

---

# ROSIDAE AND THEIR RELATIONSHIPS TO OTHER NONMAGNOLIID DICOTYLEDONS: A PHYLOGENETIC ANALYSIS USING MORPHOLOGICAL AND CHEMICAL DATA<sup>1</sup>

Larry Hufford<sup>2</sup>

---

## ABSTRACT

Parsimony analysis was used to develop phylogenetic hypotheses for Rosidae and other nonmagnoliid dicotyledons, especially Asteridae. Rosidae were placed among "lower" Hamamelidae as the sister group of *Platanus* and Hamamelidaceae. "Higher" Hamamelidae (Fagales, Juglandales, and Casuarinaceae), Dilleniidae, and Asteridae nest within a paraphyletic Rosidae. With some expansion, the traditional Asteridae are monophyletic. For example, the problematic *Columellia* was placed among Asteridae as the sister group of Caprifoliaceae. Asteridae were placed as the sister group of Ericales among rosids circumscribed as Corniflorae in recent classifications of Dahlgren. Special attention was given to problematic groups that have been allied variously with Asteridae, Dilleniidae, and Rosidae. For example, Actinidiaceae and Fouquieriaceae were placed among Ericales. Loasaceae and Sarraceniaceae formed the sister group of Hydrangeaceae in the Corniflorae grade of Rosidae. Dilleniidae were not monophyletic. For example, *Paeonia* was placed as the sister taxon of the rest of the Rosidae (including dilleniids and asterids), and Ochnaceae as the sister taxon of Linales. Dilleniaceae and Theaceae form a monophyletic group with *Paracryphia* placed as the sister group of Rhizophoraceae and Anisophylleaceae.

---

Rosidae are central to understanding phylogenetic patterns among nonmagnoliid dicotyledons. As circumscribed by Takhtajan (1969, 1980, 1987) and Cronquist (1981, 1988), Rosidae may be paraphyletic with respect to Asteridae, Dilleniidae, and some Hamamelidae. To understand better the evolution and diversification of nonmagnoliid dicotyledons, more precise and viable hypotheses of relationships among these major groups are necessary.

Rosidae have been considered "more advanced" than Magnoliidae and "less advanced" than Asteridae (Cronquist, 1981). Cunoniaceae, Rosaceae, and other members of the broadly circumscribed Rosales of Cronquist (1981; or Rosanae of Takhtajan, 1987) have been considered primitive Rosidae because their morphological, anatomical, and chemical attributes are similar to those of many Hamamelidae. Hamamelidae (sensu Takhtajan, 1980, 1987; Cronquist, 1981), however, may be polyphyletic (Crane & Blackmore, 1989). Rosidae may be nested, or positioned, among Hamamelidae,

particularly among the so-called "lower" hamamelids, such as Hamamelidaceae and Platanaceae (Hufford & Crane, 1989). Certain so-called "higher" hamamelids, such as Fagales and Juglandales, have been suggested to be more closely related to Rosidae than to "lower" Hamamelidae (Wolfe, 1973, 1989, Hickey & Wolfe, 1975; Hickey & Doyle, 1977; Thorne, 1976; Nixon, 1989).

Our understanding of rosid phylogeny may be complicated by the systematic treatment of Dilleniidae. Takhtajan (1980, 1987) and Cronquist (1981) presented Dilleniidae as a monophyletic group rooted among Magnoliidae. Character analyses of putatively primitive Dilleniidae and Rosidae have called attention to the similarities shared by these two groups (e.g., Bate-Smith, 1973; Walker & Doyle, 1975; Cronquist, 1981; Wolfe, 1989), and uncertainty often surrounds the placement of particular taxa in one or the other. These character similarities and the uncertain placement of taxa highlight the possibility of Rosidae and Dilleniidae

---

<sup>1</sup> I thank P. R. Crane, W. S. Judd, M. J. Sanderson, D. E. Soltis, K. P. Steele, and an anonymous reviewer for helpful suggestions.

<sup>2</sup> Department of Biology, University of Minnesota, Duluth, Minnesota 55812-2496, U.S.A.



composing part of a more inclusive monophyletic group that is nested among Hamamelidae (cf. Ehrendorfer, 1989).

A monophyletic Rosidae may include taxa circumscribed as Asteridae (sensu Cronquist, 1981). Recent discussions of the origin of Asteridae have focused on alternative placements among Rosidae, but no consensus has emerged about their rosid sister group. Cronquist (1988: 414; see also 1981) suggested that the origin of Asteridae "very probably lies in the order Rosales." The similarly circumscribed Asteridae in Takhtajan (1980) were illustrated to be the sister group of a branch including Cornales and Araliales; these groups together were shown to originate among Saxifragales. The placement of Asteridae also depends upon their monophyly, which has been questioned repeatedly (Dahlgren, 1927; Wunderlich, 1959; Philipson, 1974, 1975, 1977; Dahlgren, 1975, 1977). Jensen et al. (1975) allied the iridoid-containing asterids with Cornales and Ericales and the noniridoid-containing asterids with Araliales and Rurales. Hickey & Wolfe (1975) used leaf architectural data to suggest that some asterid taxa were most similar to Dilleniidae and others to Rosidae. Takhtajan (1987) circumscribed asterids in three groups, Dipsacales, Lamiidae, and Asteridae sens. str., which he envisioned to have separate origins in or near Cornanae.

Numerous problematic taxa may have important ramifications for our understanding of the evolution of nonmagnoliid dicotyledons. The systematic placement of Ericales, Actinidiaceae, Fouquieriaceae, Loasaceae, and Sarraceniaceae has been questioned repeatedly. They share iridoid compounds and embryological characteristics with some Asteridae and Rosidae, but Cronquist (1981, 1988) has placed them all in Dilleniidae. Similarly, Takhtajan (1987) placed all of these taxa, except Loasaceae, among Dilleniidae. In contrast, Dahlgren (1977, 1980, 1983) circumscribed all of these taxa, except Loasaceae, in his superorder Corniflorae. He placed Loasaceae in a monotypic superorder allied with Corniflorae. If Dahlgren's Corniflorae and associated groups, such as Loasaceae, are the rosid groups most closely related to asterids, then the traditional placement of these problematic taxa among Dilleniidae may have limited our understanding of Asteridae evolution.

Broadly based cladistic analyses of rosids and potentially related groups may begin to resolve the problems outlined above. Large-scale studies of higher taxa are important because they include the mosaic distribution of character states at this level and provide accurate tests of prior hypotheses of

relationship for problematic groups suggested to have a range of alliances. Large-scale cladistic analyses of higher-level taxa provide more precise hypotheses about relationships than current classifications and, thus, critically set the stage for subsequent, smaller-scale studies by narrowing the set of ingroup and outgroup taxa that must be considered. This preliminary, exploratory investigation of Rosidae and allied groups focuses on: (1) testing hypotheses of monophyly for Asteridae and providing hypotheses about potential sister groups of asterids; (2) testing the placement of the problematic Ericales, Actinidiaceae, Fouquieriaceae, Loasaceae, and Sarraceniaceae that have been allied with Dilleniidae, Rosidae, and Asteridae; and (3) developing hypotheses about relationships among rosid groups, giving special consideration to the placement of Dilleniidae and Hamamelidae.

## MATERIALS AND METHODS

### TAXA

Eighty-five taxa (Table 1), including commonly accepted (e.g., in Takhtajan, 1969, 1980, 1987; Cronquist, 1981, 1988) members of the Hamamelidae, Dilleniidae, Asteridae, and Rosidae as well as numerous problematic taxa of uncertain systematic placement, were investigated. Winteraceae served as the outgroup for polarizing character states and rooting cladograms.

Families of Cronquist's (1981) Rosales are represented by one or more taxa because this order may be paraphyletic and includes groups suggested to be basal in the subclass. Place-holders represent most other orders of Cronquist's (1981) Rosidae. The orders Haloragales, Podostemales, Rafflesiales, and Santalales are not included because they (1) are considered to be most closely related to or nested within one of the other included groups; (2) have exceptionally derived traits that are not critical for understanding basal Rosidae and Asteridae or other problems outlined above; and (3) have not been implicated in the relationship of Rosidae to Hamamelidae, Dilleniidae, or Asteridae.

Hamamelidae in the study include the "lower" hamamelids (except *Eucommia*) investigated by Hufford & Crane (1989); a set of "higher" hamamelids, such as Fagales and Juglandales, suggested recently to be more closely related to Rosidae than to "lower" hamamelids (Wolfe, 1973, 1989; Hickey & Wolfe, 1975; Hickey & Doyle, 1977; Thorne, 1976; Nixon, 1989); and the problematic Buxaceae and Casuarinaceae.

Sampling Dilleniidae is difficult because their monophyly is questionable; thus, the subclass may



TABLE 1. Taxa used in the phylogenetic analysis. When particular taxa served as a basis for coding higher level groups they are indicated in parentheses.

---



---

Actinidiaceae ( <i>Actinidia</i> Lindley)
Alangiaceae ( <i>Alangium</i> sect. <i>Conostigma</i> Bloemb.)
Alseuosmiaceae ( <i>Alseuosmia</i> Cunn.)
Anisophylleaceae ( <i>Anisophyllea</i> R. Br. ex Sabine)
<i>Anodopetalum</i> A. Cunn. ex Endl.
Apiaceae
Araliaceae
Asteraceae
<i>Bauera</i> Banks ex Andrews
Betulaceae ( <i>Betula</i> L.)
<i>Brunellia</i> Ruiz & Pavón
Bruniaceae
Buxaceae ( <i>Buxus</i> L. and <i>Pachysandra</i> Siebold & Zucc.)
Campanulaceae
Caprifoliaceae
Casuarinaceae
Celastrales (Celastraceae)
<i>Cercidiphyllum</i> Siebold & Zucc.
Clethraceae ( <i>Clethra</i> L.)
<i>Columellia</i> Ruiz & Pavón
Connaraceae ( <i>Cnestis</i> Juss.)
Cornaceae
Crassulaceae
Crossosomataceae ( <i>Crossosoma</i> Nutt.)
<i>Deutzia</i> Thunb.
<i>Davidsonia</i> F. Muell.
Dilleniaceae ( <i>Dillenia</i> L.)
Ericaceae
Escalloniaceae ( <i>Escallonia</i> Mutis ex L.)
<i>Eucryphia</i> Cav.
Euphorbiales (Euphorbiaceae)
<i>Euptelea</i> Siebold & Zucc.
Fabaceae (Mimosoideae)
Fagaceae ( <i>Fagus</i> L.)
Fouquieriaceae
Garryaceae
Geraniales (Oxalidaceae)
Hamamelidaceae subfamily Altingioideae
Hamamelidaceae subfamily Disanthoideae
Hamamelidaceae subfamily Exbucklandoideae
Hamamelidaceae subfamily Hamamelidoideae
Hamamelidaceae subfamily Rhodoleioideae
<i>Hydrangea</i> L.
Juglandaceae ( <i>Engelhardia</i> Leschen. ex Blume)
Linales (Linaceae)
Loasaceae ( <i>Mentzelia</i> L.)
Loganiaceae
Myricaceae ( <i>Myrica</i> L.)
<i>Myrothamnus</i> Welw.
Myrtales (Lythraceae)
Nepenthaceae
Nyssaceae ( <i>Nyssa</i> L.)
Ochnaceae
<i>Paeonia</i> L.
<i>Paracryphia</i> Baker
<i>Penthorum</i> L.

---

TABLE 1. Continued.

---



---

<i>Philadelphus</i> L.
Pittosporaceae
<i>Platanus</i> L.
Polemoniaceae (tropical genera emphasized in coding decisions)
Polygalales (Malpighiaceae)
Proteales (Proteaceae)
Rhamnales (Rhamnaceae)
Rhizophoraceae ( <i>Crossostylis</i> Forster & Forster)
<i>Rhoiptelea</i> Diels & Hand.-Mazz.
Rosaceae (tribes Quillajae and Spiraeae)
Rubiaceae
Sapindaceae
Sarraceniaceae ( <i>Heliamphora</i> Benth.)
Saxifragaceae
Scrophulariaceae
Solanaceae
<i>Spiraeanthemum</i> A. Gray
Staphyleaceae
<i>Tetracarpaea</i> Hook.
<i>Tetracentron</i> Oliver
Theaceae
<i>Trochodendron</i> Siebold & Zucc.
<i>Viburnum</i> L.
Winteraceae

---

not be represented adequately by a few placeholder taxa. Selecting putatively primitive Dilleniidae as place-holders is problematic because prior phylogenetic hypotheses for the subclass may have been influenced heavily by suggestions that it originated among Magnoliidae rather than among Hamamelidae or Rosidae. Dilleniaceae, Theaceae, Ochnaceae, and *Paeonia* are included to represent putatively basal dilleniid groups.

In order to test hypotheses of monophyly and systematic placement for Asteridae, nine representatives of its major orders (sensu Takhtajan, 1969, 1980, 1987; Cronquist, 1981, 1988) are included. The representatives include divergent groups identified in treatments by Takhtajan (1987), Dahlgren (1980, 1983), Dahlgren et al. (1981), and Thorne (1976, 1981, 1983) in which asterids are not monophyletic.

I accept provisionally the monophyly of certain families and orders discussed by Cronquist (1981). For example, Rosaceae are included despite their potential paraphyly; if higher rosid families and orders actually nested within it also are included as terminal taxa, then misleading results may occur. The higher rosid orders, Celastrales, Geraniales, Linales, Myrtales, Polygalales, Proteales, and Rhamnales, may be nested within other terminal taxa in the analysis. Prior phylogenetic hypotheses



for these groups are not sufficiently precise to determine their relationship with other terminal taxa. Hence, I opt to include various higher rosid families and orders to examine the composition of major clades. This analysis may serve subsequently as the basis for more detailed analyses of major rosid clades.

