al., 2003). The circumscription of this order in APG II (2003) is divergent from that of Cronquist (1981, 1988) and other evolutionary-taxonomic classifications, which used the order as something of a taxonomic dumping ground for taxa with plesiomorphic pentamerous flowers. Cronquist (1981) stated that the order was exceedingly diverse and included ''what is left over after all the more advanced, specialized orders [of Rosidae] have been delimited.'' He included in Rosales, for example, Connaraceae, Cephalotaceae, and Cunoniaceae (here in Oxalidales), Dialypetalanthaceae (embedded in Rubiaceae of Gentianales; Fay et al., 2000), Pittosporaceae (Apiales), Byblidaceae sensu lato (divided and placed in Ericales and Lamiales), Hydrangeaceae (Cornales), Columelliaceae (campanulids), Neuradaceae (Malvales), Chrysobalanaceae (Malpighiales), Crossosomataceae (Crossosomatales), Grossulariaceae (as narrowly delimited, in Saxifragales, but as considered by Cronquist, with genera now placed in several other families and orders), Crassulaceae and Saxifragaceae (Saxifragales), Surianaceae (Fabales), and Rhabdodendraceae (caryophyllids)! Rosales, as here delimited, include only one family in common with Cronquist's Rosales—Rosaceae! As currently delimited (APG II, 2003), the order also includes Rhamnaceae, Elaeagnaceae, Dirachmaceae, and Barbeyaceae, and also the former families of Urticales (Ulmaceae, Cannabaceae, including *Celtis* and relatives, Moraceae, and Urticaceae, including Cecropiaceae). Rosales are still heterogeneous morphologically, but a reduction (or lack) of endosperm may be synapomorphic. The presence of a hypanthium may also be synapomorphic, and this structure is evident in Rosaceae, Rhamnaceae, Elaeagnaceae, Dirachmaceae, and some Ulmaceae. Loss of the hypanthium probably is a synapomorphy of the clade comprised of Cannabaceae, Moraceae, and Urticaceae. Rosaceae are sister to the remaining families and are plesiomorphic, but their monophyly may be supported by numerous stamens; molecular studies have supported their monophyly (Morgan et al., 1994; Evans et al., 2000). Families such as Rhamnaceae and Elaeagnaceae, although bearing showy flowers with an obvious hypanthium, are more closely related to the former Urticales than to Rosaceae. This relationship is supported by DNA sequences and a trans-spliced intron in the mitochondrial gene *nad1* (Qiu et al., 1998), as well as the possession of single whorl of stamens opposite the petals. The monophyly of the urticoid subclade within Rosales (APG II, 2003) is well supported (Savolainen et al., 2000b; Soltis et al., 2000, 2003; Sytsma et al., 2002; Hilu et al., 2003), and they have long been recognized by their leaves with urticoid teeth, at least one prominent prophyllar bud, reduced, inconspicuous flowers with five or fewer stamens, and bicarpellate unilocular ovaries with a single apical (to basal) ovule (Humphries and Blackmore, 1989; Judd et al., 1994, 2002; Stevens, 2003). Ulmaceae are probably sister to a clade containing Cannabaceae (including Celtidaceae), Moraceae, and Urticaceae. These three families share imperfect flowers, curved embryos, and the loss of a hypanthium. Cannabaceae (Celtidaceae, in Judd et al., 2002) are sister to Moraceae + Urticaceae, the members of which share laticifers and milky latex (reduced in many Urticaceae, a family which should include *Cecropia* and relatives; Sytsma et al., 2002).

Malvids (eurosids II)—The APG II (2003) circumscription of malvids includes three orders (Brassicales, Malvales, and Sapindales) and one unplaced family (Tapisciaceae). The malvids were first recognized as ''rosids II'' by Chase et al. (1993), but with Crossomatales and part of Geraniales and included; this clade was later renamed ''eurosids II'' and included Myrtales, but not Geraniales or Crossosomatales (APG, 1998).

Brassicales are characterized by the presence of glucosinolates, which react with myrosinase (usually contained in specialized spherical myrosin cells) to release mustard oils (isothiocynates; Dahlgren, 1977; Rodman, 1981, 1991; Rodman et al., 1993, 1996; Judd et al., 1994, 2002; Stevens, 2003), but indeterminate (racemose) inflorescences are also diagnostic and, at the cellular level, an endoplasmic reticulum with dilated cisternae provides additional support for the order (Jorgensen, 1981). It is noteworthy that glucosinolates have also evolved in *Drypetes* and *Putranjiva* (Putranjivaceae) of Malpighiales. Monophyly of Brassicales also is supported by DNA studies (Rodman et al., 1993, 1996; Soltis et al., 1997, 2000, 2003; Källersjö et al., 1998; Karol et al., 1999; Savolainen et al., 2000b; Hilu et al., 2003). Despite their monophyly and chemical distinctiveness, Brassicales are morphologically heterogeneous, as is evident from the fact that Cronquist (1981) placed these families in seven orders (i.e., Batales, Capparales, Celastrales, Geraniales, Polygalales, Sapindales, and Violales, in two subclasses, Dilleniidae and Rosidae). Akaniaceae and Tropaeolaceae are sisters and have large zygomorphic flowers with a hypanthium. Moringaceae and Caricaceae form another clade, which, with the previous group, form the first two groups successively sister to the rest of Brassicales. These members of the order have pentamerous flowers and seeds with endosperm and a straight embryo. Most core members of Brassicales (e.g., Bataceae, Salvadoraceae, Koeberliniaceae, Resedaceae, Tovariaceae, and Brassicaceae s. l.) have tetramerous flowers and seeds with a curved embryo that more or less lacks endosperm; they also have vestured pits in the vessel elements. Bataceae and Salvadoraceae are sisters, sharing opposite leaves with two-trace nodes and paracytic stomata; these two families, along with Koeberliniaceae, form a clade that shows adaptations to dry and/or salty habitats; they also have a base chromosome number of 11 (Stevens, 2003). Brassicaceae (including Capparaceae) are by far the largest family in the order, and their monophyly is strongly supported by DNA sequences (Soltis et al., 2000; Hall et al., 2002) as well as morphology (Judd et al., 1994, 2002; Stevens, 2003). Both molecular and morphological data indicate that Capparaceae, as previously circumscribed (Cronquist, 1981; Kubitzki, 2003), are nonmonophyletic. The family comprises three clearly differentiated and monophyletic subfamilies: Capparoideae, Cleomoideae, and Brassicoideae (Hall et al., 2002). The question of whether or not to treat these three clades as subfamilies (as here and in APG II, 2003) or as closely related families (as recommended by Hall et al., 2002) is not easily answered because there are no unambiguous criteria for determination of rank.

