RELATIONSHIP OF THE ORDER *APIALES* TO SUBCLASS *ASTERIDAE*: A RE-EVALUATION OF MORPHOLOGICAL CHARACTERS BASED ON INSIGHTS FROM MOLECULAR DATA

G. M. Plunkett*

Phylogenetic relationships involving the angiosperm order *Apiales* (*Apiaceae* and *Araliaceae*) are troublesome at nearly every taxonomic level and have eluded several generations of botanists. Because of difficulties in interpreting and polarizing morphological character states at deeper phylogenetic levels, most studies in *Apiales* have focused on relationships between the two families and among/within the apialean genera. In the present study, however, recent contributions from molecular analyses are reviewed and combined using a 'supertree' approach to test traditional hypotheses of relationships involving *Apiales*, and to re-evaluate assumptions of character-state evolution in the order. Results from this study confirm that *Apiales* form a monophyletic group with *Pittosporaceae* (along with *Griselinia* G. Forst., *Melanophylla* Baker, *Torricellia* DC. and *Aralidium* Miq.), and should be transferred out of subclass *Rosidae* (away from both *Cornales* and *Sapindales*) to the *Asteridae* (in a position close to *Asterales* and *Dipsacales*). These findings are also supported by several lines of morphological, anatomical, and phytochemical evidence, and provide a more satisfactory framework for interpreting relationships and character-state evolution within the major clades of *Apiales*.

Keywords. *Apiaceae*, *Araliaceae*, *Cornales*, phylogenetic supertree, *Pittosporaceae*, *Umbellales.*

INTRODUCTION

The notion that umbelliferous plants comprise a 'natural group' has its origins in the ancient world, arguably stretching back to the Myceneans and Egyptians, with parallels in east Asian and pre-Columbian western civilizations (see Constance, 1971; Rodríguez, 1971; Reduron, 1989). The formal circumscription of this group as a taxonomic order (*Apiales*, also *Umbellales* or *Araliales*) can be traced back to the natural systems of the eighteenth century (e.g. Adanson, 1763; de Jussieu, 1789; see Rodríguez, 1971). Within this order, two constituent families have been traditionally recognized, *Araliaceae* and *Apiaceae* (= *Umbelliferae*), but most nineteenth- and early twentieth-century treatments also included *Cornaceae sensu lato* (comprising *Cornus* L. and a dozen or more loosely allied genera). These three families were often envisioned as forming a phyletic progression, with *Cornaceae* as the most 'primitive',

---

* Department of Biology, Virginia Commonwealth University, PO Box 842012, Richmond, VA 23284, USA. E-mail: gmplunke@vcu.edu

and *Apiaceae* as the most 'advanced' (see Rodríguez, 1971). This vision carried with it implicit hypotheses of character-state polarity for many features, including floral morphology, habit and stem anatomy, leaf architecture, mating systems, biochemical characters, and geographic distributions. These assumptions were based on (and in turn reinforced) the common understanding that *Apiales* were derived from *Rosales*, either directly or indirectly (e.g. Bessey, 1915, and most recent treatments except that of Dahlgren, 1980). At present, most systems exclude *Cornaceae* from *Apiales*, but an affinity between these groups is often maintained at higher taxonomic levels (e.g. Thorne's 1992 superorder *Cornanae*, and Takhtajan's 1997 subclass *Cornidae*).

The assumption that *Apiales* are closely related to *Cornaceae*, in or near subclass *Rosidae*, has also profoundly influenced interpretations of relationships at lower taxonomic levels. Within the order, *Araliaceae* and its characteristic features have generally been interpreted as ancestral; *Apiaceae*, on the other hand, have usually been viewed as a specialized group derived from araliaceous or 'proto-araliaceous' ancestors (see Rodríguez, 1971). Consequently, the distinctive features defining *Apiaceae* were interpreted as advanced or derived almost without exception. Within *Apiaceae*, three subfamilies have generally been recognized: *Hydrocotyloideae* Link, *Saniculoideae* Burnett, and *Apioideae* Drude (Drude, 1898; see reviews in Plunkett *et al.*, 1996b; Plunkett & Downie, 1999). Extending the evolutionary progression to these subfamilies, many workers have viewed the hydrocotyloids as a phyletic link or 'bridge' from the primitive araliads to the more advanced saniculoids, and ultimately to the most specialized group, the apioids.

Despite their long taxonomic history, *Apiales* have presented successive generations of botanists with persistent difficulties at nearly every phylogenetic level (reviewed in Plunkett *et al.*, 1997). Until recently, however, most attention has been focused on problems at and below the interfamilial level, leaving the issue of interordinal relationships largely unaddressed. Difficulties in discerning relationships at such 'deeper' levels of evolutionary history are not unique to *Apiales*. Quite to the contrary, this problem has marked many diverse groups of organisms, reflecting the challenges of interpreting morphological homologies and polarities after such characters have undergone considerable modification (e.g. by divergence, convergence or parallelism). The development of objective methods of data analysis (e.g. Sokal & Sneath, 1963; Hennig, 1966; and many subsequent refinements), followed by rapid progress made in identifying and applying molecular markers to systematic questions (Soltis *et al.*, 1992, 1998), has provided opportunities to evaluate earlier hypotheses of higher-level relationships in many groups. For *Apiales*, considerable progress in placing the order among the higher dicots has recently been made. The present paper reviews this progress and offers a re-evaluation of morphological characters in light of these findings.

METHODS

The circumscription of *Apiales* almost always includes *Apiaceae* and *Araliaceae* (see Hutchinson, 1967, for the rare exception), but various treatments often include one or more additional families (*Helwingiaceae*, *Torricelliaceae*, and/or *Pittosporaceae*, *inter alia*; see Dahlgren, 1980; Cronquist, 1988; Thorne, 1992; Takhtajan, 1997; Angiosperm Phylogeny Group, 1998). Because of this complexity, Cronquist's (1981, 1988) very narrow circumscription (comprising only *Apiaceae* and *Araliaceae*) is applied for the purposes of this study to avoid confusion among competing definitions. Three publications, each appearing in 1970 or 1971, succinctly summarized the prevailing understanding of apialean relationships prior to the application of cladistics, phenetics, and/or molecular approaches to phylogenetics (viz. Philipson, 1970; Eyde & Tseng, 1971; Rodríguez, 1971). For the present study, these works, together with the ordinal and familial treatments of Cronquist (1981), were used as primary sources to construct a 'consensus view' regarding relationships and interpretations of character-state polarities within *Apiales* and their presumed close relatives. This picture of relationships and character evolution was then tested against the findings of recent molecular studies, including those based on cpDNA restriction site data (Downie & Palmer, 1992; Plunkett & Downie, 1999), and sequence data from several sources, including *rbc*L (Olmstead *et al.*, 1992, 1993; Chase *et al.*, 1993; Xiang *et al.*, 1993, 1998; Plunkett 1994; Plunkett *et al.*, 1996a,b; Xiang & Soltis, 1998); *mat*K (Plunkett *et al.*, 1997; Xiang *et al.*, 1998), two plastid introns (*rpo*C1, Downie *et al.*, 1996, 1998; and *rps*16, Downie & Katz-Downie, 1999), nuclear ITS (Downie & Katz-Downie, 1996; Downie *et al.*, 1998; Plunkett & Lowry, 2001; Wen *et al.*, 2001), nuclear 18S (Nickrent & Soltis, 1995; Soltis *et al.*, 1997), and a combined *rbc*L + *atp*B + 18S data set (Soltis *et al.*, 1999).