#### CHARACTERS AND STATE CODING

Structural and chemical data (Table 2) were obtained largely from the literature (sources in Appendix 1). Few characters with over 10% missing data are included, and these are attributes (e.g., stomatal pattern) emphasized in prior systematic discussions of the taxa. *Bruniaceae*, *Columellia*, *Paracryphia*, *Rhoiptelea*, and *Tetracarpaea*, taxa that have proven difficult to place in traditional systematic treatments, are included, despite relatively extensive missing data, to provide provisional hypotheses about sister groups. Characters are coded as missing (unknown) when no single state or pair of states could be reasonably hypothesized to be plesiomorphic for a particular taxon. Wood characters for Saxifragaceae and Crassulaceae are coded as missing because these groups are hypothesized to be primitively herbaceous, and, thus, wood characters are not applicable. Numerous taxa are coded as polymorphic for certain characters primarily because of variability in the genera and higher-level groups in the analysis. Multistate characters compose 47% of the total.

#### DATA ANALYSIS

Wagner parsimony was used to search for most parsimonious trees with PAUP (version 3.0, Swofford, 1989). Multistate characters were treated as unordered to provide the least biased approach possible for state evolution. Different taxon addition sequences, including simple, closest, and random (see Swofford, 1989, for details), were used to initiate trees for branch-swapping procedures, although the most parsimonious trees were consistently found using simple sequences. To minimize computer run times, heuristic search procedures were performed using a sequential regime of branch-swapping options, beginning with nearest-neighbor interchanges, followed by subtree pruning-regrafting, and concluded with tree bisection-reconnection (Swofford, 1989). All of the trees saved from a prior swapping procedure were used to initiate a subsequent swapping procedure. A consensus tree was formed using the strict option in PAUP (Swofford, 1989). MacClade (version 2.97c+, Maddison & Maddison, 1989) was used in conjunction with

PAUP to explore character state evolution and alternative topologies.

#### RESULTS AND DISCUSSION

Fifty-six equally most parsimonious trees (consistency index = 0.18) with 682 character state changes were identified. The strict consensus tree (Fig. 1) shows that variation among the 56 equally most parsimonious trees is restricted to four regions: (1) among subfamilies of Hamamelidaceae; (2) among *Hydrangea*, *Deutzia*, and *Philadelphus*, representative genera of Hydrangeaceae; (3) among Fabaceae, Rhamnaceae, and Sapindaceae; and (4) among *Rhoiptelea*, Betulaceae, and the Casuarinaceae–Juglandaceae–Myricaceae clade. One of the 56 equally most parsimonious trees (Fig. 2) is used to discuss character state evolution.

The Hamamelidae of Takhtajan (1980, 1987) and Cronquist (1981, 1988) are shown to be polyphyletic (Fig. 2). "Lower" Hamamelidae (sensu Endress, 1986, 1989a; Hufford & Crane, 1989) are a paraphyletic assemblage at the base of Rosidae, and "higher" Hamamelidae (i.e., Fagales, Juglandales, and Casuarinaceae) are nested among Rosidae. Patterns of relationship among "lower" hamamelids reflect those shown by Hufford & Crane (1989). Buxaceae, a family sometimes placed in Rosidae (Scholz, 1964; Cronquist, 1981, 1988), form the sister taxon of *Cercidiphyllum* and *Myrothamnus*, with which they share a decussate leaf arrangement, unisexual flowers, and pollen with a papillate secondary tectal sculpturing. Drinnan et al. (1991) discussed the similarities of the Mid-Cretaceous fossil *Spanomera* with Buxaceae and *Myrothamnus*, and it may form part of the monophyletic group that includes those taxa and *Cercidiphyllum*.

Rosids are placed among "lower" Hamamelidae as the sister group of *Platanus* and Hamamelidaceae. Derived features shared by rosids include flowers with a disc nectary, anthers with unbifurcated stomia, and pollen with endoapertures (although all three attributes occur as parallelisms among Hamamelidaceae). The rosid group includes taxa circumscribed as Asteridae and Dilleniidae in recent treatments by Takhtajan (1980, 1987) and Cronquist (1981, 1988).

*Paeonia*, often placed among dilleniids (e.g., Thorne, 1976; Cronquist, 1981; Takhtajan, 1980; Dahlgren, 1983), is a basal branch of Rosidae in my results (Fig. 2). In recent classifications, Thorne (1983) and Takhtajan (1987) transferred *Paeonia* from a position near Dilleniaceae to one near Glauclidiaceae (near Berberidales and Nelumbonales).



TABLE 2. Character state assignments for taxa used in the phylogenetic analysis. Question marks indicate missing data. Characters and character states are listed in Appendix 1.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Winteraceae</i>	0	0	0	0	0	0	0	0/2	0	0	?	?	?	?	?	0	0	0	0	0
<i>Trochodendron</i>	2	0	0	0	0	1	0	1	0	0	?	?	?	?	?	0	0	0/1	0	0
<i>Tetracentron</i>	0	0	0	0	1	1	0	1	1	0	?	?	?	?	?	0	0	1	0	0
<i>Euptelea</i>	1	0	0	0	0	2	1	0	0	1	0	1	0	1	0	0	1	1	0	0
<i>Cercidiphyllum</i>	0	1	0	0	1	1	0	0	1	1	0	0	0	1	1	0	0	2	0	0
<i>Myrothamnus</i>	0	1	0	0	1	1	1	0	0	1	0	2	0	2	1	0	1	6	0	0
<i>Platanus</i>	2	0	0	0	1	1	1	?	0	1	?	1	1	2	1	0	0	7	0	0
Hamamelidoideae	0	0	0	0	1	2	0	?	0	1	0	0	0	1	0	0	0	0/1	0	1
Disanthoideae	0	0	0	0	1	1	0	?	0	1	1	0	0	1	0	0	0	0/1	0	1
Exbucklandoideae	0	0	0	0	1	1	0	?	0	1	0	0	0	1	0	0	0	3	0	1
Rhodoleioideae	0	0	0	0	1	2	0	?	0	1	0	0	0	1	0	0	0	0/1	0	1
Altingioideae	0	0	0	0	1	1	0	?	0	1	0	0	0	1	0	0	0	0/1	0	1
Juglandaceae	0	0	1	0	0	0	2	0	0	1	1	1	2	4	1	2	1	1/2	0	0
Myricaceae	0/1	0	0	0	0	0	1	0	0	1	1	1	1	2	1	0	1	1/2	0	0
Fagaceae	0	0	0	0	1	0	1	0	0	1	?	1/2	1	3	?	4	1	7	0	0
Casuarinaceae	1	2	0	0	0	?	?	2	0	1	2	2	1	2	1	2	1	7	0	0
Buxaceae	1	1	0	0	0	0	0	3	0	1	0	2	0	2	1	0	1	1	0	0
Rhoipteleaceae	0	0	1	0	1	0	2	0	0	1	1	1	1	4	1	2	1	0	0	0
<i>Bauera</i>	?	1	0	0	1	0	?	?	0	1	2	2	0	2	1	2	1	2	0	0
<i>Anodopetalum</i>	0	1	0	0	1	0	2	0	0	1	2	1	0	2	1	2	1	1	0	0
<i>Spiraeanthemum</i>	0	1	0	0	1	0	0	2	0	1	0	1	0	1	0	2	0/1	1	0	0
<i>Brunellia</i>	0	1	1	0	1	0	1	0	0	1	1	0/1	0	1	1	2	?	0/3	0	0
<i>Eucryphia</i>	0	1	0/1	0	1	0	1	2	0	1	1	1	0	1	1	2	1	1/7	0	0
<i>Davidsonia</i>	0	0	1	0	1	0	1	2	0	1	?	1	1	1	1	2	0	7	0	0
Connaraceae	0	0	1	0	0	0	?	?	0	1	2	1	1	4	1	4	1	6	0	0
<i>Tetracarpaea</i>	1	0	0	0	0	0	1	0	0	1	1	2	0	1	1	0	2	2	0	0
Pittosporaceae	0	0	0	0	0	0	2	2	0	1	2	1/2	0	?	2	3	1	1	0	0
Nepenthaceae	?	0	0	1	0	0	?	0	0	1	2	2	2	4	0	0	2	4	0	0
Sarraceniaceae	?	0	0	1	0	?	?	0	0	1	0	2	0	0	1	0	1	4	0	0
Crossosomataceae	0	0	0	0	0	0	?	0	0	1	2	2	0	4	0	0	1	4	0	0
Sapindaceae	0	0	1	0	0	0	2	0	0	1	2	2	1	4	2	4	1	7	0	0
Fabaceae	0	0	1	0	1	0	0	2	0	1	2	2	2	4	1	4	1	4/6	0	1
Bruniaceae	?	0	0	0	0	?	?	?	0	1	0	0	0	1	1	0	1	1/4	0	0
Alseuosmiaceae	0	0	0	0	0	0	0/2	0	0	1	0	1	0	3	1	4	1	?	0	0
Rosaceae	0	0	0	0	0	0	2	0	0	1	2	1	0	4	1	0	1	5	0	0



TABLE 2. Continued.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Anisophylleaceae	?	0	0	0	0	0	0	?	0	1	2	1	2	4	1	2	0	1	0	0
Rhizophoraceae	0	1	0	0	1	0	0	?	0	1	2	1	2	4	1	2	0	1	0	0
Saxifragaceae	0	0	0	0	0	0	2	0	0	1	?	?	?	?	?	?	?	?	?	?
Crassulaceae	0/1	0	0	0	0	0	2	?	0	1	?	?	?	?	?	?	?	?	?	?
<i>Penthorum</i>	1	0	0	0	0	0	2	0	0	1	0	1	0	4	1	2	1	4	0	0
<i>Columellia</i>	1	1	0	0	0	?	?	0	0	1	1	1	0	4	0	0	1	6	0	0
<i>Hydrangea</i>	0	1	0	0	0	2	0	2	0	1	0	1	0	0	1	1	1	0	0	0
<i>Deutzia</i>	0	1	0	0	0	2	2	?	0	1	0	1	0	3	1	1	1	0	0	0
<i>Philadelphus</i>	0	1	0	0	0	1	0/2	0	0	1	0	1	0	3	1	1	1	0	0	0
Escalloniaceae	1	0	0	0	1	0	0/2	0	0	1	0	2	0	1	1	0	1	0	0	0
Alangiaceae	0	0	0	0	0	1	3	0	0	1	1	0	2	4	2	4	0	0/1	0	0
Nyssaceae	0	0	0	0	0	1	3	2	0	1	0	0	1	2	1	2	0	0	0	0
Cornaceae	0	1	0	0	0	1	3	0	0	1	0	0	1	2	1	0	0/1	0	0	0
Garryaceae	0	1	0	0	0	1	3	2	0	1	1	2	0	2/4	1	1	1	4	0	0
Loasaceae	0	0	0	0	0	1	2	0	0	1	2	2	1	0	0	2	1/2	4	0	0
Ericaceae	0/1	0/1	0	0	1	0	0	0	0	1	2	1	0	2	0	0	1	1	0	1
Fouquieriaceae	1	0	0	0	0	?	0	0	0	1	2	2	0	4	1	2	1	4	0	0
Actinidiaceae	1	0	0	0	0	0	1	0	0	1	2	1	?	2	0/1	0	?	0	0	0
Clethraceae	1	0	0	0	0	0	0	?	0	1	0	0	0	2	0	2	0/1	0	0	0
Staphyleaceae	0	0/1	1	0	1	0	2	?	0	1	0	0/1	1/2	1	1	1	0	0/1	0	0
Geraniales	0	0	1	0	0	0	3	2	0	1	2	2	2	4	1	4	1	0/6	0	0
Celastrales	1	0/1	0	0	0/1	0	0	1/2	0	1	?	1	1/2	4	1	5	0/1	?	0	0
Euphorbiales	?	0	0	0	1	2	2	2	0	1	2	0/1	?	4	2	4	?	0	0	0
Rhamnales	0	0	0	0	1	0	2	0	0	1	2	2	1	4	2	4	1	?	0	1
Linales	0	0/1	0	0	1	0	?	2	0	1	2	2	0	4	1	1	0/1	?	0	0
Polygalales	0	1	0	0	1	0	0	2	0	1	2	0/1	0/2	4	2	4	0/1	0/1	0	0
Proteales	0	0	0/1	0	0	0	2	2	0	1	2	2	1/2	4	1	1	0	4	0	0
Myrtales	1	1	0	0	0	0	0	0	0	1	2	2	1	4	1	4	1	?	0	1
Betulaceae	0	0	0	0	1	0	1	0	0	1	?	1	1	4	2	1	0/1	7	0	0
Apiaceae	2	0	1	0	0	0	?	?	0	1	2	2	1	3	1	4	?	2	1	0
Araliaceae	2	0	1	0	0	0	?	2	0	1	?	1	1	?	2	4	1	1/2	1	0
Dilleniaceae	0	0	0	0	?	0	2	?	0	1	0	0	2	3	1	1	0	0/1	?	0
<i>Paeonia</i>	0	0	1	0	0	?	?	0	0	1	1	2	0	3	1	1	1	1/2	0	0
Loganiaceae	1	1	0	0	1	0	0	?	0	1	2	1	1	4	2	1	0/1	1/5	0	0
Solanaceae	1	0	0	0	0	0	0	0	0	1	2	2	?	?	2	1	1	4/5	0	0



TABLE 2. Continued.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Rubiaceae	1	1	0	0	1	0	0	2	0	1	2	1	1	4	1	1	0/1	4	0	0
Campanulaceae	1	0	0	0	0	0	?	0	0	1	2	2	1	4	1	4	?	5	0	0
<i>Viburnum</i>	?	1	0	0	1	0	2	0	0	1	0	1	1	4	0	0	0/1	4	0	0
Caprifoliaceae	?	1	0	0	0	0	2	0	0	1	2	1	1	4	0	0	0/1	0	0	0
Polemoniaceae	1	0/1	0	0	1	0	0	0	0	1	2	2	0	4	2	2	2	1	0	0
Asteraceae	0	0	0	0	1	0	0	0	0	1	2	2	1	4	2	4	1	1/2	0	0
Scrophulariaceae	1	0/1	0	0	1	0	2	0	0	1	2	2	1	4	2	3	1	0/4	0	0
Theaceae	1	0	0	0	0	0	0	?	0	1	0	0	1	1	0	1	0	0	0	0
Ochnaceae	0	0	0	0	1	0	0	0/2	0	1	2	1	1	4	1	2	1	0	0	1
<i>Paracryphia</i>	0	2	0	0	1	0	0	0	0	1	0	0	0	0/1	1	2	0	0	0	0

TABLE 2. Continued.