Malvales are clearly monophyletic (Alverson et al., 1998; Fay et al., 1998a; Källersjö et al., 1998; Bayer et al., 1999; Savolainen et al., 2000b; Soltis et al., 2000; Kubutzki and Chase, 2003) and may be diagnosed by their stratified phloem with fibrous and soft layers, wedge-shaped rays in the wood, mucilage canals and cavities, stellate hairs, malvoid teeth, and cyclopropenoid fatty acids (Judd and Manchester, 1998; Ste-

vens, 2003). The stamens are usually numerous (by secondary increase, with centrifugal initiation. Stevens (2003) noted that the seeds of Malvales have the exotegmen thickened, lignified, and with a palisade. Basal nodes within Malvales are unsupported in the DNA studies, but include the following lineages: (1) Bixaceae (including Cochlospermaceae and Diegodendonaceae), (2) Cistaceae, Dipterocarpaceae, and Sarcolaenaceae, (3) Thymelaeaceae (including Tepuianthaceae), (4) Muntingiaceae, and (5) Neuradaceae. The largest group within the order is Malvaceae s. l. (including Tiliaceae, Sterculiaceae, and Bombacaceae—Alverson et al., 1998, 1999; Baum et al., 1998; Bayer, 1998, 1999; Judd and Manchester, 1998; Bayer et al., 1999), a clade diagnosed by their inflorescence architecture (bicolor unit), nectaries of densely packed multicellular glandular hairs (usually on the adaxial surface of the connate calyx), and possibly palmate venation and the loss of vestured pits (Judd et al., 2002; Bayer and Kubitzki, 2003).

Sapindales are trees or shrubs that previously have been considered to be related on the basis of their usually alternate and spiral, pinnately compound, exstipulate leaves and rather small tetra- or pentamerous flowers with imbricate perianth parts and a distinct nectar disk. Their monophyly has been confirmed by DNA studies (Chase et al., 1993; Gadek et al., 1996; Källersjö et al., 1998; Savolainen et al., 2000b; Soltis et al., 2000). The pinnately compound leaves and distinct nectar disk are likely synapomorphic features. Anacardiaceae and Burseraceae form a clade supported by the presence of resin canals, biflavonoids in the leaves, and more or less drupaceous fruits. A Meliaceae + Rutaceae + Simaroubaceae clade is reinforced by the presence of bitter triterpenoids. The distinctive, small families Berbersteiniaceae, Kirkiaceae, and Nitrariaceae are as yet unplaced within the order. Finally, Sapindaceae are here broadly defined (including Aceraceae and Hippocastanaceae; see Judd et al., 1994; Gadek et al., 1996; Soltis et al., 2000; APG II, 2003). Monophyly of Sapindaceae s. l. is supported by their cyclopropane amino acids (such as hypoglycin), appendaged petals, stamens eight or fewer, filaments pubescent or papillose, ovules sessile, extrastaminal nectar disk, embryo curved, and a fold or pocket in the seed coat (Judd et al., 1994, 2002). Their seeds are often arillate. Aceraceae and Hippocastanaceae appear to form a clade within Sapindaceae that is supported by opposite leaf arrangement and palmate venation (Gadek et al., 1996; Savolainen et al., 2000b; Soltis et al., 2000), but these two segregate families were not sister groups in the morphological phylogenetic study of Judd et al. (1994).

ASTERIDS

The remaining angiosperm orders belong to the asterid clade (Fig. 1). Support for the monophyly of this subgroup of the tricolpate clade and relationships within it are derived from molecular studies (Olmstead et al., 1992a, 1993, 2000; Chase et al., 1993; Soltis et al., 1997, 2000, 2003; Savolainen et al., 2000b; Albach et al., 2001a, b; Bremer et al., 2002; Hilu et al., 2003). Clarification of the phylogenetic relationships of asterids to other major tricolpate clades, as well as of those for the basalmost nodes of the asterids, is critical to our ability to understand the patterns of diversification of this large group. Floral features, such as tenuinucellate and unitegmic ovules, epipetalous stamens, and sympetaly (and formation of a floral tube), certainly are significant asterid innovations (Endress, 2001). However, homoplasy and uncertain phylogenetic to-

pologies make it difficult to accurately assess their levels of universality (Albach et al., 2001a, b).

Morphological synapomorphies for the asterids in the broad sense may include unitegmic and tenuinucellate ovules, although both features are homoplasious. Iridoids are widespread in the clade and could also be synapomorphic. Most asterids have sympetalous flowers, although families with separate or nearly separate petals occur, especially in Cornales and Ericales. Connate petals have provided a traditional defining character for the core of this group (Cronquist, 1988), hence the traditional name, Sympetalae. Taxa with seemingly separate petals have in many cases been shown to have a ring primordium early in floral development (Erbar, 1991; Erbar and Leins, 1996), indicating that sympetaly may be a general asterid feature. This clade has long been recognized in angiosperm classifications, although Cornales, Ericales, and Apiales were frequently excluded (e.g., Cronquist, 1981, 1988; summarized in Judd et al., 2002). Cornales and Ericales probably are successive sister groups to the rest of the asterid clade (APG II, 2003; but we note that the position of these two clades is reversed in Hilu et al., 2003). The core asterids, supported by molecular data (Olmstead et al., 2000; Bremer et al., 2002; Hilu et al., 2003), are diagnosed by the number of stamens equaling the petals, epipetalous stamens, and an obviously sympetalous corolla. Sympetalous flowers with epipetalous stamens have also evolved in some Ericales, but in that group the number of stamens is usually at least twice the number of corolla lobes. In addition, core asterids usually have bi- or occasionally tricarpellate gynoecia. The core asterids include two major clades (Fig. 1), here called lamiids (euasterids I; Garryales, Gentianales, Lamiales, and Solanales) and campanulids (euasterids II; Aquifoliales, Apiales, Dipsacales, and Asterales; Bremer et al., 2002; APG II, 2003). Endress (2001) suggested that lamiids largely show late sympetaly (i.e., petals appearing as distinct primordia and the fused parts appearing only later in floral development), whereas campanulids are characterized by early sympetaly (i.e., the fused part appears first as a ring meristem on which the individual petals appeared later; Erbar, 1991; Erbar and Leins, 1996).