The task of building a coherent picture of relationships for *Apiales* on the basis of these studies is complicated, not merely by the large number of analyses (and resulting trees) involved, but also by the diverse source and nature (e.g. evolutionary rate) of the data, and the disparate sampling schemes used in each analysis. It may be argued that assembly and analysis of all the raw data from these studies might provide the most rigorous approach to exploring phylogenetic relationships (the 'total evidence' approach; see Kluge & Wolf, 1993), but this would necessitate the addition of vast amounts of missing characters to accommodate differences in taxon sampling, and would also require attempts to align sequence data across many distantly related taxa (an especially troublesome task for non-coding sequences). To avoid these pitfalls, a modification of the phylogenetic 'supertree' approach has instead been followed (see Sanderson *et al.*, 1998). Although use of supertrees remains controversial, the trees constructed in the present study are herein viewed as graphical synopses or condensations depicting relationships suggested by recent molecular studies rather than consensus trees in a strict cladistic sense.

Two distinct (but interrelated) problems must be addressed to examine higher taxonomic relationships in *Apiales*: the placement of the order among the other groups of higher dicots, and the relationships between its two constituent families. Sampling strategies in many of the molecular studies have closely paralleled these two levels: in most interordinal (and angiosperm-wide) analyses, a very small number of exemplar taxa are generally used as placeholders for entire families, whereas interfamilial studies typically include many taxa from within each family, but only one or several more distantly related taxa (and then often as the outgroup). For this reason, two separate supertrees were constructed at the interordinal and interfamilial levels. After reviewing the sampling scheme employed in the molecular studies listed above, 18 strict consensus trees (resulting from parsimony analyses) were selected as 'source trees'. In cases where two studies were published using highly redundant sampling schemes and data sources (e.g. the *rbc*L trees from Olmstead *et al.*, 1992 vs. 1993; and the 18S trees from Nickrent & Soltis, 1995, vs. Soltis *et al.*, 1997), only the tree resulting from the more comprehensive study was retained. For the interordinal supertree, trees from the following seven studies were employed: Downie & Palmer (1992, their Fig. 2); Chase *et al.* (1993, their Figs 12–15); Olmstead *et al.* (1993, their Fig. 3); Plunkett *et al.* (1996a, their Fig. 1); Xiang &

Soltis (1998, their Fig. 2); Soltis *et al.* (1999); and Soltis *et al.* (1997, their Fig. 2D; due to the small sample of apialean taxa employed in this last study and the spurious placement of *Lomatium* Raf. at the base of *Apiales*, this taxon was excluded). For the interfamilial supertree, 11 source trees were selected, including those from Plunkett *et al.* (Fig. 2 in 1996a; Fig. 2 in 1996b; Fig. 3 in 1997); Downie *et al.* (Figs 2, 6 in 1998); Downie & Katz-Downie (Fig. 2 in 1999); Plunkett & Downie (Fig. 1 in 1999); Wen *et al.* (Fig. 1 in 2001); and Plunkett & Lowry (Figs 1–3 in 2001).

Topologies from each source tree were translated into data matrices of binary characters following the matrix representation with parsimony (MRP) method (Baum, 1992; Ragan, 1992; see also Sanderson *et al.*, 1998). Inclusion of a taxon in a given clade was scored as 1 and its exclusion as 0; taxa not sampled in a given source tree were coded as missing data. An all-zero outgroup (a terminal scored with zeros at all characters) was added to each matrix as a root for the resulting trees. To reduce the number of terminals, monophyletic groups of species in the same genus were scored as a single taxon (e.g. *Hydrocotyle* L., *Eryngium* L., *Myodocarpus* Brongn. & Gris.). Likewise, two large clades of taxa (*Lamiidae* sensu Takhtajan and *Ericales* plus their allies) were treated as a single terminal because source trees indicated that these clades did not include *Apiales* or any of their putative relatives. Lastly, many taxonomic groups known to be unrelated to *Apiales* (e.g. gymnosperms, lower dicots, monocots, and many lower eudicot groups) were eliminated altogether from the angiosperm-wide source trees (e.g. Chase *et al.*, 1993; Soltis *et al.*, 1997). Both data matrices are available from the author upon request. Interordinal and interfamilial supertrees were constructed using PAUP* (Swofford, 1998). In both sets of analyses, preliminary trials yielded tens of thousands of shortest trees, quickly exhausting computer memory. To balance the need to explore multiple islands of most parsimonious trees with the desire to examine a large but manageable total number of trees, a two-step analysis was completed for each matrix (using TBR branch swapping, MULPARS, and ACCTRANS options throughout). In the first step, 100 random addition searches were performed saving no more than 100 trees per replicate. The resulting trees were then used as starting trees for a final heuristic search (with the same options), saving a maximum of 10,000 trees and swapping to completion. Consensus trees resulting from these final searches were used to explore relationship of *Apiales* and other groups of higher dicots and to test 'traditional' notions of evolutionary patterns compiled from earlier studies.

RESULTS AND DISCUSSION

Based on concepts prevailing before the widespread application of molecular data and cladistic approaches (Philipson, 1970; Eyde & Tseng, 1971; Rodríguez, 1971; Cronquist, 1981), the traditional assumptions regarding apialean evolution held that the order is most closely related to *Cornales* or perhaps to *Sapindales* (especially *Burseraceae* and/or *Rutaceae*), and were derived from within *Rosidae* (*sensu* Cronquist). The common ancestor of *Apiales* was widely assumed to be a woody tree or shrub with schizogenous secretory canals, multilacunate nodes, compound leaves (probably pinnately so) with spiral phyllotaxy, and flowers arranged in racemes or panicles. Although Cronquist (1981) argued for pentamerous flowers as the primitive character state (except in the androecia), most authors postulated that 'moderate' polymery (> 5) was ancestral (Philipson, 1970; Eyde & Tseng, 1971); flowers with smaller numbers of parts were viewed as reduced and derived. Moreover, there was general agreement that the ancestral flowers had minute calyx lobes, polypetalous corollas, a single whorl of stamens, and an epigynous gynoecium with axile placentation in which each of the 5+ carpels contained a single functional ovule.