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Winteraceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Trochodendron</i>	0	0	0	0	0	0	1	0	0	0	1	0	2	0	1	0	0	0	0	0
<i>Tetracentron</i>	0	0	2	0	0	0	1	1	0	0	1	2	2	0	1	0	0	0	0	0
<i>Euptelea</i>	0	?	?	?	?	0	0	?	0	0	1	0	0	1	0	2	0	0	1	0
<i>Cercidiphyllum</i>	2	?	?	?	?	0	0	0	0	0	1	5	0	1	?	2	0	0	0	0
<i>Myrothamnus</i>	2	0	2	0	0	0	?	1	0	0	1	2/3	0	0	1	0	0	0	0	0
<i>Platanus</i>	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	2	1
Hamamelidoideae	0	1	1	0	0	0	2	1	0	0	1	4	2	0	2	1	0	0	2	0
Disanthoideae	0	1	1	0	0	0	3	1	0	0	0	4	1	0	2	1	1	0	1	0
Exbucklandoideae	0	1	1	0	0	0	?	2/4	0	0	1	4	2	0	2	1	0	0	1	0
Rhodoleioideae	0	1	3	0	0	0	2	2	0	0	1	4	2	0	2	1	0	0	0	0
Altingioideae	1	?	?	?	?	0	0	1/2	0	0	1	4	3	0	2	1	0	0	0	0
Juglandaceae	1	0	2	0	0	0	0	1/2	0	1	?	4	3	0	2	1	0	2	4	1
Myricaceae	1	?	?	?	?	0	0	1/4	0	1	0	4	0	0	2	1	0	2	4	1
Fagaceae	1	0	3	0	0	0	0	1/2	0	1	0	3	3	0	2	1	0	0	3	0



TABLE 2. Continued.

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Casuarinaceae	1/2	?	?	?	?	0	0	?	0	0	0	4	0	0	2	1	0	3	3	0
Buxaceae	1	0	2	0	0	0	1	1	0	1	0	2/3	1	0	2	0	0	1	3	0
Rhoipteleaceae	0	0	2	0	0	0	?	?	0	1	?	4	0	0	2	1	0	2	2	0
<i>Bauera</i>	0	1	1/2	0	0	0	?	2	0	1	0	4	2	0	3	1	1	0	1	0
<i>Anodopetalum</i>	1	1	2	?	0	0	2	4	0	1	0	4	1	0	2	1	1	0	?	0
<i>Spiraeanthemum</i>	2	0	2	1	0	0	2	4	0	1	0	6	1	0	1	1	1	0	3	0
<i>Brunellia</i>	0/2	0	1	0	0	0	2	4	0	1	0	0	1	0	1	1	0	0	3	0
<i>Eucryphia</i>	0	1	2	0	0	0	2	3	0	1	0	0	0	0	2	1	1	0	0	0
<i>Davidsonia</i>	0	1	1	1	0	0	2	4	0	1	0	4	0	0	2	1	1	1	1	0
Connaraceae	0	1	1/2	0/1	0/1	0	2	4	0	1	0	1	1	0	1	1	1	0	3	0
<i>Tetracarpaea</i>	0	1	2	0	0	0	0	1/4	0	0	0	1/2	0	1	0	1	1	0	0	0
Pittosporaceae	0	1	1	0/1	0/1	0	2	1	0	?	0	4	0	0	3	1	1	3	0	0
Nepenthaceae	2	1	2	0	0	0	3	2/4	0	?	0	2	0	0	2	1	1	0	0	0
Sarraceniaceae	0	1	1	0	0	0	2	2/4	0	0	0	3	0	0	3	1	1	0	0	0
Crossosomataceae	0	1	1/2	0	0	0	2	3	0	0	0	6	0	1	0	1	1	0	1	0
Sapindaceae	0	1	1/2	0/1	0	0	?	1/4	0	1	0	3	0	0	3	1	1	0	2	0
Fabaceae	0	1	1	1	0/1	0	?	2/4	0	1	0	5	0	1	?	1	1	0	2	0
Bruniaceae	0	1	1	0	0	0	2	1	0	1	0	4	3	0	2	1	1	0	2/3	0
Alseuosmiaceae	0	1	1	0	1	1	2	1	0/1	1	0	4	3	0	3	1	1	0	1	0
Rosaceae	0	1	1	1	0	1	2	3	0	1	0	1	0	?	0	1	1	0	0/1	0
Anisophylleaceae	0	1	2	0	0	?	2	4	0	1	0	2	3	0	2	1	1	0	2	0
Rhizophoraceae	0	1	2	?	?	?	2	3	0	?	0	0	3	0	3	1	1	1	?	0
Saxifragaceae	0	1	1	1	0	0	2	4	0	0	0	3/4	1/2	0	1	1	1	0	0	0
Crassulaceae	0	1	1/2	0/1	0/1	0	2	4	0/1	?	0	1/2	2	0	0	1	1	0	0	0
<i>Penthorum</i>	0	1	1	1	0	0	?	4	0	0	0	0/1	2	0	1	1	1	0	0	0
<i>Columellia</i>	0	1	1	1	1	0	2	1	1	1	0	4	3	0	3	1	1	0/3	0	0
<i>Hydrangea</i>	0	1	1/2	1	0	1	2	4	0	1	0	6	3	0	2	1	1	0/3	1	0
<i>Deutzia</i>	0	1	1	1	0	0	2	4	0	?	0	2	3	0	2	1	1	0	0	0
<i>Philadelphus</i>	0	1	2	1	0	0	2	4	0	0	0	2	3	0	2	1	1	0	0	0
Escalloniaceae	0	1	1	1	0/1	0	2	1	0	1	0	4	3	0	3	1	1	0/3	0	0
Alangiaceae	0	1	1/2	1	1	0	2	1	0	0	0	4	3	0	3	1	1	3	2	0
Nyssaceae	0	1	1	0	0	0	2	4	0	0	0	4	3	0	3	1	0	1	2	0
Cornaceae	0	1	2	1	0	0	2	1	0	1	0	4	3	0	3	1	1	0	2	0
Garryaceae	2	0	2	?	0	0	0	1	0	0	0	4	3	0	2	1	1	3	2	0
Loasaceae	0	1	1	0	0	0	2	3	0	0	0	3	3	0	3	1	1	3	0	0
Ericaceae	0	1	1	0	1	0	2	4	0	1	0	1	0	0	3	1	1	0	0	0



TABLE 2. Continued.

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Fouquieriaceae	0	1	1	1	1	0	2	2/4	0	1	0	3	0	0	3	1	1	0	1	0
Actinidiaceae	2	1	1/2	1	0	0	0	3	0	1	0	0	0	0	2	1	1	0	0	0
Clethraceae	0	1	1	1	1	0	2	4	0	1	0	3	0	0	3	1	1	0	0	0
Staphyleaceae	0	1	1	0	0	1	2	1	0	1	0	3	0/2	0	2	1	1	0	1	0
Geraniales	0	1	1	0	1	0	2	4	0	1	0	1	0	0	2	1	1	0	1	0
Celastrales	0	1	1/2	1	0	0	2	1/4	0	?	?	6	0/2	0	3	1	1	0	3	0
Euphorbiales	1/2	1	1	0	0	0	2	1/2	0	?	0	3	0	0	2	?	0	1	2/3	0
Rhamnales	0	1	1/2	0	0	1	2	1	0	1	0	4/5	2/3	0	3	1	1	2	2	0
Linales	0	1	1	0/1	0	0	2	1	0	0	0	6	0	0	3	1	1	1	3	0
Polygalales	0	1	1	0/1	0	0	0	4	0	1	0	3	0	0	2	1	1	0	2	0
Proteales	0	1	2	1	?	0	2	1	0	0	0	5	0/2	0/1	?	1	1	0	2/3	0
Myrtales	0	1	2	0	0	1	2	4	0	1	0	6	0	0	3	1	1	0	1	0
Betulaceae	0	0	3	0	0	0	0	1	0	1	0	4	2	0	2	1	1	0	2/3	0
Apiaceae	0	1	1	0	0	0	2	1	0	1	0	4	3	0	2	1	1	1	2	0
Araliaceae	0	1	1	0	0	0	2	2	0	1	0	6	3	0	2	1	1	1	2	0
Dilleniaceae	0	1	1	0	0	0	0/2	5	0	0	0	0/6	0	0/1	0/1	1	1	0	1	0
<i>Paeonia</i>	0	1	1	0	0	0	2	5	0	0	0	6	0	0	0	0	0	0	0	0
Loganiaceae	0	1	1/2	1	1	0	0/2	1	1	1	0	3/4	0	0	3	1	1	0	0	0
Solanaceae	0	1	1	1	1	0	2	1	1	1	0	4	0	0	3	1	1	0	0	0
Rubiaceae	0	1	1/2	1	1	0	2	1	1	1	0	4	3	0	3	1	1	0	1	0
Campanulaceae	0	1	1	1	1	0	2	1	0	?	0	6	3	0	3	1	1	0	0	0
<i>Viburnum</i>	0	1	1	1	1	0	2	1	1	1	0	3	3	0	3	1	1	0	1	0
Caprifoliaceae	0	1	1	1	1	0	2	1	1	1	0	6	3	0	3	1	1	0/3	1	0
Polemoniaceae	0	1	1	1	1	0	2	1	1	1	0	3	0	0	3	1	1	0	0/1	0
Asteraceae	0/1	?	1	?	1	0	2	1	1	1	0	4	3	0	3	1	1	2	4	0
Scrophulariaceae	0	1	1	1	1	0	2	1	1	1	0	4	0	0	3	1	1	0	0	0
Theaceae	0	1	1	0/1	0/1	0	2	5	0	1	0	6	0	0	2/3	1	1	0	0	0
Ochnaceae	0	1	1	0	0	0	0/2	?	0	0	0	0/6	0	0	3	1	1	0	0/1	0
<i>Paracryphia</i>	0	0	2	0	0	0	?	4	0	0	0	0	0	0	2	1	0	0	1	0



TABLE 2. Continued.

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Winteraceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Trochodendron</i>	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0
<i>Tetracentron</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
<i>Euptelea</i>	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	3	1	0	0	2
<i>Cercidiphyllum</i>	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	3	1	0	0	0
<i>Myrothamnus</i>	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	2	1	0	?	0
<i>Platanus</i>	0	0	0	1	1	0	0	1	0	0	1	?	2	1	0	0	0	0	0	2
Hamamelidoideae	0	0	0	1	1	0	0	1	1	0	1	0	2	1	0	0	0	0	0	0
Disanthoideae	0	0	0	1	1	0	0	0	1	0	1	0	2	1	0	0	0	0	0	0
Exbucklandoideae	0	0	0	1	1	0	0	1	?	0	1	0	2	1	0	3	0	0	0	0
Rhodoleioideae	0	0	0	1	1	0	0	?	?	0	1	0	2	1	1	3	0	0	0	0
Altingioideae	0	0	0	1	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0
Juglandaceae	1	0	1	1	2	0	0	1	1	0	1	?	0	0	1	4	0	1	2	2
Myricaceae	1	0	?	1	2	0	0	1	1	0	1	0	0	0	1	4	0	1	2	3
Fagaceae	0	0	1	1	2	0	?	1	1	0	1	0	2	1	1	5	0	0	1	2
Casuarinaceae	0	0	1	1	2	0	?	1	1	0	1	0	0	0	1	4	0	1	2	2
Buxaceae	0	0	?	0	0	0	?	0	0	0	1	0	2	0	1	3	1	0	0	1
Rhoipteleaceae	0	0	?	1	2	?	?	1	?	?	1	0	2	0	1	4	0	1	2	2
<i>Bauera</i>	0	0	0	1	0	?	0	1	?	?	1	1	2	1	1	0	0	0	0	0
<i>Anodopetalum</i>	0	0	0	1	0	0	0	1	0	0	1	1	2	1	1	8	0	0	1	4
<i>Spiraeanthemum</i>	0	0	0	1	0	0	0	1	0	0	1	1	2	1	1	8	0	0	1	0
<i>Brunellia</i>	0	0	0	?	0	?	0	1	?	?	1	1	2	1	1	8	0	0	1	0
<i>Eucryphia</i>	0	0	0	?	0	0	0	1	0	0	1	1	2	1	1	8	0	0	1	0
<i>Davidsonia</i>	0	0	0	?	2	0	0	1	0	0	1	1	2	1	1	8	0	0	1	2
Connaraceae	0	0	0	1	0/1	0	0	1	0	0	1	0	2	1	1	8	0	0	1	0
<i>Tetracarpaea</i>	0	0	0	1	0	?	0	0	?	0	1	1	2	1	1	5	0	0	1	0
Pittosporaceae	1	1	0	1	0	0	1	0	0	0	1	0	2	1	1	0	0	0	0	1
Nepenthaceae	0	0	0	?	0	0	0	0	0	0	1	1	?	?	?	4	0	?	?	1
Sarraceniaceae	1	1	0	0	0	1	0	0	0	0	1	0	2	1	1	7	0	?	1	1
Crossosomataceae	0	0	0	1	0/1	0	0	?	1	1	1	0	2	1	1	0	0	0	0	0
Sapindaceae	0	0	0	1	2	0	1	1	0	0	1	0	2	1	1	1	0	0	1	?
Fabaceae	0	0	0	?	2	0	1	1	0	0	1	0	2	1	1	8	0	0	1	0
Bruniaceae	1	0	0	?	0	0	0	1	0	0	1	0	2	1	1	0	0	0	0	2
Alseuosmiaceae	1	1	0	?	0	0	0	0	?	?	1	0	2	1	1	6	0	0	2	4
Rosaceae	0	0	0	1	1/2	0	0	1	0	0	1	0	2	1	1	1	0	0	1	0
Anisophylleaceae	1	0	0	1	2	0	0	0	?	?	1	0	2	1	1	8	0	0	1	2



TABLE 2. Continued.