Cornales have been supported as monophyletic by DNA sequences (Xiang et al., 1993, 1996, 1998; Hempel et al., 1995; Olmstead et al., 2000; Savolainen et al., 2000b; Soltis et al., 2000, 2003; Albach et al., 2001a, b; Fan and Xiang, 2003; Hilu et al., 2003) and are diagnosed by their flowers with inferior ovaries, an epigynous nectar disk, and usually reduced sepals. Many have drupaceous fruits, but capsules are characteristic of Loasaceae and Hydrangeaceae. Relationships are still unclear within Cornales, but Loasaceae and Hydrangeaceae apparently form a clade (Olmstead et al., 2000; Soltis et al., 2000; Bremer et al., 2002; Hilu et al., 2003), a hypothesis supported by their capsular fruits, tuberculate trichomes with basal pedestals (Hufford, 1992), parietal placentation, numerous ovules, and iridoid chemistry (Stevens, 2003). The circumscription of Cornaceae has been surprisingly problematic, with an independent Nyssaceae containing the mastixioids (*Mastixia* and *Diplopanax*) and the nyssoids (*Nyssa*, *Davidia*, and *Camptotheca*) recognized as an alternative option in APG II (2003). If segregated, Cornaceae (*Cornus* and *Alangium*) would have perfect, tetramerous flowers and Nyssaceae would have usually unisexual, pentamerous flowers. Alternatively, all three clades, i.e., Nyssaceae, Mastixiaceae, and Cornaceae, have been recognized at familial rank (Xiang et al., 2002; Fan and Xiang, 2003). Hydrostachyaceae, an unusual group of

aquatics with deeply divided leaves and imperfect flowers that lack a perianth and have only a single stamen, show many morphological and molecular apomorphies. Their position within the order is unclear, and their placement within Hydrangeaceae in some analyses (e.g., Hempel et al., 1995; Olmstead et al., 2000; Soltis et al., 2000) may be an artifact of divergent plastid DNA sequences (Xiang et al., 2002). The small families Curtisiaceae and Grubbiaceae also belong in Cornales.

Ericales, as presently circumscribed, are strongly supported, but were not recognized prior to DNA-based studies (Olmstead et al., 1992a, 1993, 2000; Chase et al., 1993; Kron and Chase, 1993; Morton et al., 1997a, b; Källersjö et al., 1998; Savolainen et al., 2000b; Soltis et al., 2000; Albach et al., 2001a, b; Bremer et al., 2002; Hilu et al., 2003), and morphological markers for the clade are unclear. Possible synapomorphies are leaves bearing single-veined teeth with an opaque-deciduous cap (i.e., theoid teeth), sometimes with a multicellular hair replacing the cap, and gynoecia with protruding diffuse placentae (Hickey and Wolfe, 1975; Nandi et al., 1998; Judd et al., 2002; Stevens, 2003). The group is also distinctive within asterids in typically having ellagic acid. Phylogenetic relationships of most families within the order remain uncertain, but have been partially resolved by Anderberg et al. (2002). Sister to the rest of the order is a clade of Balsaminaceae, Marcgraviaceae, and Tetrameristaceae (including Pellicieraceae), which may be diagnosed, in part, by the presence of raphide sacs and short styles. Fouquieriaceae + Polemoniaceae represent the next clade sister to the rest, and this group has strongly connate petals and tricarpellate gynoecia with lobed stigmas. The remaining families form a clade, within which relationships are mostly unresolved, except for a few small groups of families. *Lissocarpa* (Lissocarpaceae of several authors, e.g., Cronquist, 1981) should be included in Ebenaceae (Berry et al., 2001; Anderberg et al., 2002; Bremer et al., 2002). Sapotaceae may be sister to Lecythidaceae; both have seeds with multiplicative, more or less lignified testa. Diapensiaceae may be sister to Styracaceae (including *Halesia*); both families lack glandular hairs. The monophyly of the primuloid clade (often treated as Primulales previously), including Maesaceae, Theophrastaceae, Primulaceae, and Myrsinaceae (including several "primuloid" genera, especially those with resinous dots or streaks), is well supported (Anderberg and Ståhl, 1995; Morton et al., 1997a; Anderberg et al., 1998, 2000, 2002). Numerous genera in the broader but paraphyletic Primulaceae have been transferred to Myrsinaceae and Theophrastaceae, leaving a smaller Primulaceae (Källersjö et al., 2000). The clade has long been recognized and is easily diagnosed by its flowers having stamens equal to and opposite the corolla lobes and a gynoecium with a large, free-central placenta. Core Ericales comprises Roridulaceae, Actinidiaceae, Sarraceniaceae, Clethraceae, Cyrillaceae, and Ericaceae, and their monophyly is supported by anthers more or less inverted (late to early) in development, style somewhat impressed into the apex of the ovary, and details of pollen-wall ultrastructure (Anderberg, 1992, 1993; Judd and Kron, 1993; Kron and Chase, 1993; Bayer et al., 1996; Kron, 1996; Anderberg et al., 2002; Bremer et al., 2002). Sarraceniaceae, the American carnivorous pitcher plants, are most closely related to Actinidiaceae and Roridulaceae; the last with leaves bearing stalked, capitate, viscid hairs. Ericaceae are circumscribed broadly (Kron et al., 2002) to include Empetraceae, Epacridaceae, Monotropaceae, Pyrolaceae, and Vacciniaceae