Inspection of recent phylogenetic studies and the results of the interordinal supertree analysis (Fig. 1) strongly challenge earlier ideas of apialean relationships. All molecular studies to date suggest that *Apiales* are not closely related to *Sapindales*

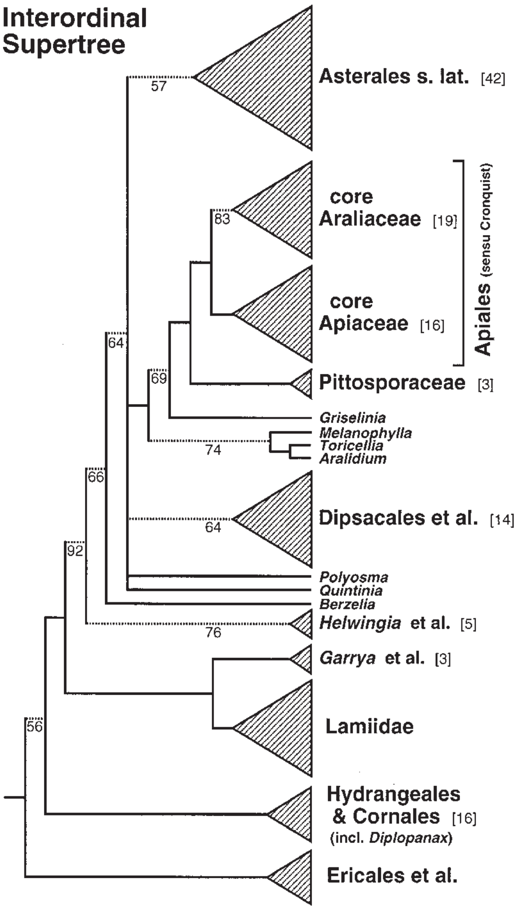

FIG. 1. Consensus tree of 10,000 shortest trees (each of 281 steps) resulting from matrix representation with parsimony (MRP) analysis of the data matrix (236 characters and 128 terminals, including the all-zero outgroup) based on seven interordinal or angiosperm-wide studies (see text). To highlight interordinal relationships involving *Apiales* and their presumed close relatives, the majority-rule (50%) tree is presented in abbreviated form; dashed lines (with majority rule percentages) indicate those branches not found in all shortest-length trees; the strict consensus can be derived by collapsing these dashed branches. Bracketed numbers in the clade labels, adjacent to abbreviated (triangular) clades, indicate the number of terminals represented; *Lamiidae* and ericalean clades were scored as a single terminal.

(which recent studies retain in *Rosidae*) or to *Cornales* (which are sister to *Hydrangeaceae*). Instead, the order forms a monophyletic group with *Pittosporaceae* (cf. Dahlgren, 1980), and this *Apiales–Pittosporaceae* clade is sister to four genera formerly allied to *Cornaceae* (viz. *Griselinia* G. Forst., *Melanophylla* Baker, *Torricellia* DC. and *Aralidium* Miq.). Together, these groups form what Plunkett *et al.* (1996a) called the 'apialean alliance'. Further, this entire alliance is placed not in subclass *Rosidae*, but instead within the *Asteridae*, where they form a clade with several derived groups, including *Asterales* and *Dipsacales*.

Although molecular data largely disagree with the 'traditional' taxonomic systems regarding *Apiales*, careful analysis shows that non-molecular data from many sources provide strong support for the molecular topologies. For example, the close relationship of *Pittosporaceae* to *Apiales* is not a novel idea, despite Cronquist's (1981) and Eyde & Tseng's (1971) emphatic dismissal of the notion. In fact, successive studies dating to the late nineteenth century offer evidence for this relationship, including the shared presence of schizogenous secretory canals in the stems (van Tieghem, 1884), similar ovule structure and development (Jurica, 1922), the same basic chromosome number (Jay, 1969), and similar phytochemical compounds (Hegnauer, 1971, 1982; Dahlgren, 1980; Jensen, 1992).

In a similar manner, there are many links between *Apiales* and several groups of higher asterids. Subclass *Asteridae* is generally defined as having sympetalous corollas, haplostemonous androecia, and unitegmic, tenuinucellate ovules (see Hufford, 1992; Wagenitz, 1992). The polypetalous *Apiales* may appear out of place among these sympetalous lineages, but Erbar & Leins (1988, 1996) have demonstrated that the corollas of *Apiales* (and of *Pittosporaceae*) are initiated from a continuous ring of primordium tissue, corresponding exactly to corolla development in both *Asterales* and *Dipsacales* (see also Erbar, 1988; Donoghue *et al.*, 1992; Backlund and Bremer, 1996; Roels & Smets, 1996). In the two latter groups, however, the corollas retain their 'early sympetally' throughout development, whereas those of most *Apiales* eventually form what appear to be distinctly free petals. In a few notable exceptions, basal fusion is more evident in *Araliaceae* (as in *Osmoxylon* Miq.), and basally fused petals are common among the closely related *Pittosporaceae*. Significantly, this shared developmental character is lacking in the asterids falling outside of the *Asterales–Dipsacales–Apiales* clade (e.g. *Lamiales* and related orders). Among these other *Asteridae*, the corolla is initiated from several distinct primordia; only later in development do these primordia fuse to form a single corolla tube ('late sympetaly' *sensu* Erbar & Leins, 1996). In addition to petal development, several other characters serve to link *Apiales* to the *Asteridae*, including a single integument, mostly tenuinucellate ovules (although many araliads are crassinucellate), and S-type sieve-tube plastids (Hufford, 1992; Wagenitz, 1992). There are also many phytochemical connections between *Apiales* and *Asterales*, such as similar triterpenic sapogenins, polyacetylenes, alkaloids, flavonols, and acetate-derived arthroquinones, as well as isopentenyl-substituted coumarins and several other classes of compounds; both groups also lack iridoids and tannins (Hegnauer, 1971, 1982; Jensen, 1992; Watson

& Dallwitz, 1992). It must be noted, however, that the biochemistry of *Griselinia*, *Torricellia*, and *Aralidium* is somewhat different; these genera produce seco-iridoids (especially griselinoside), which are lacking in *Apiales* and *Asterales*, but are known to occur in both *Cornaceae* and *Dipsacales* (Jensen & Nielsen, 1980; Jensen, 1992; Watson & Dallwitz, 1992).

Molecular data have also provided a means to resolve the placement of many 'bridging' genera once thought to link *Cornales* to *Apiales* (see Rodríguez, 1971; Philipson & Stone, 1980; Eyde, 1988). As a result of studies focusing on both orders (e.g. Xiang *et al.*, 1993, 1998; Plunkett *et al.*, 1996a, 1997; Xiang & Soltis, 1998), a growing consensus is emerging as to the placement of these taxa. Some genera can now be excluded from both *Cornales* and *Apiales* (e.g. *Helwingia* Willd., *Kaliphora* Hook.f.). Many others have been placed within or near one of the two orders. For example, *Aralidium* and *Diplopanax* Hand.-Mazz. have both been referred to *Araliaceae* (Miquel, 1855; Bentham, 1867; Harms, 1898; Handel-Mazzetti, 1933), but a number of vegetative and floral features made their placement in this family problematic (see Philipson & Stone, 1980; Eyde & Xiang, 1990). Molecular data suggest that *Diplopanax* is allied to *Cornales*, in a clade with *Nyssa* L., *Camptotheca* Decne., *Davidia* Baill., and *Mastixia* Blume. (Fig. 1; see also Xiang *et al.*, 1993, 1998; Xiang & Soltis, 1998). *Aralidium* can also be excluded from *Araliaceae*, but it appears to comprise a clade (or grade) along with *Torricellia*, *Melanophylla*, and *Griselinia* at the base of the *Apiales–Pittosporaceae* clade (Fig. 1).