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Rhizophoraceae	0	0	0	1	0/1	0	0	?	1	0	1	1	2	1	1	6	0	0	1	2
Saxifragaceae	0	0	0	0	0	0	0	1	0	0	1	?	2	1	1	0/1	0	0	1	0
Crassulaceae	0	0	0	0	0	0	0	1	0	0	1	?	2	1	1	1	0	0	1	0
<i>Penthorum</i>	0	0	0	0	0	?	0	0	1	0	1	1	2	1	1	1	0	0	1	0
<i>Columellia</i>	1	1	0	?	0	0	0	0	?	0	1	0	2	1	1	0	0	0	?	0
<i>Hydrangea</i>	1	1	0	0	0	1	0	1	0	0	1	1	2	0	1	0	0	0	0	1
<i>Deutzia</i>	1	1	0	0	0	1	0	0	0	0	1	1	2	0	1	0	0	0	0	1
<i>Philadelphus</i>	1	1	0	0	0	0	0	0	0	0	1	1	2	?	1	8	0	0	1	1
Escalloniaceae	1	1	0	1	?	1	0	0	0	0	1	1	2	1	1	3	0	0	1	0
Alangiaceae	1	0	0	0/1	0	1	0	0	0	1	1	0	2	1	1	0/3	0	0	1	3
Nyssaceae	1	1	0	0	0	1	0	0	1	1	1	0	2	1	1	8	0	0	1	3
Cornaceae	1	0	0	0	0	1	0	0	1	0	1	0	2	1	1	8	0	0	1	3
Garryaceae	1	0	0	0	0	1	0	0	0	1	1	0	2	1	1	0	1	0	0	3
Loasaceae	1	1	0	0	0	1	0	0	0	1	1	?	2	1	1	1	0	0	1	1
Ericaceae	1	1	0	0	0	1	0	1	1	1	1	0	2	1	1	6	0	0	2	0/1
Fouquieriaceae	0	1	0	0	1	1	0	0	1	0	1	0	2	1	1	0	0	0	0	1
Actinidiaceae	1	1	0	0	0	1	0	0	?	0	1	1	2	1	1	6/7	0	0	2	1/4
Clethraceae	1	1	0	0	0	1	0	0	0	0	1	0	2	1	1	6	0	0	2	1
Staphyleaceae	0	0	0	1	0	0	0	0	0	0	1	0	2	1	1	0	0	0	1	0
Geraniales	0	1	0	1	0	?	0	0	0	0	1	0	2	1	1	0	0	0	1	1
Celastrales	0	0	0	1	0	0	0	0/1	0	0	1	?	2	1	1	0	0	0	0	?
Euphorbiales	0	0	0	1	0	0	1	0	1	0	1	?	2	1	1	0	0	0	0	4
Rhamnales	0	0	0	1	1/2	0	0	0	0	0	1	0	2	1	1	8	0	0	1	3
Linales	0	0	0	1	1	0	0	0	0	1	1	0	2	1	1	4/7	0	0	1	0
Polygalales	0	0	0	1	2	0/1	0	0	0	0	1	0	2	1	1	0	0	0	1/2	2/4
Proteales	0	0	0	1	2	0	0	1	0	0	1	0	0/1	0/1	1	?	0	0	1	?
Myrtales	0	0	0	1	2	0	0	1	1	1	1	0	2	1	1	1/3	0	0	1	0
Betulaceae	1	0	1	1	1/2	0	0	1	1	0	1	0	0	0	1	4	0	1	2	2
Apiaceae	1	1	0	1	0	0	1	1	0	1	1	0	2	1	1	1/3	0	0/1	1	4
Araliaceae	1	0	0	1	0	0	1	0	0	1	1	0	2	1	1	0	0	0/1	0	3/4
Dilleniaceae	0	0	0	1	0	0	0	1	1	0	1	0	2	1	0/1	8	0	0	1	0
<i>Paeonia</i>	0	0	0	1	0	0	0	0	0	1	1	0	2	1	1	0	0	0	0	0
Loganiaceae	1	1	0	1	0	1	0	0	0	1	1	0	2	1	1	0	0	0	0	0
Solanaceae	1	1	0	0/1	0	0	0	0/1	0	1	1	0	1	1	1	1/4	0	0	1	0/4
Rubiaceae	1	1	0	0/1	0/2	1	0	1	0	0	1	0	2	1	1	0	1	0	0	0/4
Campanulaceae	1	1	0	0	0	0	1	0	0	1	1	0	2	1	1	6/8	0	0	1	0



TABLE 2. Continued.

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
<i>Viburnum</i>	1	0	0	0	0	1	0	0	?	?	1	?	2	1	1	0	0	0	0	3
Caprifoliaceae	1	1	0	0	0	1	0	0	1	0	1	0	2	1	1	4	0	0	2	4
Polemoniaceae	1	1	0	1	0	0	0	0/1	0	1	1	0	0	0	1	0/1	0	0	0	1
Asteraceae	1	1	0	0/1	2	0	1	0	1	1	1	0	0/1	0/1	1	0/4	0	0	0	2
Scrophulariaceae	1	1	0	0	0	1	0	0	0	1	1	0	2	1	1	0	0	0	1	0
Theaceae	0	1	0	1	0	0	0	1	1	1	1	0	2	1	1	4	0	0	1	0
Ochnaceae	0	1	0	1	0/2	0	0	0	0	0	1	0	2	1	1	6/7	0	0	1	0
<i>Paracryphia</i>	1	0	0	?	0	?	0	?	?	?	1	0	2	1	1	3	0	0	1	0

Worsdell (1908) earlier suggested a relationship between *Paeonia* and Ranunculaceae, and Sawada (1971) argued that floral structure implied a position among magnoliids. This cladistic analysis is not sufficiently inclusive to evaluate the placement of *Paeonia* among groups such as Ranunculaceae, Berberidales, and Nelumbonales. Extensive attention has been given to the distinctive coenocytic proembryo of *Paeonia* (Cave et al., 1961; Murgai, 1959; Yakovlev & Yoffe, 1957), but this autapomorphy currently has no bearing on our understanding of its sister group relationship. The nectarial disc surrounding the base of the apocarpous gynoecium of *Paeonia* (Hiepko, 1965, 1966) is a derived feature shared by the rosid group (including dilleniids and asterids) but not by Magnoliidae (including Ranunculaceae, Berberidales, and Nelumbonales). Corner (1946) was among the first to suggest that *Paeonia* was more closely related to Dilleniaceae than to Ranunculaceae or other Magnoliidae. Corner (and more recently others), however, emphasized attributes such as centrifugal androecial development, arillate seeds with a hard testa, and exstipulate leaves, which are present among rosids as well as Dilleniales and Theales (sensu Cronquist, 1981).

The sister group of *Paeonia* comprises two groups (Fig. 2): (1) Crossosomataceae and their sister group (treated as the "core rosid group") and (2) Bruniaceae and their sister group (treated as the "Corniflorae-asterid group").

#### THE CORE ROSID GROUP

Crossosomataceae, placed as the sister taxon of the rest of the core rosid group, have been allied with *Paeonia*, Ranunculaceae, Dilleniaceae, Rosaceae, and Fabaceae. Kapil & Vani (1963) treated *Crossosoma* as more closely related to Dilleniaceae and Rosaceae than to *Paeonia* and Ranunculaceae. Richardson (1970) and DeBuhr (1978) used leaf and wood structure to ally Crossosomataceae more closely with Rosaceae than Dilleniaceae. Similarity indices based on chemical attributes showed Crossosomataceae to be equally similar to *Paeonia*, Dilleniaceae, and rosids (Tatsuno & Scogin, 1978). Crossosomataceae appear to have diverged little from the basic character states of the core rosid group, although its stipitate carpels and polystemony are parallelisms with those of other rosids.

The Rosaceae-Crassulaceae-Saxifragaceae clade is supported by striate pollen and five-carpellate gynoecia (although the carpel number for both Crassulaceae and Saxifragaceae was coded as polymorphic). Missing data may have influenced



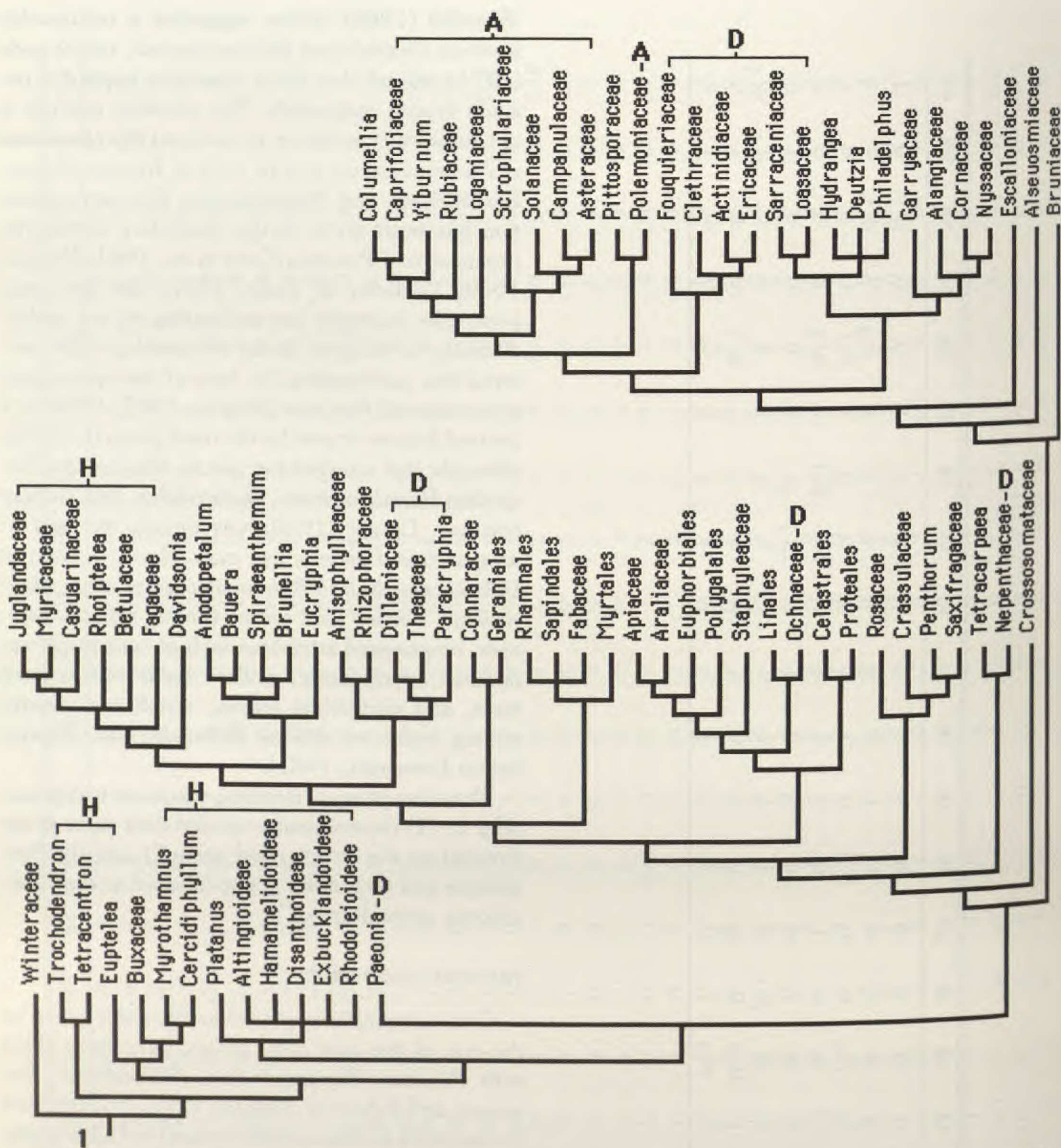


FIGURE 1. A strict consensus tree based on the set of 56 equally most parsimonious trees. Groups circumscribed by Cronquist (1981) as Asteridae, Dilleniidae, and Hamamelidae are indicated. (Key: A, Asteridae; D, Dilleniidae; H, Hamamelidae.)

the placement of the Crassulaceae–Saxifragaceae group (including *Penthorum*). Crassulaceae and Saxifragaceae were considered primitively herbaceous (see Hart & Koek-Noorman, 1989), and all wood characters were coded as nonapplicable (i.e., missing) for these taxa. Engler (1930) broadly circumscribed Saxifragaceae to include the so-called “woody saxifrages,” groups such as Escalloniaceae and Hydrangeaceae. My results show that “woody” saxifrages are more closely related to certain members of the Corniflorae–asterid group than to Saxifragaceae sens. str. (the “herbaceous” saxifrages).

This is supported by chloroplast DNA data (Downie & Palmer, 1992; Olmstead et al., 1992). Saxifragaceae sens. str. lack the iridoid chemistry and some embryological states that help to define the Corniflorae–asterid group. The Crassulaceae–Saxifragaceae group demonstrates evolution of ab initio cellular endosperm and the formation of endosperm haustoria parallel with members of the Corniflorae–asterid group. This may help to explain its previous alliance with groups such as Escalloniaceae and Hydrangeaceae. *Penthorum* has been treated as intermediate between Saxifragaceae and Crassu-



laceae (e.g., Agababian, 1961; Huber, 1963; Hildebrand & Ferguson, 1976; Grund & Jensen, 1981; Haskins & Hayden, 1987; Spongberg, 1972), although my results are consistent with suggestions (Dahlgren, 1930; Jay, 1970; Wakabayashi, 1970) that it is more closely related to the former.