and diagnosed by pendulous, urceolate-campanulate flowers. Ericaceae are probably sister to Cyrillaceae, which together are sister to Clethraceae; all three have a reduced seed coat, and micropylar and a chalazal endosperm haustorium (Anderberg et al., 2000; Judd et al., 2002). Several families (e.g., Actinidiaceae, Lecythidaceae, Sarraceniaceae, Styracaceae, Symplocaceae, Theaceae, and Ternstroemiaceae) have numerous stamens, initiated in centrifugal sequence, indicating a secondary increase in number of stamens (from an ancestral condition of two, pentamerous whorls). Other clades have reduced the androecium to a single whorl (e.g., Balsaminaceae, Polemoniaceae, and the primuloid clade). In the primuloid clade, the outer whorl is sometimes represented by staminodia (e.g., Theophrastaceae), whereas in Diapensiaceae, this is true for the inner whorl. Finally, the parasitic Mitrastemonaceae has recently been placed within Ericales on the basis of mitochondrial DNA sequence data (Barkman et al., 2004), and mycoparasitism has evolved within Ericaceae (Kron et al., 2002).

Lamiids (euasterids I)—The APG II circumscription of lamiids includes four orders (Garryales, Gentianales, Lamiales, Solanales) and four families unassigned to order. The lamiids were first recognized as "asterids I" by Chase et al. (1993) with essentially this circumscription; they were later renamed "euasterids I" (APG, 1998; APG II, 2003). Although the clade received strong molecular support (Olmstead et al., 2000; Bremer et al., 2002; Hilu et al., 2003) at present it cannot be diagnosed morphologically. Relationships at basal nodes within the lamiids are unclear, especially those involving placement of some members of "Icacinaceae," which may form a complex along with Oncothecaceae (Kårehed, 2001; Bremer et al., 2002) and Garryales, although *Icacina* (and genera related to it) was weakly associated with Garryales in the analysis of Soltis et al. (2000) and *Oncotheca* with Garryales in Savolainen et al. (2000b). Apart from the uncertainty surrounding the placement of *Icacina* and *Oncotheca*, Garryales are sister to a clade comprising Boraginaceae, Vahliaceae, Solanales, Gentianales, and Lamiales. Garryales, when narrowly defined, contains only the monotypic Eucommiaceae and Garryaceae, the latter including Aucubaceae (Bremer et al., 2002; APG II, 2003; Hilu et al., 2003). The group can be diagnosed by several putative apomorphies (sclerids in the leaf mesophyll, dioecy, valvate corolla lobes, more or less atectate pollen, unilocular gynoecia with one or two apical ovules, a short style, and indehiscent fruits). *Garrya* and *Acuba* (Garryaceae) share tetramerous flowers with an inferior ovary and a nectar disk (reduced in *Garrya*; Liston, 2003) and previously have been placed in Cornales (e.g., Cronquist, 1981). *Eucommia* (Hamamelidae, Cronquist, 1981) and *Garrya* are both wind-pollinated.

Placement of Boraginaceae is unclear, but the family is here circumscribed broadly, including Hydrophyllaceae (capsular fruits), as well as the parasitic Lennoaceae (Ferguson, 1999; Gottschling et al., 2001; Långström and Chase, 2002). Analyses (e.g., Soltis et al., 2000; Albach et al., 2001a) have indicated a relationship with Lamiales, Lamiales + Solanales (Bremer et al., 2002), Gentianales + Solanales + Lamiales (Hilu et al., 2003), or just Solanales (Chase et al., 1993; Olmstead et al., 2000); the last placement is also supported by their plicate corollas. Morphological support for monophyly of Boraginaceae s. l. comes from their characteristic scorpioid cymes (Buys and Hilger, 2003).

Monophyly of Gentianales (Chase et al., 1993; Olmstead et

al., 1993; Bremer et al., 1994, 2002; Endress et al., 1996; Källersjö et al., 1998; Backlund et al., 2000; Savolainen et al., 2000b; Soltis et al., 2000; Albach et al., 2001a; Hilu et al., 2003) is supported by morphology: vestured pits, stipules (sometimes reduced to a stipular line or lacking), and colleters on the adaxial surface of the stipules, along the nodal line, or at the base of the petiole (Wagenitz, 1959, 1992; Bremer and Struwe, 1992; Nicholas and Baijnath, 1994; Struwe et al., 1994; Stevens, 2003). Other potential synapomorphies include opposite leaves, a particular array of complex indole alkaloids, and corollas convolute in bud (Bremer and Struwe, 1992; Wagenitz, 1992). Rubiaceae are the sister group of the remaining four families and should include *Dialypetalanthus* (former Dialypetalanthaceae; Fay et al., 2000; Soltis et al., 2000). The remaining families (Gentianaceae, Loganiaceae, Gelsemiaceae, and Apocynaceae) share the apomorphy of internal phloem, but their interrelationships are unclear (Bremer et al., 2002). Gentianaceae should be expanded to include *Saccifolium* (Saccifoliaceae; Struwe et al., 1998; Thiv et al., 1999) and *Fagraea*, *Anthocleista*, and *Potalia*, formerly of "Loganiaceae" (Backlund et al., 2000; Savolainen et al., 2000a; Struwe and Albert, 2000), but they should exclude *Menyanthes* and relatives (Olmstead et al., 1993; Bremer et al., 1994, 2002), which are members of Asterales. Loganiaceae are now defined narrowly with a number of previously included genera transferred to several clades within Lamiales, as well as Gentianaceae and Gelsemiaceae. The segregate family Gelsemiaceae is characterized by their styles/stigmas being twice forked (Struwe et al., 1994). Apocynaceae are circumscribed broadly, including Asclepiadaceae (Chase et al., 1993; Judd et al., 1994; Endress et al., 1996; Sennblad and Bremer, 1996; Civeyrel et al., 1998; Endress and Bruyns, 2000; Endress and Stevens, 2001; Potgieter and Albert, 2001), and supported by several distinctive apomorphies: laticifers with milky latex, the two carpels connate by styles and/or stigmas only with the ovaries distinct, and the apical portion of the style expanded and highly modified, forming a head that secretes viscin.