Within *Apiales*, the overall relationships illustrated in the interfamilial supertree (Fig. 2) agree closely to the findings of Plunkett *et al.* (1996a, 1997) and Downie *et al.* (1998, 2001). There are two major clades corresponding closely to the traditional circumscriptions of the two families (informally named 'core *Araliaceae*' and 'core *Apiaceae*'). Several groups of taxa, however, are excluded from both core groups. Among these are some members of *Apiaceae* subfamily *Hydrocotyloideae*, which all molecular studies to date suggest is polyphyletic (forming as few as three and as many as eight distinct groups within *Apiales*). Also excluded are five araliad genera, which form two distinct clades in *Apiales* (Plunkett & Lowry, 2001). These two clades closely match the traditional araliad tribes *Myodocarpeae* (*Myodocarpus–Delarbrea* Vieill.–*Pseudosciadium* Baill.) and *Mackinlayeae* (*Mackinlaya* Hook.f.–*Apiopetalum* Baill.), the latter of which also includes several hydrocotyloid genera (e.g. *Centella* L., *Micropleura* Lag., and *Actinotus* Labill.). Within core *Araliaceae*, *Osmoxylon* and *Astrotricha* DC. are successive sister groups to the remaining araliads. The genus *Hydrocotyle* is sister to core *Araliaceae*, and another hydrocotyloid, *Trachymene* Rudge (syn. *Didiscus* DC.), is nested within the core-*Araliaceae* clade. The core-*Apiaceae* clade comprises several major subclades, including one closely matching the circumscription of subfamily *Apioideae*, another including the saniculoids (as sister to a clade of two woody African apioids and the African hydrocotyloid *Arctopus* L.), and a third clade or grade of hydrocotyloids (including *Azorella* Lam., *Bolax* Juss., and *Eremocharis* Phil., *inter alia*).

The growing consensus among molecular studies regarding relationships within

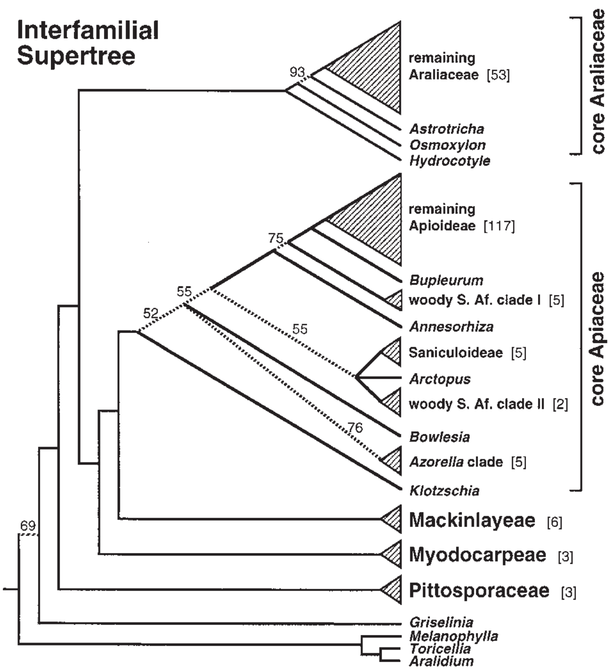

FIG. 2. Consensus tree of 10,000 shortest trees (each of 553 steps) resulting from matrix representation with parsimony (MRP) analysis of the data matrix (461 characters and 212 terminals, including the all-zero outgroup) based on 11 inter- or infrafamilial source trees (see text). To highlight relationships among the major clades of *Apiales* and their close relatives, the majority-rule (50%) tree is presented in abbreviated form; dashed lines (with majority rule percentages) indicate those branches not found in all shortest-length trees; the strict consensus can be derived by collapsing these dashed branches. Bracketed numbers in the clade labels, adjacent to abbreviated (triangular) clades, indicate the number of terminals represented. Taxa labelled 'woody south African clade I' include the apioids *Anginon* Raf., *Heteromorpha* Cham. & Schltdl., *Dracosciadium* Hilliard & B. L. Burtt, *Polemannia* Eckl. & Zeyh., and *Glia* Sond.; the 'woody south African clade II' comprises the apioids *Polemanniopsis* B. L. Burtt and *Steganotaenia* Hoscht. (see Downie & Katz-Downie, 1999); taxa in the *Mackinlayeae* clade includes the araliads *Mackinlaya* and *Apiopetalum*, and four hydrocotyloids (*Centella*, *Micropleura*, *Actinotus* and *Xanthosia* Rudge); the *Myodocarpeae* clade comprises *Delarbrea* plus *Pseudosciadium* (scored as a single terminal) and *Myodocarpus*, plus the hydrocotyloid *Spananthe* Jacq. The *Pittosporaceae* clade includes *Pittosporum* Gaertn., *Hymenosporum* F. Muell., and *Sollya* Lindl. Relationships within the core *Apiaceae* clade are further detailed in Downie *et al.* (2001), and those in the core *Araliaceae* clade by Lowry *et al.* (2001), Wen *et al.* (2001) and Plunkett & Lowry (2001).

Apiales (and among the higher asterids in general) provides an opportunity to re-examine evolutionary patterns in morphological and other non-molecular characters, and to compare these with the traditional concepts of apialean evolution described above. A similar effort was attempted previously in a study of *rbc*L sequence data by Plunkett *et al.* (1996a). In that study, the authors concluded that the ancestor of *Apiales* was likely a paleotropical shrub or small tree with simple leaves, pentamerous perianths and androecia, basally fused petals (at least in development), bicarpellate (or perhaps 3–4-carpellate) gynoecia, a polygamous mating system, paniculate inflorescences, and a basic chromosome number of $x = 12$. These findings, however, were based on a single marker (*rbc*L) and left several critical taxa unsampled.

In the present analysis, data have been summarized from many more taxa and from several additional molecular markers (see above). In general, the resulting supertrees (Figs 1, 2) strengthen and clarify the conclusions of the earlier *rbc*L study. For example, the previous analysis suggested that bicarpelly was ancestral in *Apiales*, in opposition to the traditional assumption of pentacarpelly or pluricarpelly. The interfamilial supertree (Fig. 2), reflecting the findings of several recent studies, places bicarpellate taxa in basally branching positions in each of the major clades. The flowers of all members traditionally assigned to *Apiaceae* have two carpels, and so it is not surprising that all taxa in core *Apiaceae* are thus characterized. However, the position of *Hydrocotyle*, *Osmoxylon*, and *Astrotricha* as successive sister groups to the remaining members of core *Araliaceae* suggests bicarpelly may have occurred in the early araliads as well. Further, the taxa comprising the segregate tribes *Myodocarpeae* and *Mackinlayeae* are also characterized almost exclusively by bicarpelly. Among the close relatives of *Apiales*, the polarity of this character is less clear, but low carpel numbers (2–4) predominate, and pentacarpelly is known only very rarely in *Pittosporaceae* (viz. *Pittosporum sinuatum* Bl. and *P. spinescens* (F. Muell.) L. Cayzer, Crisp & I. Telford; Cayzer, 1998). Bicarpelly is also common among the early diverging lineages in *Asterales* and *Dipsacales* (e.g. Chase *et al.*, 1993; Olmstead *et al.*, 1993; Backlund, 1996; Backlund & Bremer, 1996).