Some "higher" rosid orders and Dilleniidae are placed in the core rosid group between Cunoniaceae and Rosaceae, taxa hypothesized to be among the most primitive Rosidae (Dickison, 1989a). This result might be expected, given that "higher" rosids often are suggested to "originate" among Rosales (e.g., Cronquist, 1981). Two caveats are needed with regard to the placement of "higher" rosid orders. First, the "higher" rosid orders actually may nest within one of the represented terminal taxa. For example, Rosaceae may be a paraphyletic group with other recognized "families" or "orders" nesting within it. Including paraphyletic terminal taxa in addition to monophyletic segregates may have caused misleading results. It is particularly important that the monophyly of putatively primitive rosids such as Rosaceae and Cunoniaceae (see Hufford & Dickison, in press) be more rigorously assessed. Second, additional core rosid taxa, especially those sharing derived characters with "higher" rosid orders, should be included to assess more reasonably the sister group relationships of higher rosids.

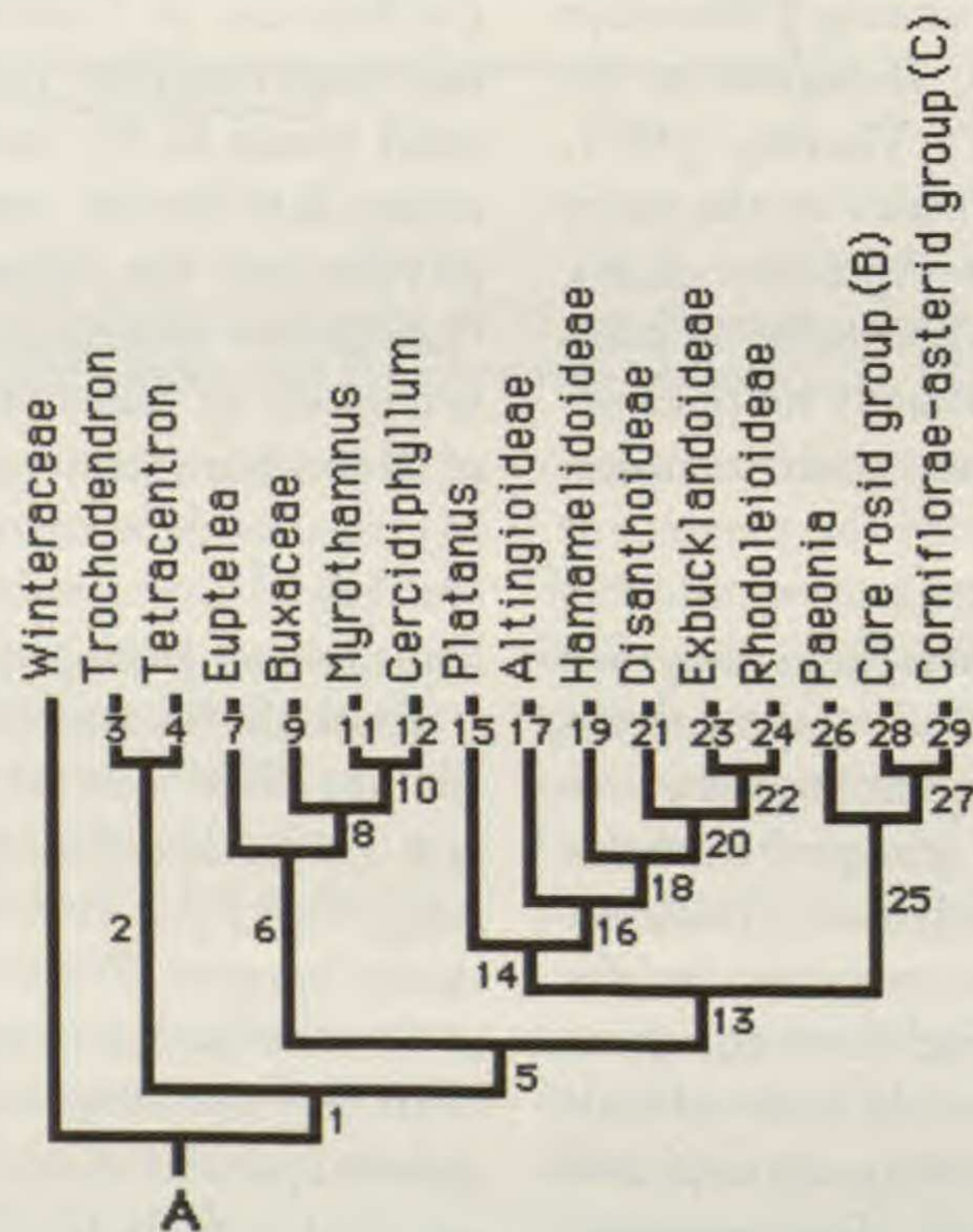
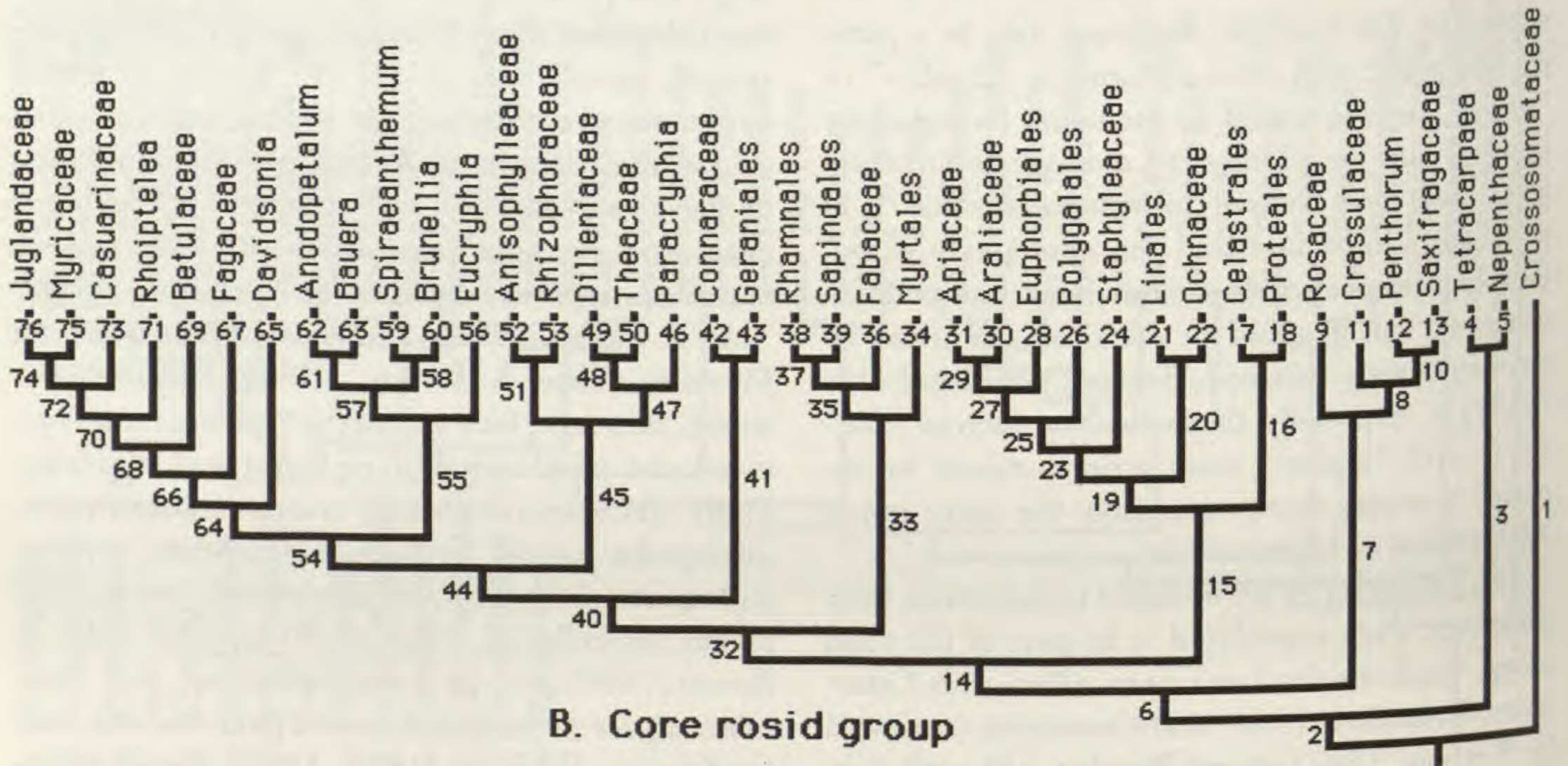
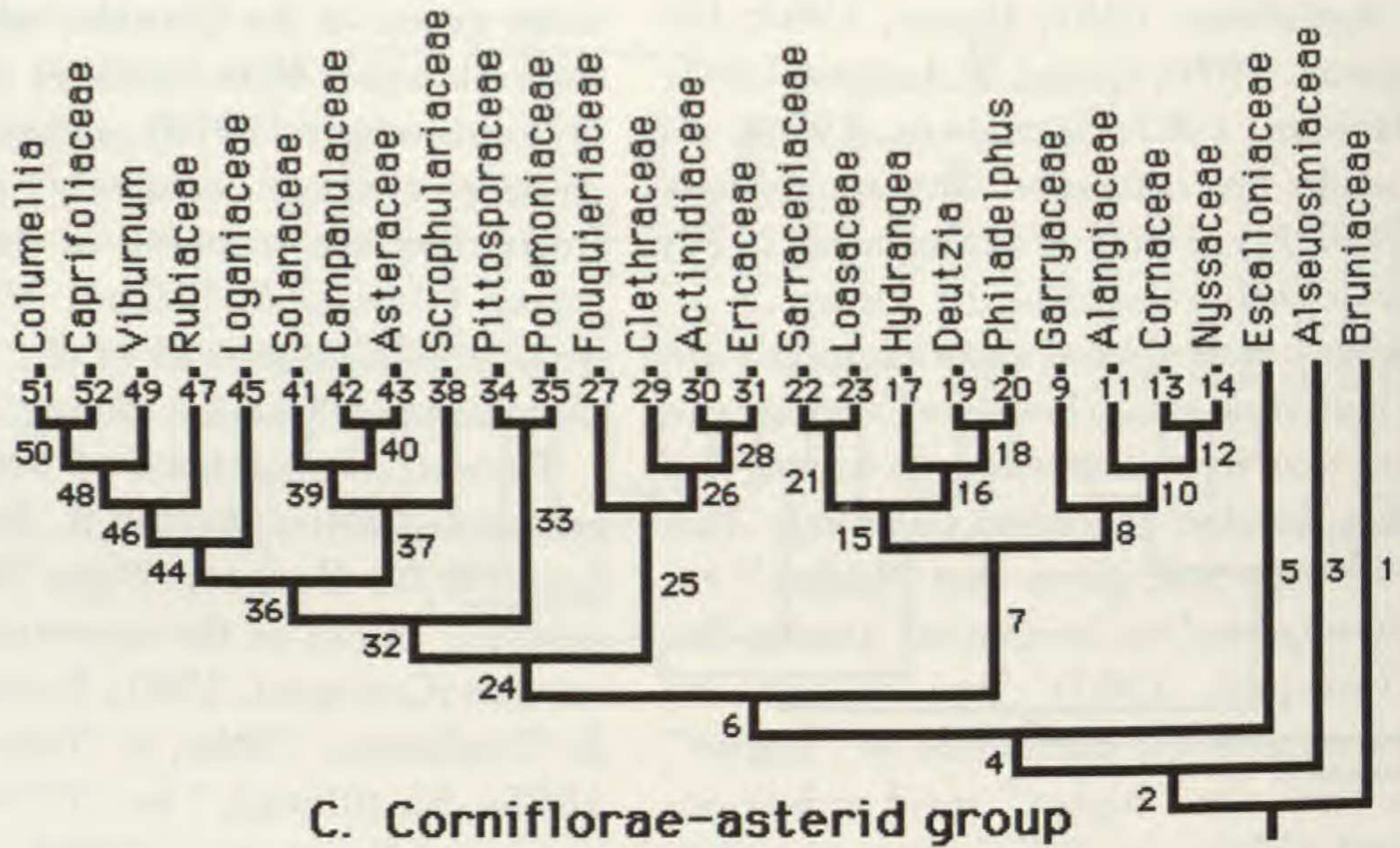
The Euphorbiales are included to determine their placement when considered to be part of the rosid group. Euphorbiales have been allied with Celastrales (Cronquist, 1981) and Geraniales (reviewed by Webster, 1987) among Rosidae, although they are perhaps most often placed among Dilleniidae near Malvales (Dahlgren, 1983; Dahlgren et al., 1981; Takhtajan, 1980, 1987; Thorne, 1981, 1983). My results place Euphorbiales as the sister group of Araliales (the Araliaceae–Apiaceae clade), a relationship supported by the presence of polyacetylenes. If Euphorbiales are actually more closely related to higher dilleniids, then their inclusion in the analysis may have influenced the placement of Araliales. For example, Dahlgren et al. (1981) allied Araliales with Pittosporaceae, and they are often suggested (e.g., Huber, 1963) to be related to Cornales. Altering the cladogram topology to place Pittosporaceae as the sister group of Araliales in the core rosid group adds only one character state change to the total number required for the most parsimonious trees. Changing the topology to place a Pittosporaceae–Araliales clade in various positions in the Corniflorae–asterid group adds five or more character state changes. For example, placing the Pittosporaceae–Araliales clade as the

sister group of the Cornales adds seven character state changes. Bate-Smith et al. (1975) and Lee & Fairbrothers (1978) suggested, however, that Araliales are only "remotely" related to Cornales. Restriction site mapping of the cpDNA inverted repeat (Downie & Palmer, 1992) and *rbcL* sequence data (Olmstead et al., 1992) support the placement of Araliales among Asteridae.