Lamiales are clearly monophyletic (Downie and Palmer, 1992; Olmstead et al., 1992a, b, 1993, 2000; Olmstead and Reeves, 1995; Wagstaff and Olmstead, 1997; Källersjö et al., 1998; Savolainen et al., 2000b; Soltis et al., 2000; Albach et al., 2001a; Bremer et al., 2002; Hilu et al., 2003). They are characterized by gland-headed hairs, oligosaccharides (which replace starch in carbohydrate storage), parenchyma tissue extending from anther connectives into the locules, often diacytic stomata, endosperm with a conspicuous micropylar haustorium, and protein inclusions in the nuclei of mesophyll cells (Yamazaki, 1974; Dahlgren, 1983; Wagenitz, 1992; Judd et al., 1994, 2002), although the precise level of universality of some of these characters is in doubt, because of uncertain phylogenetic placements or lack of knowledge of some groups potentially sister to the rest, especially Plocospermataceae and Tetrachondraceae. We note that Boraginaceae, which may be related, also have protein bodies in their nuclei. Plocospermataceae, Oleaceae, and Tetrachondraceae are probably successively sister groups to the remaining members of the order (Oxelman et al., 1999; Savolainen et al., 2000a; Bremer et al., 2002; APG II, 2003; Hilu et al., 2003). Carlemanniaceae may be sister to Oleaceae (Savolainen et al., 2000a), and both families have flowers with only two stamens. The flowers of Tetrachondraceae (*Tetrachondra*, *Polypremum*) are also actinomorphic and tetramerous, but they have four stamens, not two. Most other members of Lamiales have zygomorphic flowers

with two petals forming an upper corolla lobe and three petals forming a lower lobe (i.e., the corolla is more or less bilabiate), but they are secondarily radial and tetramerous in some Scrophulariaceae (e.g., *Buddleja*). They have four didynamous stamens, although one pair sometimes has been lost or reduced to staminodia. This clade is also diagnosed by endosperm haustoria at micropylar and chalazal ends, lamellar protein inclusions in the nuclei, six- and/or eight-oxygenated flavones, and shikimic-acid-derived anthraquinones. All of these features are likely synapomorphic for this large clade, the core Lamiales, which in APG II (2003) contains 17 families that are often difficult to distinguish. Recent phylogenetic analyses have resulted in many changes in circumscription. More phylogenetic studies of core Lamiales are needed to clarify phylogenetic relationships, and thus familial limits. Among core Lamiales, Calceolariaceae, Gesneriaceae, and Plantaginaceae (or Veronicaceae, see Olmstead et al., 2001) may represent successive sister groups to the rest (Olmstead et al., 2000; Bremer et al., 2002). Calceolariaceae, segregated recently by Olmstead et al. (2001) and represented mainly by the large genus *Calceolaria*, have only two stamens, and a saccate lower corolla lip with oil-producing masses of hairs.

The large family Scrophulariaceae, as previously delimited, is not monophyletic and has only symplesiomorphies such as flowers with bilabiate corollas, four stamens, bicarpellate ovaries with axile placentation, numerous ovules, and more or less globose capsules with small, endospermous seeds. It is, therefore, not surprising that DNA-based studies (e.g., Olmstead and Reeves, 1995; Young et al., 1999; Olmstead et al., 2001; Beardsley and Olmstead, 2002) have shown that members of "Scrophulariaceae" belong to at least eight different lineages within core Lamiales. Most former members of "Scrophulariaceae" now belong to one of three families, each of which is apparently monophyletic: Plantaginaceae, Scrophulariaceae s. s., and Orobanchaceae. Plantaginaceae include most of the autotrophic "scrophs" with biloculate anthers, such as *Penstemon*, *Veronica*, *Linaria*, *Lindernia*, *Antirrhinum*, *Gratiola*, and *Digitalis*, along with *Globularia* and relatives (Olmstead et al., 2001; Bremer et al., 2002), the derived aquatics *Callitriche* and *Hippuris* (Olmstead and Reeves, 1995), and a genus of wind-pollinated herbs, *Plantago* (Olmstead et al., 1993, 2001; Wagstaff and Olmstead, 1997). Scrophulariaceae s. s. (contra Judd et al., 2002) include five tribes of mostly South African distribution, the former Myoporaceae of predominantly Australian distribution, and two more cosmopolitan groups, tribe Scrophularieae (e.g., *Verbascum* and *Scrophularia*) and the former Buddlejaceae (Olmstead et al., 2001; Beardsley and Olmstead, 2002). Corollas that are actinomorphic or nearly so occur throughout Scrophulariaceae, including *Buddleja*, which has tetramerous corollas.

Orobanchaceae constitute the third major clade (de Pamphilis et al., 1997; Nickrent et al., 1997; Young et al., 1999; Olmstead et al., 2001). These plants are mainly hemiparasites (which were included within "Scrophulariaceae") to holoparasites, all with haustorial connections to their hosts, and orobanchin, which causes the leaves or the entire plant to turn black on drying (de Pamphilis et al., 1997; Judd et al., 2002). Some have parietal placentation. The autotrophic genus *Lindenbergia* may be the sister group of the parasitic genera of Orobanchaceae; morphological apomorphies linking *Lindenbergia* to these parasites may include the abaxial lobes of the corolla outside the adaxial, details of hair morphology, and indeterminate inflorescences. A few other small groups, not

yet mentioned here, have recently been removed from traditional "Scrophulariaceae"; e.g., *Mimulus* is related to *Phryma* and treated in an expanded Phrymaceae (Beardsley and Olmstead, 2002), and the problematic *Paulownia* and *Schlegelia*, which have been tossed back and forth between "Scrophulariaceae" and Bignoniaceae, are treated in Paulowniaceae and Schlegeliaceae, respectively (Olmstead et al., 2001; APG II, 2003).