Other comparisons among the close relatives of *Apiales* and the basally branching lineages within the order are also instructive (see Table 1 for an overview of the relevant vegetative and reproductive features found in these groups). For example, the early diverging lineages of each major clade in the apialean alliance are characterized by simple leaves, refuting the traditional notion that *Apiales* 'terminate a long line of compound-leaved members of the *Rosidae*' (Cronquist, 1981: 553). Moreover, most groups are characterized by alternate phyllotaxy, sheathing petioles, and the lack of stipules. *Apiales* and *Pittosporaceae* also share schizogenous secretory canals in their stems (absent, however, in *Griselinia*, *Melanophylla*, *Torricellia*, and *Aralidium*). Reproductively, it would appear that the various umbellate inflorescences of *Apiales* were derived from panicles, racemes, or perhaps cymes, which predominate in *Pittosporaceae* and the other four genera. Mating systems throughout the apialean alliance are quite variable, but among the four genera, *Griselinia*, *Aralidium*, and *Torricellia* are each dioecious (except some monoecious species of *Torricellia*); only *Melanophylla* is hermaphroditic (see Wangerin, 1910; Philipson, 1967; Philipson & Stone, 1980; Eyde, 1988; Dillon & Muñoz-Schick, 1993). *Pittosporaceae* exhibit a wide variety of mating systems, including (but not limited to) dioecy, gynodioecy, monoecy, and andromonoecy, in addition to hermaphroditism (Cayzer, 1998).

TABLE 1. Comparison of vegetative and reproductive characters of major groups in the 'apialean alliance'. Character states for core *Apiaceae*, core *Araliaceae*, and *Pittosporaceae* do not include rare exceptions (e.g. opposite leaves in only one genus of *Araliaceae*). *, basic chromosome number of $x = 10$ for *Aralidium* based on report of $2n = 40 \pm 2$ by Hellmayr *et al.* (1994). Other references: Harms (1897), Drude (1898), Wangerin (1910), Philipson (1967, 1970), Hutchinson (1967), Eyde & Tseng (1971), Rodríguez (1971), Bate-Smith (1980), Jensen & Nielsen (1980), Philipson & Stone (1980), Cronquist (1981), Eyde (1988), Watson & Dallwitz (1992), Dillon & Muñoz-Schick (1993), Oginuma *et al.* (1994), Cayzer (1998)

	Taxon								
	Core *Apiaceae*	Core *Araliaceae*	*Myodocarpeae*	*Mackinlayeae*	*Pittosporaceae*	*Griselinia*	*Melanophylla*	*Aralidium*	*Torricellia*
Habit	Mostly herbaceous	Mostly woody	Woody	Woody or herbaceous	Woody	Woody	Woody	Woody	Woody
Schizogenous secretory canals	Present	Present	Present	Present	Present	Absent	Absent	Absent	Absent
Phyllotaxy	Alternate	Alternate	Alternate	Alternate	Alternate	Alternate	Alternate	Alternate	Alternate
Petiole base	Sheathing	Sheathing to non-sheathing	Sheathing	Sheathing	Sheathing to non-sheathing	Sub-sheathing	Sheathing to non-sheathing	Sheathing	Sheathing
Leaf shape	Compound or simple	Compound or simple	Compound or simple	Compound or simple	Simple (to pinnatifid)	Simple	Simple	Simple (pinnatifid)	Simple (to palmatifid)
Inflorescence	Umbels (often compound)	Panicles or racemes (often of umbels)	Panicles or racemes (often of umbels)	Panicles or racemes (often of umbels)	Cymes or corymbs	Racemes or panicles	Racemes	Panicles (of cymes)	Panicles or cymes

TABLE 1. (Continued.)

	Taxon								
	Core *Apiaceae*	Core *Araliaceae*	*Myodocarpeae*	*Mackinlayeae*	*Pittosporaceae*	*Griselinia*	*Melanophylla*	*Aralidium*	*Torricellia*
Mating system	Hermaphroditic or andromonoecious	Hermaphroditic, andromonoecious, monoecious, gynomonoecious, dioecious	Andromonoecious or hermaphroditic	Andromonoecious or hermaphroditic	Hermaphroditic, andromonoecious, monoecious, gynodioecious, dioecious	Dioecious	Hermaphroditic	Dioecious	Monoecious or dioecious
Sepals/Petals	5/5	3–5(–12)/(3–)5(–12)	5/5	5/5	5/5	5/(0 or) 5	5/5	5/5	(3–)5/(0 or) 5
Petal aestivation	Valvate	Imbricate (or valvate)	Imbricate	Valvate	Imbricate	(Sub)-imbricate	Imbricate	Imbricate	Valvate
Stamens	5	(3–)5(–>100)	5	5	5	5	5	5	5
Carpels	2	2–5(–>100)	2	2(–4)	2(–3)	3	2–3	3(–4)	3–4
Locules	2	2–5(–>100)	2	2(–4)	1–2(–3)	2 (only 1 ovuliferous)	2–3 (only 1 ovuliferous)	3(–4) (only 1 ovuliferous)	3–4 (only 1 ovuliferous)
Floral insertion	Epigynous	Epigynous	Epigynous	Epigynous	Hypogynous	Epigynous	Epigynous	Epigynous	Epigynous
Epigynous disc	Present	Present	Present	Present	Absent	Present	Absent	Present	Absent
Placentation	Apical to axile	Apical	Apical	Apical	Axile or parietal	Apical	Apical to axile	Apical	Apical

TABLE 1. (Continued.)