Recent investigations of Rhizophoraceae have segregated *Anisophyllea* R. Br. ex Sabine, *Combretocarpus* Hook. f., *Poga* Pierre, and *Polygonanthus* Ducke as the separate family Anisophylleaceae (Cronquist, 1981; Behnke, 1988; Juncosa & Tomlinson, 1988a, b; Tobe & Raven, 1987, 1988a, b), although Vliet (1976, using wood anatomy) and Vezev et al. (1988, using pollen structure) identified three divergent groups in Rhizophoraceae sens. lat. Tobe & Raven (1988a) hypothesized monophyly for Rhizophoraceae sens. str. on the basis of subdermally initiated laticifers in the gynoecial walls and colleters. Rhizophoraceae sens. str. have been allied with Celastraceae and Elaeocarpaceae (Juncosa & Tomlinson, 1988a; Tobe & Raven, 1988b) and Anisophylleaceae with Myrtales (Tobe & Raven, 1988a). Anisophylleaceae, however, lack intraxylary phloem and vested pits, which are derived features of Myrtales. Many characters (including crassinucellate ovules, micropyles formed by both integuments, nuclear endosperm formation, exalbuminous seeds, and pollen two-celled at "maturity") used by Tobe & Raven (1988a) to ally Anisophylleaceae with Myrtales appear to be symplesiomorphies for the core rosid group. Dahlgren (1980, 1983) placed Anisophylleaceae in Corniflorae (largely equivalent to the non-Asteridae portion of the Corniflorae–asterid group in my results). The unilacunar nodes, exstipulate leaves, and unitegmic ovules of Anisophylleaceae are present in some members of the Corniflorae–asterid group; however, it is more parsimonious to place the family as the sister group of Rhizophoraceae sens. str. in the core rosid group. My results demonstrate that it still may be reasonable to hypothesize monophyly for Anisophylleaceae and Rhizophoraceae sens. str.

Anisophylleaceae and Rhizophoraceae are placed as the sister taxa of *Paracryphia*, Dilleniaceae, and Theaceae, although this relationship is weakly supported by a reversal to long imperforate elements in wood. The bitegmic, tenuinucellate ovules of Theales (sensu Cronquist, 1981), such as Theaceae, Scyttopetalaceae, Medusagynaceae, and Clusiaceae, parallel those of some Rhizophoraceae sens. str. (e.g., *Gynotroches* Blume and *Pellacalyx* Korth; Juncosa & Tobe, 1988), and the unitegmic,







crassinucellate ovules of other Theales, such as *Paracryphia*, *Oncothecaceae*, and some *Caryocaraceae*, parallel those of some *Anisophylleaceae* (e.g., *Anisophyllea* and *Combretocarpus*; Tobe & Raven, 1987).

Dilleniaceae, Theaceae, and Ochnaceae are included as place-holders to represent Dilleniidae (sensu Takhtajan, 1980, 1987; Cronquist, 1981, 1988). The Dilleniaceae–Theaceae clade is supported by basally connate ovaries and centrifugal polystemony (a parallelism with *Paeonia*). *Paracryphia* is placed as the sister taxon of Dilleniaceae

and Theaceae on the basis of wood with long vessel elements and heterogeneous type I rays. Ochnaceae appear to be more closely related to *Linales* than to these dilleniids (Fig. 1). Experimentally placing Ochnaceae as the sister group of the *Paracryphia*–Dilleniaceae–Theaceae clade adds five character state changes. My results do not support the placement of *Actinidiaceae*, *Fouquieriaceae*, *Loasaceae*, *Sarraceniaceae*, and *Ericales* in Dilleniidae as they are treated by Takhtajan (1980, 1987) and Cronquist (1981). The chemical, ovular, and endosperm attributes of these problematic taxa sup-

FIGURE 2. One of the set of equally most parsimonious cladograms requiring 689 character state changes. Clades B (core rosid group) and C (Corniflorae–asterid group) are sister groups positioned at the indicated points on clade A. The character state changes for each branch of A, B, and C are indicated below as follows: clade letter and branch number: character number-apomorphic state.

- Al: 6-1; 18-1; 23-2; 28-1; 31-1; 53-1; A2: 8-1; 27-1; 33-2; 35-1; 56-1; A3: 1-2; 23-0; 28-0; 48-1; A4: 5-1; 9-1; 32-2; A5: 10-1; 17-1; 51-1; A6: 1-1; 56-3; 57-1; A7: 6-2; 7-1; 15-0; 34-1; 36-2; 39-1; 48-1; 60-2; A8: 2-1; 12-2; 14-2; 21-1; 32-2; 35-1; A9: 6-0; 8-3; 27-1; 30-1; 31-0; 33-1; 35-2; 38-1; 39-3; 53-2; 55-1; 60-1; A10: 1-0; 5-1; 18-2; 21-2; 49-1; A11: 7-1; 18-6; 44-1; 56-2; A12: 9-1; 12-0; 14-1; 17-0; 28-0; 32-5; 34-1; 36-2; 45-1; A13: 22-1; 23-1; 44-1; 53-2; 54-1; A14: 5-0; 17-0; 21-1; 39-2; 45-1; 48-1; A15: 1-2; 7-1; 13-1; 14-2; 18-7; 22-0; 40-1; 60-2; A16: 12-0; 15-0; 20-1; 32-4; 33-2; 35-2; 36-1; 49-1; A17: 33-3; 39-0; 46-1; 53-0; 54-0; A18: 21-0; 27-2; A19: 6-2; A20: 39-1; A21: 11-1; 27-3; 31-0; 33-1; 37-1; 48-0; A22: 28-2; 56-3; A23: 18-3; A24: 6-2; 23-3; 39-0; 55-1; A25: 6-0; 12-2; 27-2; 31-0; 32-6; 55-1; A26: 3-1; 11-1; 14-3; 16-1; 28-5; 50-1; A27: 18-4; 36-1; 37-1; A28: 11-2; 14-4; 28-4; A29: 30-1; 32-4; 33-3; 35-2; 41-1.
- B1: 15-0; 28-3; 34-1; 39-1; 49-1; 50-1; B2: 59-1; B3: 1-1; 7-1; 17-2; 23-2; 27-0; 32-2; 52-1; 56-4; B4: 11-1; 14-1; 18-2; 34-1; 56-5; B5: 4-1; 13-2; 15-0; 21-2; 27-3; 35-2; 60-1; B6: 12-1; 48-1; B7: 7-2; 24-1; 32-1; 56-1; B8: 11-0; 16-2; 33-2; 44-0; 52-1; B9: 18-5; 26-1; 28-3; 30-1; 45-1/2; B10: 35-1; B11: no changes; B12: 1-1; 48-0; 49-1; B13: 32-3/4; B14: 13-1; 16-1; 35-3; 39-1; B15: 8-2; 28-1; B16: 17-0; 23-2; 24-1; 39-3; B17: 1-1; 16-5; 59-0; B18: 7-2; 12-2; 32-5; 45-2; 53-0/1; B19: 5-1; 18-0; 48-0; B20: 56-7; B21: 12-2; 13-0; 38-1; 39-3; 45-1; 50-1; B22: 16-2; 20-1; 42-1; B23: 7-2; 30-1; 32-3; 35-2; B24: 3-1; 11-0; 14-1; 17-0; 26-1; B25: 15-2; 16-4; 39-2; 60-4; B26: 2-1; 7-0; 13-0/2; 27-0; 28-4; 45-2; B27: 1-2; 38-1; 47-1; 59-0; B28: 6-2; 21-1/2; 37-0; 49-1; B29: 3-1; 5-0; 14-3; 18-2; 19-1; 32-4; 33-3; 41-1; 50-1; B30: 28-2; 32-6; B31: 12-2; 15-1; 42-1; 48-1; 56-1/3; 59-1; B32: 16-4; 18-6; 30-1; 56-8; B33: 12-2; 20-1; 45-2; B34: 1-1; 2-1; 23-2; 26-1; 49-1; 50-1; 56-1/3; B35: 3-1; 5-1; 32-5; 39-2; 47-1; B36: 8-2; 13-2; 24-1; 34-1; B37: 7-2; 15-2; 18-7; 28-1; 60-3; B38: 3-0; 26-1; 33-2/3; 38-2; 47-0; 48-0; B39: 5-0; 20-0; 32-3; 56-1; B40: 32-1; 35-2; B41: 3-1; 7-3; 8-2; 25-1; B42: 33-1; 35-1; 39-3; B43: 12-2; 13-2; 42-1; 48-0; 56-0; 60-1; B44: 14-1; 16-2; 18-1; 23-2; 32-0; B45: 13-2; 17-0; 49-1; B46: 2-2; 13-0; 22-0; 37-0; 41-1; 56-3; B47: 11-0; 12-0; 18-0; 30-0; B48: 16-1; 23-1; 28-5; 32-6; B49: 7-2; 14-3; 35-0/1; B50: 1-1; 13-1; 15-0; 30-1; 39-0; 42-1; 56-4; B51: 14-4; 33-3; 39-2; 48-0; 60-2; B52: 32-2; 41-1; 45-2; B53: 2-1; 5-1; 28-3; 35-3; 38-1; 52-1; 56-6; B54: 5-1; 7-1; 11-1; 52-1; B55: 2-1; 13-0; B56: 8-2; 28-3; 39-0; B57: 33-1; B58: 21-2; 22-0; 35-1; 39-3; B59: 7-0; 8-2; 11-0; 15-0; 24-1; 32-6; B60: 3-1; 18-0/3; 23-1; 37-0; B61: 7-2; 11-2; 14-2; 32-4; B62: 21-1; 60-4; B63: 12-2; 18-2; 28-2; 33-2; 35-3; 56-0; 59-0; B64: 18-7; 23-1; 32-4; 45-2; 60-2; B65: 3-1; 8-2; 17-0; 24-1; 38-1; B66: 14-3; 22-0; 23-3; 27-0; 28-1; 37-0; 39-3; 43-1; 49-1; 52-0; 56-4; B67: 16-4; 21-1; 32-3; 33-3; 56-5; B68: 14-4; 53-0; 54-0; 58-1; 59-2; B69: 15-2; 16-1; 33-2; 37-1; 41-1; B70: 7-2; 23-2; 38-2; B71: 3-1; 18-0; 39-2; 53-2; B72: 5-0; 14-2; 21-1; B73: 1-1; 2-2; 8-2; 11-2; 12-2; 30-0; 38-3; B74: 18-1; 39-4; 40-1; 41-1; B75: 7-1; 16-0; 60-3; B76: 3-1; 13-2; 14-4; 33-3.
- C1: 12-0; 39-2/3; 48-1; 60-2; C2: 25-1; 35-3; 42-1; C3: 12-1; 14-3; 16-4; 26-1; 39-1; 56-6; 59-2; 60-4; C4: 1-1; 24-1; C5: 5-1; 18-0; 52-1; 56-3; 59-1; C6: 14-4; 16-2; 44-0; 60-1; C7: 1-0; 6-1; 7-2; 25-0; 30-0; C8: 7-3; 11-1; 23-2; 38-3; 39-2; 42-0; 50-1; 60-3; C9: 2-1; 8-2; 16-1; 21-2; 22-0; 27-0; 35-2; 44-1; 57-1; C10: 12-0; 13-1; 17-0; 18-0; 59-1; C11: 13-2; 15-2; 16-4; 25-1; C12: 11-0; 14-2; 38-0; 49-1; 56-8; C13: 2-1; 16-0; 30-1; 50-0; C14: 8-2; 23-1; 24-0; 28-4; 37-0; 38-1; 42-1; C15: 14-0; 28-4; 32-2; C16: 2-1; 6-2; 12-1; 16-1; 18-0; 35-2; 52-1; 54-0; C17: 7-0; 8-2; 26-1; 30-1; 32-6; 39-1; 48-1; C18: 14-3; C19: no changes; C20: 6-1; 23-2; 46-0; 56-8; 59-1; C21: 24-0; 32-3; 56-1; 59-1; C22: 4-1; 16-0; 33-0; 56-7; C23: 11-2; 13-1; 15-0; 28-3; 38-3; 50-1; C24: 11-2; 33-0; C25: 28-4; 32-3; 49-1; C26: 12-0; 14-2; 15-0; 18-0; 56-6; 59-2; C27: 39-1; 41-0; 45-1; C28: 12-1; 16-0; 32-1; C29: 11-0; 49-0; C30: 7-1; 21-2; 25-0; 27-0; 28-3; 32-0; 35-2; 52-1; C31: 18-1; 20-1; 24-0; 48-1; 50-1; C32: 15-2; 29-1; C33: 18-1; 44-1; 46-0; C34: 1-0; 7-2; 8-2; 16-3; 29-0; 38-3; 47-1; C35: 17-2; 32-3; 50-1; 53-0; 54-0; C36: 13-1; 16-1; 60-0; C37: 59-1; C38: 7-2; 16-3; C39: 18-5; 46-0; 50-1; 53-1; 56-4; C40: 16-4; 33-3; 47-1; C41: no changes; C42: 15-1; 29-0; 32-6; 53-2; 56-6/8; C43: 1-0; 18-1/2; 38-2; 39-4; 45-2; 59-0; 60-2; C44: 2-1; 5-1; 12-1; C45: 18-1/5; 44-1; 50-1; C46: 15-0; 33-3; 39-1; C47: 8-2; 15-1; 48-1; 57-1; C48: 7-2; 16-0; 49-1; C49: 11-0; 32-3; 42-0; 60-3; C50: 5-0; 18-0; 59-2; C51: 11-1; 13-0; 18-6; 39-0; 46-0; C52: 32-6; 56-4; 60-4.



port their placement in the Corniflorae-asterid group. Marcgraviaceae, although not included in my investigation, also may be more closely related to members of the Corniflorae-asterid clade than to Theales, among which it is commonly placed (e.g., Cronquist, 1981; Dahlgren, 1983; Thorne, 1983; Takhtajan, 1987). The bitegmic, tenuinucellate ovules of Marcgraviaceae are compatible with those of Theales and the Corniflorae-asterid group, but its integumentary endothelium, cellular endosperm, and endosperm haustoria (Mauritzon, 1939; Swamy, 1948a) are attributes generally found in combination only in the latter. Marcgraviaceae warrant examination for iridoid compounds, which might help to support a hypothesis of relationship to the Corniflorae-asterid group.