Lentibulariaceae are characterized by their insectivorous habit (glandular hairs secreting mucilage and digestive enzymes) and may be sister to Byblidaceae (only *Byblis*, formerly placed in Rosales; Cronquist, 1981), which also are insectivorous herbs with sticky, glandular hairs (Bremer et al., 2002). Acanthaceae are monophyletic (Hedrén et al., 1995; Scotland et al., 1995; McDade et al., 2000; Bremer et al., 2002; Hilu et al., 2003) and include Nelsonioideae, Thunbergioideae, and the mangrove genus *Avicennia*, often treated in its own family, Avicenniaceae (Scotland et al., 1995; McDade and Moody, 1999; McDade et al., 2000; Schwarzbach and McDade, 2002). Martyniaceae (New World) and Pedaliaceae (Old World) have often been considered related (e.g., Cronquist, 1981), but this grouping has received no support in phylogenetic studies. Finally, Verbenaceae and Lamiaceae often have been considered sister taxa because both have ovaries with four ovules, divided into four locules by the development of a false septum, and aromatic, ethereal oils (in glandular hairs, or parenchymatous tissues). Most molecular studies have not placed these families together (Olmstead and Reeves, 1995; Wagstaff and Olmstead, 1997; Oxelman et al., 1999; Olmstead et al., 2000, 2001; Hilu et al., 2003), indicating that the earlier listed characters have evolved in parallel, but a sister-group relationship was supported by Bremer et al. (2002) with limited taxon sampling. Even if a close relationship of these two taxa is supported, the circumscription of these two groups has been markedly restructured on the basis of phylogenetic analyses of both morphological and DNA characters (Cantino, 1992a, b; Chadwell et al., 1992; Olmstead et al., 1993; Judd et al., 1994; Wagstaff and Olmstead, 1997; Wagstaff et al., 1998), and to make Lamiaceae monophyletic, nearly two-thirds of the genera usually included within Verbenaceae have been transferred to Lamiaceae (Cantino et al., 1992). Verbenaceae now include only subfamily Verbenoideae (excluding the tribe Monochileae).

Solanales comprise Solanaceae, Convolvulaceae, Hydroleaceae, Montiniaceae, and Sphenocleaceae (Olmstead et al., 1992a, 1993, 2000; Cosner et al., 1994; Soltis et al., 2000; Albach et al., 2001a, b; Bremer et al., 2002) and can be recognized by their radially symmetrical flowers with a plicate, sympetalous corolla, and a calyx persistent in the fruit. These plants have alternate and spiral, simple, exstipulate leaves, and iridoids are absent. Montiniaceae are anomalous in having imperfect flowers with free, valvate petals. Sphenocleaceae often have been placed with or near Campanulaceae (Takhtajan, 1997; see Asterales) and Hydroleaceae (*Hydrolea*) previously were placed within Hydrophyllaceae (Cronquist, 1981; Takhtajan, 1997; here treated as Boraginaceae). Solanaceae and Convolvulaceae are sister families that share the synapomorphies of internal phloem and similar alkaloid chemistry; their corollas are usually contorted and/or induplicate–valvate. Convolvulaceae include Cuscutaceae (parasites) and Dichondraceae (gynoecia with gynobasic styles; Neyland, 2001; Stefanovic et al., 2002). Solanaceae includes Goetzeaceae, Duckeodendraceae, and Nolanaceae, the last two recognized as families by Cronquist (1981) among others (Olmstead and Palmer, 1991, 1992; Olmstead and Sweere, 1994; Olmstead et al., 1999; Fay et al., 1998b; Santiago and Olmstead, 2003).

Campanulids (euasterids II)—The APG II circumscription of campanulids includes four orders (Apiales, Aquifoliales, Dipsacales, and Asterales) and eight families unassigned to order. The campanulids were first recognized as "asterids II" by Chase et al. (1993) with the same circumscription and later renamed "euasterids II" (APG, 1998; APG II, 2003). Aquifoliales are the sister group of the remaining orders: Apiales, Dipsacales, and Asterales (Olmstead et al., 1993, 2000; Bremer et al., 2002), which share polyacetylenes and frequently have inferior ovaries. Among the unassigned families, Paracryphiaceae and *Quintinia* (Escalloniaceae) are probably sister groups and together are weakly placed as sister to Dipsacales (Bremer et al., 2002). *Columellia* (Columelliaceae) is likely sister to *Desfontainia* (Desfontainiaceae; Bremer et al., 2002); these may be combined as Columelliaceae s. l. (APG II, 2003) and Bruniaceae may be their sister (Bremer et al., 2002). Tribelaceae, Polyosmaceae, Eremosynaceae, and some Escalloniaceae possibly form a clade (Lundberg, 2001; Bremer et al., 2002) that may be supported by their free petals, but at present this hypothesis is only weakly supported; some species of *Escallonia* are sympetalous. Lundberg (2001) recommended that the circumscription of Escalloniaceae be expanded by inclusion of Tribelaceae, Polyosmaceae, and Eremosynaceae.

Aquifoliales, in their current circumscription (APG II, 2003), were not recognized until the advent of molecular phylogenetics (Chase et al., 1993; Olmstead et al., 2000; Savolainen et al., 2000b; Soltis et al., 2000; Albach et al., 2001a; Bremer et al., 2002). The order is poorly characterized, but gynoecia with axile–apical placentation and only one or two ovules per locule and drupaceous fruits may be synapomorphies. Two clear subclades are evident: Cardiopteridaceae and Stemonuraceae, each containing several genera previously placed in "Icacinaceae" (Kårehed, 2001), are characterized by trilacunar nodes, entire, exstipulate leaves, and drupes with a single pit, whereas the Phyllonomataceae + Helwingiaceae + Aquifoliaceae (only *Ilex*) clade have unilacunar nodes, usually serrate leaves associated with small stipules, and berries, or drupes with several pits. Patterns of polarity among these characters are unclear. Members of the order tend to have small, often imperfect flowers with the petals at most slightly connate. Phyllonomataceae and Helwingiaceae both have epiphyllous flowers and fimbriate stipules. They may be sister families (Bremer et al., 2002).