	Taxon								
	Core *Apiaceae*	Core *Araliaceae*	*Myodocarpeae*	*Mackinlayeae*	*Pittosporaceae*	*Griselinia*	*Melanophylla*	*Aralidium*	*Torricellia*
Functional ovules per locule	1	1	1	1	4–∝	1	1	1	1
Fruit type	Schizocarp	Drupe or berry	Drupe or schizocarp	Drupe or schizocarp	Capsule or berry	Berry	Drupe	Drupe	Drupe
Seeds	Endosperm copious, embryos small	Endosperm copious, embryos small	Endosperm copious, embryos small	Endosperm copious, Embryos small	Endosperm copious, embryos small	Endosperm copious, embryos small	Endosperm copious, embryos small	Endosperm copious, embryos small	Endosperm copious, embryos small
Chromosomes	$x = 8$ or 11	$x = 12$	$x = 12$	Not known	$x = 12$	$x = 9$	Not known	$x = 10$*	$x = 12$
Distribution	Cosmopolitan (mostly north temperate)	Cosmopolitan (mostly paleotropics)	Australasia (mostly New Caledonia)	Paleotropics (mostly Australasia)	Paleotropics (mostly Australasia)	New Zealand and Chile	Madagascar	Australasia	E Himalayas and China

Apiales were traditionally considered to be ancestrally hermaphroditic, but andromonoecy is very common in *Apiaceae* and among many araliads. The 'basal' placement of tribes *Myodocarpeae* and *Mackinlayeae*, whose members are almost all andromonoecious, provides further evidence for this theory, and is discussed in greater detail by Schlessman *et al.* (2001). The floral formula of *Apiaceae* is extremely stable, but that of other groups in the apialean alliance appears to be somewhat more variable. Nevertheless, flowers with pentamerous perianths and androecia (and bicarpellate gynoecia) are found in many taxa from each of the major groups of the alliance, suggesting that this may be the original formula from which all others have been derived. Floral insertion is uniformly epigynous with the notable exception of *Pittosporaceae* and of a single species of *Araliaceae*, *Tetraplasandra gymnocarpa* (Hillebr.) Sherff. Eyde & Tseng (1969), however, convincingly demonstrated that 'hypogyny' in *T. gymnocarpa* was secondarily derived from epigyny (see also Costello & Motley, 2001). The placement of *Pittosporaceae* in the supertrees (nested among exclusively epigynous taxa; Figs 1, 2) clearly suggests that their superior ovaries are also secondarily derived, but developmental studies are needed to test this hypothesis. Several other features can also be interpreted as ancestral, such as seeds with copious endosperm and small embryos, a basic chromosome number of $x = 12$, a woody habit, and a paleotropical distribution.

The emergence of a stable phylogeny for *Apiales* (and the angiosperms in general), together with resultant hypotheses of character-state evolution, provides a framework for understanding why the systematics of this group has been so perplexing. Viewing apialean morphologies along a continuum, many workers interpreted the features predominating in *Araliaceae* as ancestral ('primitive'), and those in *Apiaceae* as derived ('advanced'). This vision left many taxa with a confounding mixture of ancestral and derived features, blurring the delimitation between the two families. Among such 'intermediate' or 'bridging' genera were most members of *Hydrocotyloideae*, *Myodocarpeae*, and *Mackinlayeae*. Molecular data have now helped to resolve the placement of many of these groups. *Myodocarpeae* and *Mackinlayeae*, for example, do not appear to belong to core *Araliaceae*, but instead should be recognized as distinct clades within *Apiales* (see Lowry *et al.*, 2001, and Plunkett & Lowry, 2001). Relationships among the various polyphyletic lineages of *Hydrocotyloideae* are complex, but the alliance of some groups to core *Apiaceae* and others to core *Araliaceae* and *Mackinlayeae* makes it easy to see why these taxa were viewed as intermediates. Moreover, the molecular topologies provide a clearer picture of character-state evolution, as taxa occupying the earliest diverging lineages in all the major clades of *Apiales* present a relatively unified repertoire of morphologies. In core *Araliaceae*, for example, the Australasian shrubby genera *Osmoxylon* and *Astrotricha* are basally branching, and in core *Apiaceae*, there are several woody, southern African umbellifers at the base of both the apioid and saniculoid subclades (Fig. 2). Together with the Australasian (and largely New Caledonian) representatives of *Myodocarpeae* and *Mackinlayeae*, these taxa include mostly woody, paleotropical shrubs or small trees with bicarpellate flowers, andromonoecious mating systems, and (in many cases) simple leaves (cf. Lowry *et al.*, 2001). These findings suggest that many of the difficulties in understanding evolutionary relationships in the order *Apiales* and its placement among the higher dicots were due to faulty assumptions regarding character-state polarity, and further complicated by the persistent influence of a phyletic model of evolutionary transformations.

Acknowledgements

The author gratefully acknowledges financial support from the National Science Foundation (DEB 92-11400 and 99-81641), National Geographic Society (5793-96), and the Thomas F. Jeffress and Kate Miller Jeffress Memorial Trust (J-506), and the assistance of P. P. Lowry II, A. A. Oskolski, S. R. Downie, D. S. Katz-Downie, B.-Y. Lee, D. E. Soltis, P. S. Soltis, Q. Xiang, R. K. Kuzoff, A. Backlund, and the staffs of ORSTOM (Nouméa, New Caledonia) and CSIRO (Atherton and Canberra).

References

Adanson, M. (1763). *Familles des Plantes*. Paris: Vincent.

Angiosperm Phylogeny Group (1998). An ordinal classification of flowering plants. *Ann. Missouri Bot. Gard.* 85: 531–553.

Backlund, A. (1996). Phylogeny of the *Dipsacales*. *Acta Univ. Ups*. 243: 1–34.

Backlund, A. & Bremer, B. (1996). Phylogeny of the *Asteridae s. str.* based on *rbc*L sequences, with particular reference to the *Dipsacales*. *Plant Syst. Evol.* 207: 225–254.

Bate-Smith, E. C. (1980). The systematic position of *Aralidium* Miq. – a multidisciplinary study. 5. A note on the phenolic constituents. *Taxon* 29: 412.

Baum, B. R. (1992). Combining trees as a way of combining data sets for phylogenetic inference, and the desirability of combining gene trees. *Taxon* 41: 3–10.

Bentham, G. (1867). *Araliaceae*. In: Bentham, G. & Hooker, J. D. (eds) *Genera Plantarum*, Vol. 1, pp. 931–947. London: Reeve & Co.

Bessey, C. E. (1915). Phylogenetic taxonomy of flowering plants. *Ann. Missouri Bot. Gard.* 2: 109–164.

Cayzer, L. W. (1998). *Revision of the family* Pittosporaceae *in Australia*. PhD dissertation, Australian National University, Canberra.

Chase, M. W., Soltis, D. E., Olmstead, R. G. *et al.* (1993). Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbc*L. *Ann. Missouri Bot. Gard.* 80: 528–580.

Constance, L. (1971). History of the classification of *Umbelliferae* (*Apiaceae*). In: Heywood, V. H. (ed.) *The Biology and Chemistry of the Umbelliferae*, pp. 1–11. London: Academic Press.

Costello, A. & Motley, T. J. (2001). Molecular systematics of *Tetraplasandra*, *Munroidendron* and *Reynoldsia sandwicensis* (*Araliaceae*) and the evolution of superior ovaries in *Tetraplasandra*. *Edinb. J. Bot.* 58 (2): 229–242.

Cronquist, A. (1981). *An Integrated System of Classification of Flowering Plants*. New York, NY: Columbia University Press.

Cronquist, A. (1988). *The Evolution and Classification of Flowering Plants.* New York, NY: New York Botanical Garden.

Dahlgren, R. M. T. (1980). A revised system of classification of the angiosperms. *Bot. J. Linn. Soc*. 80: 91–124.