Core Cunoniaceae, represented by *Anodopetalum* and *Spiraeanthemum*, form a monophyletic group along with *Bauera* and *Brunellia*, supporting the results of a phylogenetic analysis of the family by Hufford & Dickison (in press). The more inclusive analysis by Hufford & Dickison has shown *Eucryphia* to be nested within Cunoniaceae and not its sister group as might be interpreted from these results (Fig. 1). The Cunoniaceae clade, including *Bauera*, *Brunellia*, and *Eucryphia*, is supported by small pollen grains.

The close placement of Rhizophoraceae and Cunoniaceae is interesting, given the interpetiolar stipules (often enclosing the terminal bud and sometimes associated with colleters) in both groups. *Dialypetalanthus* Kuhl., generally placed in the monotypic Dialypetalanthaceae allied with Myrtales and Rubiaceae (Cronquist, 1981; Rizzini & Occhioni, 1949), has interpetiolar stipules and other attributes similar to Cunoniaceae and Rhizophoraceae. Although Juncosa & Tomlinson (1988a) regarded suggestions of relationship for Rhizophoraceae sens. str., Cunoniaceae, and Dialypetalanthaceae as "indefensible," this warrants testing in a broadly based phylogenetic analysis that includes Myrtales and Rubiaceae.

Cunoniaceae are placed as the sister group of a clade consisting of *Davidsonia*, Fagaceae, and other taxa often considered to be "higher" Hamamelidae (Fig. 1). This result supports contentions that "higher" hamamelids are more closely related to rosids than to "lower" hamamelids (Wolfe, 1973, 1989; Hickey & Wolfe, 1975; Hickey & Doyle, 1977; Nixon, 1989). Although Fagaceae-Betulaceae, Juglandaceae-Myricaceae-Rhoipteleaceae, and Casuarinaceae are commonly discussed as three separate monophyletic groups (e.g., Cronquist, 1981), they are seldom placed in a single group as shown by my results (although, see Stone &

Broome, 1971, 1975; Zavada & Dilcher, 1986; Kedves, 1989; Nixon, 1989). Fagaceae and their sister group are defined by chalazallogamy (not present in all Fagaceae) and nonpersistent endosperm. Betulaceae and their sister group share pollen traits, including poroid apertures and poorly developed columellae ("granular" columellae sensu Zavada & Dilcher, 1986). Zavada & Dilcher (1986) identified other pollen characteristics, including a microchanneled tectum and thin footlayer, that may help define this group (these attributes are not included in this analysis because of insufficient sampling among other rosids).

#### THE CORNIFLORAE-ASTERID GROUP

Ovular traits are important for developing hypotheses about relationships in the Corniflorae-asterid group as emphasized by Dahlgren (1975). The Corniflorae-asterid group, consisting of Bruniaceae and their sister group (Fig. 2), shares unitegmic ovules. Although Bruniaceae retain crassinucellate ovules, their sister group is defined by tenuinucellate ovules. Among Cornales, Garryaceae, Alangiaceae, and Cornaceae have a reversal to crassinucellate ovules. *Fouquieria* has a reversal to bitegmic ovules but has retained its single-layered nucellus.

Dahlgren (1975) also used endosperm attributes to circumscribe Corniflorae (a group corresponding largely to the nonasterid members of the Corniflorae-asterid group of Fig. 2). The presence of ab initio cellular endosperm defines the sister group of *Escallonia*, although reversals to nuclear endosperm occur in some members of this group (e.g., Garryaceae, Loganiaceae, Pittosporaceae, and Polemoniaceae). Some of the taxa in this group are polymorphic for endosperm formation (e.g., Asteraceae, Solanaceae, Rubiaceae, and Alangiaceae). The ab initio cellular endosperm of the Corniflorae-asterid group is a reversal to a trait present among "lower" hamamelids (which may have retained it from Magnoliidae; cf. Dahlgren, 1975). The formation of endosperm haustoria was not used as a character because of limited data availability, but mapping its occurrence on the cladogram indicates numerous parallel origins are likely. Although lost in *Actinidia*, endosperm haustoria are shared by most members of the ericalean clade, including *Fouquieria*.

The placement of Alseuosmiaceae (Fig. 1) reflects Takhtajan's (1980) classification in which they are listed between Bruniaceae and Pterostemonaceae. Airy Shaw (1973) and Gardner (1978) noted affinities between them and Escalloniaceae.



Many members of the Corniflorae-asterid group retain a suite of wood attributes generally considered to be "primitive," but Alseuosmiaceae have derived tendencies toward raylessness and scarcity of axial parenchyma (Dickison, 1986c). Other members of the Corniflorae-asterid group, such as Loasaceae, Polemoniaceae, and Scrophulariaceae (Carlquist, 1988, 1992), also have trends toward raylessness and/or scarcity of axial parenchyma, which have been associated with paedomorphic wood evolution (Carlquist, 1962). Paedomorphosis must have occurred numerous times in wood of the Corniflorae-asterid group.

The Cornales (represented by Garryaceae, Alangiaceae, Nyssaceae, and Cornaceae) are defined by uniovulate carpels (parallel with some core rosids), fleshy (berry- to drupelike) fruits, and campodromous secondary venation in leaves. A reversal to crassinucellate ovules also supports the clade, although Nyssaceae are secondarily tenuinucellate. Among Nyssaceae, *Nyssa* and *Camptotheca* are tenuinucellate, and *Davidia* is crassinucellate (Mohana Rao, 1972a; Schmid, 1978a; Tandon & Herr, 1971). Based on Eyde's (1988) phylogenetic hypothesis for Nyssaceae, the thick nucellus of *Davidia* is a parallelism with that of other Cornales. Two additional features, endosperm with hemicellulose and the formation of a nucellar cap, also may support the hypothesis of monophyly for Cornales, but neither was used in this analysis because of limited data availability.

My results support Eyde's (1988) placement of Cornaceae and Nyssaceae as sister groups on the basis of shared foveolate pollen exine. Alangiaceae share with Cornaceae and Nyssaceae reversals to long vessel and imperforate elements in their wood (Adams, 1949; Titman, 1949; Metcalfe & Chalk, 1950; Li & Chao, 1954, report shorter measurements for Alangiaceae than other authors). *Garrya* diverges from other Cornales in floral attributes. The dioecy, loss of a nectary, and other floral simplifications probably are associated with the evolution of wind pollination in *Garrya* (see Dahling, 1978). Dahling (1978) suggested that pollen of *Garrya* strongly resembles that of Cornaceae, but it differs in having a papillate secondary tectal sculpture that parallels that of *Euptelea*, *Buxaceae*, *Cercidiphyllum*, and *Myrothamnus*. Paliwal & Kakkar (1970) noted that *Garrya* diverged from Cornaceae in unique leaf features.

Actinodromous leaf venation and basifixed anthers support the monophyly of Cornales, Hydrangeaceae (represented by *Hydrangea*, *Deutzia*, and *Philadelphus*), Loasaceae, and Sarraceniaceae (Fig. 2). The Hydrangeaceae-Loasaceae-Sarraceni-

aceae group is supported by diplostemonous androecia, although Loasaceae are coded as polystemonous. Diplostemony is present among Loasaceae only in *Schismocarpus* (Hufford, 1989, 1990). A generic-level cladistic analysis of Loasaceae, however, has shown polystemony to be plesiomorphic for the family even when the outgroup is coded as diplostemonous (Hufford, unpublished results). Among Sarraceniaceae, only *Heliamphora* includes diplostemonous members (Maguire, 1978). Both *Darlingtonia* and *Sarracenia* are polystemonous (Maguire, 1978). Based on Thanikaimoni & Vasanthi's (1972) and Maguire's (1978) hypothesis that *Heliamphora* is the most primitive member of Sarraceniaceae, the family was coded using it. The Loasaceae-Sarraceniaceae clade is supported by tricarpellate gynoecia. Coding for gynoecial states is based on *Mentzelia* for Loasaceae and *Heliamphora* for Sarraceniaceae, although both families have variation in gynoecial merosity, with five carpels being the most common in each.

Loasaceae have been placed in Dilleniidae in some treatments (e.g., Gilg, 1925; Cronquist, 1981) largely on the basis of their parietal placentation and putatively centrifugally developing polystemonous androecia. Various androecial developmental patterns are present among Loasaceae, but none are strictly centrifugal (Hufford, 1990). Those Loasaceae with a centrifugal phase during androecial development actually begin with centripetal development and have complex androecia that are probably derived within the family. Emphasis has been given to trichomes in taxonomic studies of Loasaceae, although they have not been used to develop hypotheses of relationship for the family because of their presumed uniqueness. Among Loasaceae, the tuberculate trichomes with and without a prominent pedestal of basal cells may be homologous with similar tuberculate trichomes, including some with distinct basal cells, of Hydrangeaceae (Hardin & Pilatowski, 1981). Loasaceae and Hydrangeaceae are among the few groups found to possess 10-carboxyl (and 10-decarboxylated) iridoids (Dahlgren et al., 1981). Other groups with these iridoid forms include Ericaceae, Oleaceae, Retziaceae, Stilbaceae, and Verbenaceae. Seco-iridoids are present in Loasaceae and Sarraceniaceae as well as in Hydrangeaceae, Gentianales, Dipsacales, and a few other members of the Corniflorae-asterid group (Dahlgren et al., 1981).

Sarraceniaceae have been allied with magnoliids, such as Ranunculaceae and Papaveraceae (Lindley, 1847; Thanikaimoni & Vasanthi, 1972;



Takhtajan, 1980), or dilleniids, such as Theales and Parietales (Markgraf, 1955; DeBuhr, 1977). This analysis does not test the placement of Sarraceniaceae among magnoliids, but its evolution among them seems unlikely given its derived features. Sarraceniaceae have been allied with Nepenthaceae in some classifications (e.g., Cronquist's, 1981, Nepenthales) on the basis of shared ascidiate leaves involved in insectivory. My results, which place Nepenthaceae in the core rosoid group, are not consistent with those classifications.

Although Sarraceniaceae are placed as the sister taxon of Loasaceae in these results, I call attention to their potential evolution among Ericales. DeCandolle (1873) noted similarities among Sarraceniaceae and Monotropeoideae and Pyroloideae of Ericaceae. Jensen et al. (1975) more recently called attention to similarities between Sarraceniaceae and Ericales. For example, the placentation of Sarraceniaceae, Monotropeoideae, and Pyroloideae is axile in the lower part of the gynoecium and parietal in the upper (Abbott, 1936; Maguire, 1978; Hufford, unpublished obs.). Inversion of the anthers is common among Ericales, although it has not been described for Cyrillaceae. Anther inversion occurs relatively early during stamen development among most Ericales, although in *Clethra* and some Ericaceae it occurs at anthesis. In Sarraceniaceae, anther inversion at anthesis occurs in *Heliampora* (Maguire, 1978), although it is unknown in *Darlingtonia* and *Sarracenia*. The umbrellalike stigma of Sarraceniaceae may represent an elaboration of the capitate stigma common among Ericales. Numerous cells of the flowers of Sarraceniaceae and Ericales are tanniferous (Hufford, unpublished obs.). These attributes are notably not shared by Sarraceniaceae and Loasaceae, but may be derived states shared by the former and some Ericales. Within Sarraceniaceae, Loasaceae, and Ericales, gynoecia with three to five carpels are present.

The clade composed of Ericales (with Fouquieriaceae) and Asteridae (with Pittosporaceae and *Columellia*) is supported by unilacunar nodes and sympetally (Fig. 2). Unilacunar nodes and sympetaly were used historically to hypothesize monophyly of Asteridae. Both traits occur as parallelisms in *Escallonia*.

The core ericalean groups, Clethraceae and Ericaceae, form part of a monophyletic group including *Actinidia* and Fouquieriaceae. Fouquieriaceae have been allied primarily with parietalean dilleniids (Bentham & Hooker, 1862; Niedenzu, 1895; Behnke, 1976; Cronquist, 1981; Takhtajan, 1980, 1987). Various chemical compounds, including ellagitannins and iridoids, in Fouquieri-

aceae do not support their placement in Dilleniidae (Bate-Smith, 1964; Scogin, 1977, 1978, Jensen & Nielsen, 1982). Dahlgren et al. (1976) used the chemical profile, polyandrous flowers, and tricarpellate gynoecia of Fouquieriaceae to suggest they were more closely related to Ericales (as part of Dahlgren's Corniflorae) than to dilleniids, which is consistent with my results and those of Olmstead et al. (1992).

Nash (1903), Henrickson (1967), Thorne (1977, 1981, 1983) and Downie & Palmer (1992) allied Fouquieriaceae with Polemoniaceae, which is especially interesting when the former is compared with *Acanthogilia* [*Gilia*] *gloriosa*. Nash (1903) suggested that Fouquieriaceae were similar to *Gilia* located in the same area. *Acanthogilia* is a basally branched shrub of north-central Baja California (Day & Moran, 1986). It is similar to Fouquieriaceae not only in its overall shoot morphology but also in its long shoot/short shoot dimorphism and leaf development. Leaves on long shoots of *Acanthogilia* sclerify as spines. Short shoots arise in the axils of spinose leaves. The leaves formed on short shoots have deciduous blades but persistent bases reminiscent of Fouquieriaceae. The pollen of both *Fouquieria* and *Acanthogilia* is colpate with a reticulate exine. Neither of these genera has the specialized pollen characteristics of many Polemoniaceae. Day & Moran (1986: 125) suggested that *Acanthogilia* is most closely related to *Cantua* in being a "specialized desert descendant of a diploid line also ancestral to *Cantua*," although it shares numerous derived features with *Fouquieria*.