Apiales are well supported by both molecular (Olmstead et al., 2000; Soltis et al., 2000; Kårehed, 2001, 2003; Bremer et al., 2002; Hilu et al., 2003) and morphological characters (e.g., corolla lobes well developed, stamens free from the corolla or nearly so, only one or two ovules per carpel, and possibly also drupaceous fruits with only one carpel fertile; Stevens, 2003). Relationships and familial circumscriptions among the small clades Pennantiaceae, Torricelliaceae, Aralidiaceae, Melanophyllaceae, and Griseliniaceae are ambiguous, and it has been noted that "some of the families . . . could possibly be merged when well-supported sister-group relationships have been established" (APG II, 2003). Torricelliaceae, Aralidiaceae, Melanophyllaceae, and Griseliniaceae have trans-septal vascular bundles in their ovaries, as in Cornales, in which they were once placed. Core Apiales include Pittosporaceae and the complex including Araliaceae, Mackinlayaceae, Myodocarpaceae,

and Apiaceae, within which relationships are problematic (see Plunkett et al., 1996a, b, 1997; Plunkett, 2001; Plunkett and Lowry, 2001; Judd et al., 2002). Araliaceae, Apiaceae s. s., Mackinlayaceae, and Myodocarpaceae were combined, as Apiaceae s. l., in Judd et al. (2002), but each of these was recognized at familial rank in APG II (2003). Monophyly of core Apiales receives strong phenotypic support, having aromatic, ethereal oils and resins in canals associated with the conducting tissues (pericycle), falcarinone polyacetylenes, a characteristic arrangement of the lateral roots, shoots with reduced, bractlike leaves at the base, trinucleate pollen, gynoecia with both carpels fertile, hemicellulosic seed reserves, and minute embryos. Pittosporaceae may be sister to Apiaceae s. l. (Judd et al., 2002; Kårehed, 2003). Apiaceae s. l. are supported as monophyletic by umbellate inflorescences, a stylopodium, presence of the trisaccharide umbelliferose (as a carbohydrate storage product), and petroselenic acid in the seeds, and possibly also minute sepals, an inferior ovary, and schizocarpic fruits (the last homoplasious; Judd et al., 2002). The major clades within Apiaceae s. l. are difficult to diagnose due to the lack of unambiguous morphological synapomorphies, and, therefore, Judd et al. (2002) adopted a broad familial circumscription, as did Thorne (1973).

Dipsacales comprise Adoxaceae and Caprifoliaceae (including Dipsacaceae and Valerianaceae). Monophyly of Dipsacales (Donoghue et al., 1992, 2001; Judd et al., 1994; Olmstead et al., 1993, 2000; Soltis et al., 2000; Albach et al., 2001a, b; Bell et al., 2001; Bremer et al., 2002; Hilu et al., 2003) is supported by their opposite leaves, cellular endosperm development, anthers with a three- or four-cell-layered tapetum, and nucleotide sequences. Stevens (2003) also noted that the seeds have a vascularized testa, with the exotestal cells enlarged (palisade) and variously thickened and lignified. Lundberg (2001) suggested that Columelliaceae should also be included in Dipsacales. Adoxaceae are circumscribed broadly to include *Sambucus* and *Viburnum* (Donoghue et al., 1992, 2001; Judd et al., 1994; Eriksson and Donoghue, 1997). Caprifoliaceae, including Dipsacaceae, Valerianaceae, Linnaeaceae, Diervillaceae, Caprifoliaceae s. s. sensu Backlund and Pyck (1998), are easily circumscribed on the basis of molecular (Donoghue et al., 1992; Downie and Palmer, 1992; Backlund and Bremer, 1997, 1998; Backlund and Pyck, 1998; Soltis et al., 2000; Albach et al., 2001a, b; Bremer et al., 2002) and morphological data (Judd et al., 1994). Putative synapomorphies for Caprifoliaceae s. l. include their zygomorphic corollas; nectar produced by densely packed, simple hairs on the inner surface of the lower portion of the corolla tube; large, echinate pollen grains; and elongate style with a capitate stigma.