Dillon, M. O. & Muñoz-Schick, M. (1993). A revision of the dioecious genus *Griselinia* (*Griseliniaceae*), including a new species from the coastal Atacama Desert of northern Chile. *Brittonia* 45: 261–274.

Donoghue, M. J, Olmstead, R. G., Smith, J. F. & Palmer, J. D. (1992). Phylogenetic relationships of *Dipsacales* based on *rbc*L sequences. *Ann. Missouri Bot. Gard.* 79: 333–345.

Downie, S. R. & Katz-Downie, D. S. (1996). A molecular phylogeny of *Apiaceae* subfamily *Apioideae*: evidence from nuclear ribosomal DNA internal transcribed spacer sequences. *Amer. J. Bot.* 83: 234–251.

Downie, S. R. & Katz-Downie, D. S. (1999). Phylogenetic analysis of chloroplast *rps*16 intron sequences reveals relationships among within the woody southern African *Apiaceae* subfamily *Apioideae*. *Can. J. Bot.* 77: 1120–1135.

Downie, S. R. & Palmer, J. D. (1992). Restriction site mapping of the chloroplast DNA inverted repeat: a molecular phylogeny of the *Asteridae*. *Ann. Missouri Bot. Gard.* 79: 266–283.

Downie, S. R., Katz-Downie, D. S. & Cho, K.-J. (1996). Phylogenetic analysis of *Apiaceae* subfamily *Apioideae* using nucleotide sequences from the chloroplast *rpo*C1 intron. *Molec. Phyl. Evol.* 6: 1–18.

Downie, S. R., Ramanath, S., Katz-Downie, D. S. & Llanas, E. (1998). Molecular systematics of *Apiaceae* subfamily *Apioideae*: phylogenetic analysis of nuclear ribosomal DNA internal transcribed spacer and plastid *rpo*C1 intron sequences. *Amer. J. Bot.* 85: 563–591.

Downie, S. R., Plunkett, G. M., Watson, M. F. *et al.* (2001). Tribes and clades within *Apiaceae* subfamily *Apioideae*: the contribution of molecular data. *Edinb. J Bot.* 58 (2): 301–330.

Drude, C. G. O. (1898). Umbelliferae. In: Engler, A. & Prantl, K. (eds) *Die Natürlichen Planzenfamilien*, Vol. 3 (8), pp. 63–250. Leipzig: W. Engelmann.

Erbar, C. (1988). Early developmental patterns in flowers and their value for systematics. In: Leins, P., Tucker, S. C. & Endress, P. (eds) *Aspects of Floral Development*, pp. 7–23. Berlin: Cramer.

Erbar, C. & Leins, P. (1988). Blütenentwicklungsgeschichliche Studien an *Aralia* und *Hedera* (*Araliaceae*). *Flora* 180: 391–406.

Erbar, C. & Leins, P. (1996). Distribution of the character states 'early sympetaly' and 'late sympetaly' within the 'sympetalae tetracyclicae' and presumably allied groups. *Bot. Acta* 109: 427–440.

Eyde, R. H. (1988). Comprehending *Cornus*: puzzles and progress in the systematics of the dogwoods. *Bot. Review* 54: 233–351.

Eyde, R. H. & Tseng, C. C. (1969). Flower of *Tetraplasandra gymnocarpa*: hypogyny with epigynous ancestry. *Science* 166: 506–508.

Eyde, R. H. & Tseng, C. C. (1971). What is the primitive floral structure of *Araliaceae*? *J. Arnold Arb.* 52: 205–239.

Eyde, R. H. & Xiang, Q.-Y. (1990). Fossil mastixioid (*Cornaceae*) alive in eastern Asia. *Amer. J. Bot.* 77: 689–692.

Handel-Mazzetti, H. F. von (1933). Plantae novae Chingianae, III. *Sinensia* 3: 185–198.

Harms, H. (1898). *Araliaceae*. In: Engler, A. & Prantl, K. (eds) *Die Natürlichen Pflanzenfamilien*, Vol. 3 (8), pp. 1–62. Leipzig: W. Engelmann.

Hegnauer, R. (1971). Chemical patterns and relationships of Umbelliferae. In:

HEYWOOD, V. H. (ed.) *The Biology and Chemistry of the Umbelliferae*, pp. 267–277. London: Academic Press.

HEGNAUER, R. (1982). Phytochemie und Klassifikation der Umbelliferen, eine Neubewertung im Lichte der Siet 1972 bekannt gewordenen phytochemischen Tatsachen. In: CAUWET-MARC, A.-M. & CARBONNIER, J. (eds). *Les Ombellifères: contributions pluridisciplinaires à la systématique: actes du 2ème Symposium International sur les Ombellifères, Centre Universitaire de Perpignan, 18–21 Mai 1977*, pp. 335–363. St Louis, MO: Missouri Botanical Garden.

HELLMAYR, E. M., KIEHN, M. & WEBER, A. (1994). Chromosome numbers of Malayan rain-forest angiosperms. *Beitr. Biol. Pflanzen* 68: 51–71.

HENNIG, W. (1966). *Phylogenetic Systematics*. Urbana, IL: University of Illinois Press.

HUFFORD, L. (1992). Phylogeny of *Asteridae*: an introduction. *Ann. Missouri Bot. Gard.* 79: 207–208.

HUTCHINSON, J. (1967). *The Genera of Flowering Plants*, Vol. 2. London: Oxford University Press.

JAY, M. (1969). Chemotaxonomic researches on vascular plants. XIX. Flavonoid distribution in the *Pittosporaceae*. *Bot. J. Linn. Soc.* 62: 423–429.

JENSEN, S. R. (1992). Systematic implications of the distribution of iridoids and other chemical compounds in the *Loganiaceae* and other families of the *Asteridae*. *Ann. Missouri Bot. Gard.* 79: 284–302.

JENSEN, S. R. & NIELSEN, B. J. (1980). The systematic position of *Aralidium* Miq. – a multidisciplinary study. 4. Iridoid glucosides. *Taxon* 29: 409–411.

JURICA, H. S. (1922). A morphological study of the *Umbelliferae*. *Bot. Gazette* 74: 292–307.

JUSSIEU, A. L. DE. (1789). *Genera Plantarum*. Paris: Herissant.

KLUGE, A. G. & WOLF, A. J. (1993). Cladistics: what's in a word? *Cladistics* 9: 183–199.

LOWRY II, P. P., PLUNKETT, G. M. & OSKOLSKI, A. A. (2001). Early lineages in *Apiales*: insights from morphology, wood anatomy and molecular data. *Edinb. J. Bot.* 58 (2): 207–220.

MIQUEL, F. A. G. (1855). *Plantae Junghuhnianae*, Part 3. Batavia.

NICKRENT, D. L. & SOLTIS, D. E. (1995). A comparison of angiosperm phylogenies from nuclear 18S rDNA and *rbc*L sequences. *Ann. Missouri Bot. Gard.* 82: 208–234.

OGINUMA, K., TOBE, H. & OHBA, H. (1994). Chromosomes of some woody plants from Nepal. *Acta Phytotax. Geobot.* 45: 15–22.

OLMSTEAD, R. G., MICHAELS, H. J., SCOTT, K. M. & PALMER, J. D. (1992). Monophyly of the *Asteridae* and identification of its major lineages inferred from *rbc*L sequences. *Ann. Missouri Bot. Gard.* 79: 249–265.

OLMSTEAD, R. G., BREMER, B., SCOTT, K. M. & PALMER, J. D. (1993). A parsimony analysis of the *Asteridae sensu lato* based on *rbc*L sequences. *Ann. Missouri Bot. Gard.* 80: 700–722.

PHILIPSON, W. R. (1967). *Griselinia* Forst. fil. – anomaly or link. *New Zeal. J. Bot.* 5: 134–165.

PHILIPSON, W. R. (1970). Constant and variable features of the *Araliaceae*. In: ROBSON, N. K. B., CUTLER, D. F. & GREGORY, M. (eds) *New Research in Plant Anatomy*, pp. 87–100. London: Academic Press.

PHILIPSON, W. R. & STONE, B. C. (1980). The systematic position of *Aralidium* Miq. – a multidisciplinary study. 1. Introduction and floral and general anatomy. *Taxon* 29: 391–404.

PLUNKETT, G. M. (1994). *A molecular-phylogenetic approach to the 'family-pair dilemma' in* Apiales *and* Cyperales. PhD dissertation, Washington State University, Pullman.

Plunkett, G. M. & Downie, S. R. (1999). Major lineages within *Apiaceae* subfamily *Apioideae*: a comparison of chloroplast restriction site data and DNA sequence data. *Amer. J. Bot.* 86: 1014–1026.

Plunkett, G. M. & Lowry II, P. P. (2001). Relationships among ‘ancient araliads’ and their significance for the systematics of *Apiales*. *Mol. Phyl. Evol.* 19 (in press).

Plunkett, G. M., Soltis, D. E. & Soltis, P. S. (1996a). Higher level relationships of *Apiales* (*Apiaceae* and *Araliaceae*) based on phylogenetic analysis of *rbc*L sequences. *Amer. J. Bot.* 83: 499–515.

Plunkett, G. M., Soltis, D. E. & Soltis, P. S. (1996b). Evolutionary patterns in *Apiaceae*: inferences based on *mat*K sequence data. *Syst. Bot.* 21: 477–495.

Plunkett, G. M., Soltis, D. E. & Soltis, P. S. (1997). Clarification of the relationship between *Apiaceae* and *Araliaceae* based on *mat*K and *rbc*L sequence data. *Amer. J. Bot.* 84: 565–580.

Ragan, M. A. (1992). Phylogenetic inference based on matrix representation of trees. *Molec. Phyl. Evol.* 1: 53–58.

Reduron, J.-P. (1989). La représentation végétale au travers des Ombellifères. *Bull. Soc. Industr. Mulhouse* 811–812: 29–50.

Rodríguez, R. L. (1971). The relationships of the Umbellales. In: Heywood, V. H. (ed.) *The Biology and Chemistry of the Umbelliferae*, pp. 63–91. London: Academic Press.

Roels, P. & Smets, E. (1996). A floral ontogenetic study in the *Dipsacales*. *Int. J. Plant Sci.* 157: 203–218.

Sanderson, M. J., Purvis, A. & Henze, C. (1998). Phylogenetic supertrees: assembling the trees of life. *Trends Ecol. Evol.* 13: 105–109.

Schlessman, M. A., Plunkett, G. M., Lowry II, P. P. & Lloyd, D. G. (2001). Sexual systems of New Caledonian *Araliaceae*: a preliminary phylogenetic reappraisal. *Edinb. J. Bot.* 58 (2): 221–228.

Sokal, R. R. & Sneath, P. H. A. (1963). *Principles of Numerical Taxonomy*. San Francisco: W. H. Freeman.

Soltis, P. S., Soltis, D. E. & Doyle, J. J. (1992). *Molecular Systematics of Plants.* New York: Chapman and Hall.

Soltis, D. E., Soltis, P. S., Doyle, J. J. *et al.* (1997). Angiosperm phylogeny inferred from 18S ribosomal DNA sequences. *Ann. Missouri Bot. Gard.* 84: 1–49.

Soltis, D. E., Soltis, P. S. & Doyle, J. J. (1998). *Molecular Systematics of Plants II: DNA sequencing*. Boston: Kluwer Academic Publishers.

Soltis, P. S., Soltis, D. E. & Chase, M. W. (1999). Angiosperm phylogeny inferred from multiple genes as a tool for comparative biology. *Nature* 402: 402–404

Swofford, D. L. (1998). *PAUP*: phylogenetic analysis using parsimony (*and other methods), version 4.0b2.* Sunderland, MA: Sinauer Associates, Inc.

Takhtajan, A. L. (1997). *Diversity and Classification of Flowering Plants*. New York: Columbia University Press.

Thorne, R. F. (1992). Classification and geography of flowering plants. *Bot. Review* 58: 225–348.

Tieghem, P. van (1884). Sur la structure et les affinités des Pittosporées. *Bull. Soc. Bot. France* 31: 384–385.

Wagenitz, G. (1992). The *Asteridae*: evolution of a concept and its present status. *Ann. Missouri Bot. Gard.* 79: 209–217.

Wangerin, W. (1910). *Cornaceae*. In: Engler, A. (ed.) *Das Pflanzenreich, Regni Vegetabilis Conspectus*, Vol. IV (229), pp. 1–101.

Watson, L. & Dallwitz, M. J. (1992 onwards). *The Families of Flowering Plants: descriptions, illustrations, identification, and information retrieval.* http://biodiversity.uno.edu/delta/angio/ (29 May 1999 version).

Wen, J., Plunkett, G. M., Mitchell, A. D. & Wagstaff, S. J. (2001). The evolution of *Araliaceae*: a phylogenetic analysis based on ITS sequences of nuclear ribosomal DNA. *Syst. Bot.* 26: 144–167.

Xiang, Q. Y. & Soltis, D. E. (1998). *Rbc*L sequence data define a cornaceous clade and clarify relationships of *Cornaceae sensu lato*. In: Bouffard, D. E. & Ohba, H. (eds) *Sino-Japanese Flora: its characteristics and diversification* (Bulletin no. 37), pp. 123–137. Tokyo: University Museum, University of Tokyo.

Xiang, Q. Y., Soltis, D. E., Morgan, D. R. & Soltis, P. S. (1993). Phylogenetic relationships of *Cornus* L. *sensu lato* and putative relatives inferred from *rbc*L sequence data. *Ann. Missouri Bot. Gard.* 80: 723–734.

Xiang, Q. Y., Soltis, D. E. & Soltis, P. S. (1998). Phylogenetic relationships of *Cornaceae* and close relatives inferred from *mat*K and *rbc*L sequences. *Amer. J. Bot.* 85: 285–297.

Received 15 January 2000; accepted with revision 18 June 2000