In many previous classifications (e.g., Cronquist, 1981), Asterales included only Asteraceae, which would make it one of the largest orders of angiosperms even without the 10 other smaller families included in Asterales by APG II (2003). In those classifications, the remaining families mostly were assigned to two or more related orders (e.g., Calycerales and Campanulales in Cronquist, 1981), but molecular studies have shown that these families form a grade leading to Asteraceae. Thus, we consider them all to belong to one order (Downie and Palmer, 1992; Olmstead et al., 1992a, 1993, 2000; Michaels et al., 1993; Cosner et al., 1994; Källersjö et al., 1998; Savolainen et al., 2000b; Soltis et al., 2000; Albach et al., 2001a, b; Lundberg, 2001; Bremer et al., 2002; Hilu et al., 2003; Lundberg and Bremer, 2003). Monophyly of Asterales is supported also by their valvate petals, storage of carbohydrates as the oligosaccharide inulin, presence of ellagic acid, lack of apotracheal parenchyma, and probably also plunger or brush pollen presentation mechanism. Most taxa have the stamens with their introrse anthers closely associated with one another (more or less sticking together to completely connate) and forming a tube around the style. In plunger or brush pollination, pollen is pushed out of the tube by specialized hairs on the style or by a specialized pollen-gathering cup. The style elongates to present the pollen to floral visitors. Later, the stigmas become receptive (Wagenitz, 1977, 1992; Leins and Erbar, 1990; Lammers, 1992; Yeo, 1993). All of these characters show homoplasy, but the same could be said of the diagnostic features of many of the orders discussed earlier. The absence of this secondary pollen presentation mechanism in Menyanthaceae and Alseuosmiaceae (and relatives) may result from reversals (secondary losses). Campanulaceae (including Lobeliaceae; APG II, 2003) may be most closely related to Pentaphragmataceae and Rousseaceae (Savolainen et al., 2000b; Soltis et al., 2000; Lundberg and Bremer, 2003), but Bremer et al. (2002) showed Stylidiaceae as sister to Campanulaceae, which is also indicated by floral similarity to Lobelioideae. All except Rousseaceae have inferior ovaries, and in Campanulaceae and Pentaphragmataceae, it is evident that this condition has been derived through adnation of a hypanthium to the gynoecium (Lammers, 1992; Judd et al., 2002). Stylidiaceae have bizarre trigger flowers that are zygomorphic and semiresupinate, with the two stamens adnate to the style (Laurent et al., 1998). However, Stylidiaceae are not placed with Campanulaceae, but instead form a clade with Donatiaceae in several analyses (Soltis et al., 2000; Lundberg and Bremer, 2003), and the two families are optionally combined in APG II (2003). Molecular and morphological data have strongly supported a clade comprised of Menyanthaceae, Goodeniaceae, Calyceraceae, and Asteraceae (Bremer, 1987, 1994; Kårehed et al., 1999; Olmstead et al., 2000; Soltis et al., 2000; Bremer et al., 2002; Lundberg and Bremer, 2003; Stevens, 2003). These plants have corollas with more or less fused marginal veins joining the median vein near the apex of each lobe, thick integuments, and no endosperm haustoria. Menyanthaceae are sister to a Goodeniaceae + Calyceraceae + Asteraceae clade. The monophyly of the clade composed of the last three is supported by their pollen exine with bifurcating columellae and possibly also by connate anthers (Lundberg and Bremer, 2003; Stevens, 2003). In addition, all have inferior ovaries. Calyceraceae and Asteraceae are likely sister clades (Bremer et al., 2002; Lundberg and Bremer, 2003) and they share an unusual kind of corolla venation, pollen with intercolpar depressions, uniloculate gynoecia with a single ovule, persistent and typically highly modified calyces, and achene fruits (Lundberg and Bremer, 2003). Both families also have flowers densely clustered in heads surrounded by an involucre of bracts, a likely parallelism because those of Asteraceae are centrifugally flowering, whereas those of Calyceraceae are centripetal. Their reduced gynoecia are also sometimes considered to have evolved in parallel because placentation is basal in Asteraceae and apical in Calyceraceae (Lammers, 1992). Asteraceae (or Compositae) form an easily recognized and obviously monophyletic group; both morphological and molecular synapomorphies are numerous (Bremer, 1987, 1994, 1996; Jansen et al., 1991, 1992; Keeley and Jansen, 1991; Karis et al., 1992; Kim et al., 1992; Karis, 1993; Kim and Jansen, 1995; Panero and Funk, 2002).

UNRESOLVED ISSUES AND FUTURE DIRECTIONS

Despite the intensive phylogenetic work of the last 15 years, several taxa are still of uncertain position within angiosperms. This is especially true of some highly modified holoparasitic clades, e.g., Balanophoraceae and Cynomoriaceae, which likely belong within the tricolpates. Placement of such groups is difficult because both phenotypic features and DNA sequences are highly divergent from all other organisms. The inflorescences of Balanophoraceae and Cynomoriaceae are superficially fungus-like, with numerous, minute, densely packed flowers. Balanophoraceae produce tuberous underground parts composed of both parasite and host tissues; inflorescences develop within the tuber and at maturity break through, creating a "volva" (Kuijt, 1969). The flowers are so reduced that ovules, placentas, carpels, and perianth parts often are not easily recognized. However, it is encouraging that a recent analysis of mitochondrial sequences (Barkman et al., 2004) has clarified the position of Rafflesiaceae, another group of specialized holoparasites. Their analyses supported a placement of *Rafflesia* and *Rhizanthes* with Malpighiales. This conclusion, however, should be considered very preliminary. Rafflesiaceae have a vegetative body that is mycelium-like, ramifying through the tissues of the host, and their small to gigantic, often bizarre flowers are imperfect, with connate tepals, numerous connate stamens, and an inferior ovary. Other unplaced taxa are uncommon tropical groups that have yet to be investigated phylogenetically (APG II, 2003), although rapid progress is being made in analyzing large numbers of taxa, including difficult-to-obtain tropical genera.

In addition to questions relating to the phylogenetic placement of certain problematic taxa, there are still numerous unresolved relationships among the tricolpates. Some of these are evident in Fig. 1, such as relationships among the early divergent tricolpates, i.e., Sabiaceae, Proteales, Buxales, and Trochodendraceae; relationships among the core tricolpates sister to Gunnerales, i.e., Berberidopsidales, Santalales, caryophyllids, Saxifragales, rosids, and asterids; and relationships within the rosids. As outlined earlier, other major problems involve interfamilial relationships within many of the tricolpate orders. Finally, phylogenetic relationships within those clades placed at familial rank, including circumscriptions of monophyletic genera, have been little studied. A major focus of taxonomic research in the coming years surely will be collaborative efforts aimed at elucidating phylogenetic relationships within families, as already seen for Ericaceae (Kron et al., 2002), Onagraceae (Hoch et al., 1993; Levin et al., 2003, 2004), Malvaceae (Baum et al., 1998; Judd and Manchester, 1998; Alverson et al., 1999), and Caprifoliaceae (Donoghue et al., 1992, 2001; Judd et al., 1994), among others.

Angiosperm systematists have never before learned so much about phylogenetic patterns in such a short period of time. We anticipate continued improvement in our knowledge, although it is likely that we already have a reasonably accurate picture of the broad pattern of angiosperm relationships (Fig. 1). Certainly, there can be no justification for continued use of outdated evolutionary-taxonomic systems. Systematists now have the ability to use a comprehensive and phylogenetically based classification that encompasses nearly all angiosperms (APG II, 2003) not only as a guide to their taxonomic research (and that of other biologists), but also in teaching and floristics (see Sanders and Judd, 2000; Judd et al., 2002; Stevens, 2003). We hope that the brief summary of tricolpate orders, along with the discussion of a few of the major familial clades, provided here will encourage the use of phylogenetic classifications in all aspects of our professional and educational lives.

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