My results place Polemoniaceae and Pittosporaceae as the sister group of the rest of Asteridae and Fouquieriaceae as the sister group of the rest of Ericales (Fig. 1). Chloroplast DNA sequence data (Olmstead et al., 1992) currently support the hypothesis that Fouquieriaceae and Polemoniaceae are part of a monophyletic Ericales. Polemoniaceae and asterids have distinctly epipetalous stamens. Epipetalous stamens are derived in some ericalean groups, but none were coded with this state in my analysis. The tricarpellate gynoecia and loculicidal capsules of Polemoniaceae are characteristic of Ericales, such as Clethraceae, but not of asterids, which tend to have bicarpellate gynoecia and septicidal capsules. Iridoid compounds have been lost among Ericales (e.g., in Cyrillaceae and Clethraceae) and asterids. Some of the specialized pollen of Polemoniaceae and the ericalean Epacridaceae are quite similar. Asterids that lack iridoids generally synthesize polyacetylenes and/or tropane alkaloids (Dahlgren et al., 1981; Gershenzon & Mabry, 1983), but this is not true of Polemoni-



aceae, Polemoniaceae, Clethraceae, and the Monotropoideae and Pyroloideae of the Ericaceae were the only groups to form both ketose and isoketose oligosaccharides in a broad survey by Pollard & Amuti (1981). Isoketose oligosaccharides were found in various asterids, possibly indicating this trait is shared by all members of the asterid-ericalean monophyletic group.

*Actinidia* has been allied with Dilleniaceae and Theaceae (Hutchinson, 1959; Dickison, 1972b; Schmid, 1978b; Cronquist, 1981). Its unitegmic, tenuinucellate ovules, and iridoid compounds are derived features shared with members of the Corniflorae-asterid group but not with Dilleniaceae. Some Theales share ovular characteristics with *Actinidia* but not its cellular endosperm and iridoids. Heel (1987) has shown that androecial development in *Actinidia* is not strictly centrifugal as among some dilleniids, although the putative presence of this attribute has been used to place it in Dilleniidae. Hallier (1905), Hunter (1966), and Takhtajan (1969) allied *Actinidia* with Ericales; this is supported by my results. The branch (Fig. 2) with Clethraceae, Ericaceae, and *Actinidia* is corroborated by the occurrence of 600–1,000- $\mu$ m-long vessel elements, opposite intervessel pitting, and imperforate pollen tectum in all three taxa. Like other Ericales, the anthers of *Actinidia* become inverted.

The present study significantly demonstrates the placement of Asteridae as the sister group of Ericales among taxa recognized by Dahlgren (1980, 1983) as Corniflorae. Epipetalous stamens may be a derived feature shared by all Asteridae, although the placement of Pittosporaceae as the sister group of Polemoniaceae makes this equivocal. Haplostemony is commonly used to support the hypothesis of monophyly of Asteridae, but my results show that it originates with "lower" hamamelids and is retained in the Corniflorae-asterid group. Diplostemony and polystemony are derived variously in the Corniflorae-asterid group as well as among the core rosids. Corolla connation (sympetaly) unites the asterid and ericalean groups, but it also occurs in other members of the Corniflorae-asterid group, including Alangiaceae, Alseuosmiaceae, Escalloniaceae, and Loasaceae.

*Columellia* has been allied with a wide variety of groups (see Stern et al., 1969), ranging from asterids (including Gesneriaceae, Loganiaceae, and Rubiaceae), "woody saxifrages" (such as *Phildelphus* and *Escallonia*), and dilleniids (Cucurbitaceae). My results place *Columellia* as the sister group of Caprifoliaceae. Stern et al. (1969) suggested that most attributes of *Columellia* were

shared by Escalloniaceae, and experimentally placing *Columellia* as the sister group of Escalloniaceae adds three character state changes. Including *Columellia* in more inclusive studies with Dipsacales and Escalloniaceae may lead to more decisive hypotheses about its placement.

My results are not consistent with hypotheses that *Viburnum* is more closely related to groups other than Caprifoliaceae nor with those (e.g., Dahlgren, 1983; Takhtajan, 1987) suggesting that Dipsacales, such as Caprifoliaceae, are more closely related to rosids of the Corniflorae grade than to asterids. The monophyly of *Columellia*, Caprifoliaceae, and *Viburnum* is supported by reversals in wood attributes, such as a solitary distribution of vessels and only true tracheids as imperforate elements. Chloroplast DNA data (Donoghue, 1992; Downie & Palmer, 1992; Olmstead et al., 1992) do support a placement for *Viburnum* and *Sambucus* separate from other Caprifoliaceae (with both placed among Asteridae).

The monophyly of Asteridae as traditionally circumscribed (e.g., Cronquist, 1981) is largely supported. The results do not support the Jensen et al. (1975) hypothesis of a separate rosid origin for asterids with iridoid compounds from those without iridoids. The asterids without iridoids of the Solanales, Campanulales, and Asterales are placed as a monophyletic group nested among the asterids with iridoid compounds. The results also do not support Takhtajan's (1987) classification, in which asterids are circumscribed in three groups (Dipsacales, Lamiales, and Asteridae sens. str.) with separate origins among the rosids Corniflorae.

#### CONCLUSIONS AND PROBLEMS FOR FURTHER RESEARCH

This preliminary, exploratory analysis has pertinent results for understanding the phylogeny of nonmagnoliid dicotyledons. These include: (1) Hamamelidae (sensu Takhtajan, 1980, 1987; Cronquist, 1981, 1988) are polyphyletic; (2) "lower" Hamamelidae (e.g., Trochodendrales and Hamamelidales) are a grade at the base of the nonmagnoliid dicotyledons; (3) Rosidae (sensu Takhtajan, 1980, 1987; Cronquist, 1981, 1988) are paraphyletic with respect to Asteridae, Dilleniidae, and "higher" Hamamelidae (e.g., Fagales, Juglandales, and Casuarinaceae); (4) "higher" Hamamelidae appear most closely related to *Davidsonia* and Cunoniaceae; (5) monophyly of Dilleniidae is not supported; and (6) Dahlgren's (1980, 1983) Corniflorae are the rosid grade in which Asteridae are rooted.



Rosidae are central to understanding the phylogeny of nonmagnoliid dicotyledons, and they require extensive investigation. Identification of monophyletic groups among basal rosids and ascertaining their relationship to higher rosid orders are crucial. A key step will involve investigating the monophyly of Rosaceae by analyzing their relationships with Chrysobalanaceae, Connaraceae, Fabaceae, Rhabdodendraceae, and Surianaceae, as well as higher rosid orders. Ascertaining the relationships of Engler's (1930) Saxifragaceae also is critical for understanding early evolution in both the core rosid group and the Corniflorae-asterid group (see Soltis et al., 1990). Additional analyses centered on Cunoniaceae (see Hufford & Dickson, in press) will be important for better understanding relationships of *Davidsonia* and "higher" Hamamelidae on one hand and Rhizophoraceae, Dilleniaceae, and Theales on the other. Monophyletic groups in Dilleniaceae and their relations with rosids remain virtually unexplored, but their identification will lead to better understanding of the diversification of nonmagnoliid dicotyledons. More detailed analyses of the Corniflorae (sensu Dahlgren, 1983) grade of Rosidae will be crucial for understanding the relationships of problematic taxa (including major groups such as Ericales and, possibly, Ebenales) and the evolution of character suites present among Asteridae. Defining a monophyletic Asteridae and understanding relationships among their major clades also will be contingent on more fully developed hypotheses of relationships among taxa of the Corniflorae grade. Large, broadly based cladistic analyses will be critical for developing hypotheses of relationship for higher level taxa and, especially, problematic groups.

## LITERATURE CITED

- ABBOTT, C. L. 1936. Phylogeny of the Ericales. *Trillia* 9: 62-69.
- ADAMS, J. E. 1949. Studies in the comparative anatomy of the Cornaceae. *J. Elisha Mitchell Sci. Soc.* 65: 218-244.
- AGABABIAN, V. S. 1961. Materials toward the palynological study of the family Saxifragaceae s. l. *Izv. Biol. Nauki* 14: 45-61.
- AIRY SHAW, H. K. 1973. *A Dictionary of the Flowering Plants and Ferns*. Cambridge Univ. Press, Cambridge.
- AVETISIAN, E. M. 1975. Palynomorphology of the family Loasaceae. *Palinologija* 1975: 5-18.
- BAAS, P. & R. C. V. J. ZWEYPFENNIG. 1979. Wood anatomy of the Lythraceae. *Acta Bot. Neerl.* 28: 117-155.
- BAILEY, I. W. & C. G. NAST. 1945. Morphology and relationships of *Trochodendron* and *Tetracentron*, I. Stem, root, and leaf. *J. Arnold Arbor.* 26: 143-154.
- BANGE, G. G. J. 1952. A new family of dicotyledons: Davidsoniaceae. *Blumea* 7: 293-296.
- BASAK, R. K. & K. SUBRAMANYAN. 1966. Pollen grains of some species of *Nepenthes*. *Phytomorphology* 16: 334-338.
- BATE-SMITH, E. C. 1964. Chemistry and taxonomy of *Fouquieria splendens* Engelm: a new member of the asperuloside group. *Phytochemistry* 3: 623-625.
- . 1973. Systematic distribution of ellagitannins in relation to the phylogeny and classification of the angiosperms. Pp. 93-100 in G. Bendz & J. Santesson (editors), *Chemistry in Botanical Classification*. Nobel Foundation, Stockholm.
- . 1977. Chemistry and taxonomy of the Cunoniaceae. *Biochem. Syst. Ecol.* 5: 95-105.
- , I. K. FERGUSON, K. HUTSON, S. R. JENSEN, B. J. NIELSEN & T. SWAIN. 1975. Phytochemical interrelationships in the Cornaceae. *Biochem. Syst. Ecol.* 3: 79-89.
- BAUSCH, J. 1938. A revision of the Eucryphiaceae. *Kew Bull.* 1938: 317-349.
- BEAMISH, K. I. & S. C. LIN. 1965. Fertilization and seed development in *Saxifraga integrifolia* Hook. *Canad. J. Bot.* 43: 861-865.
- BEHNKE, H.-D. 1976. Sieve-element plastids of *Fouquieria*, *Frankia* (Tamaricales), and *Rhabdodendron* (Rutaceae), taxa sometimes allied with Centrospermae (Caryophyllales). *Taxon* 25: 265-268.
- . 1988. Sieve-element plastids and systematic relationships of Rhizophoraceae, Anisophylleaceae, and allied groups. *Ann. Missouri Bot. Gard.* 75: 1387-1409.
- BENSEL, C. R. & B. F. PALSER. 1975a. Floral anatomy in the Saxifragaceae sensu lato. II. Saxifragoideae and Iteoideae. *Amer. J. Bot.* 62: 661-675.
- & ———. 1975b. Floral anatomy in the Saxifragaceae sensu lato. III. Kirengeshomoideae, Hydrangeoideae and Escallonioideae. *Amer. J. Bot.* 62: 676-687.
- & ———. 1975c. Floral anatomy in the Saxifragaceae sensu lato. IV. Baueroideae and conclusions. *Amer. J. Bot.* 62: 688-694.
- BENTHAM, G. & J. D. HOOKER. 1862. *Genera Plantarum*. Reeve, London.
- BHANDARI, N. N. 1971. Embryology of the Magnoliales and comments on their relationships. *J. Arnold Arbor.* 52: 1-39, 285-304.
- BOGLE, A. L. 1986. The floral morphology and vascular anatomy of the Hamamelidaceae: subfamily Liquidambaroideae. *Ann. Missouri Bot. Gard.* 73: 325-347.
- . 1989. The floral morphology, vascular anatomy, and ontogeny of the Rhodoleioideae (Hamamelidaceae) and their significance in relation to the 'lower' hamamelids. Pp. 201-220 in P. R. Crane & S. Blackmore (editors), *Evolution, Systematics, and Fossil History of the Hamamelidae*, Volume 1. Introduction and 'Lower' Hamamelidae. Clarendon, Oxford.
- BOHLMANN, F., T. BURKHARDT & C. ZDERO. 1973. Naturally occurring acetylenes. Academic Press, London.
- BREMER, K. 1987. Tribal interrelationships of the Asteraceae. *Cladistics* 3: 210-253.
- BRIZICKY, G. K. 1961. A synopsis of the genus *Columellia* (Columelliaceae). *J. Arnold Arbor.* 42: 363-372.
- BROUWER, J. 1924. Studies in Platanaceae. *Recurcul. Trav. Bot. Néerl.* 1924: 369-382.
- BRUSH, W. D. 1917. Distinguishing characters of North



- American sycamore woods. Bot. Gaz. (Crawfordsville) 64: 480-496 + 7 pls.
- BURKETT, G. W. 1932. Anatomical studies within the genus *Hydrangea*. Proc. Indiana Acad. Sci. 41: 83-95.
- CARLQUIST, S. 1962. A theory of paedomorphosis in dicotyledonous woods. Phytomorphology 12: 30-45.
- . 1964. Wood anatomy of Veronieae (Compositae). Aliso 5: 451-467.
- . 1966. Wood anatomy of Compositae: a summary, with comments on factors controlling wood evolution. Aliso 6: 25-44.
- . 1969. Wood anatomy of Lobelioideae (Campanulaceae). Biotropica 1: 47-72.
- . 1976. Wood anatomy of *Myrothamnus flabellifolia* (Myrothamnaceae) and the problem of multiperforate perforation plates. J. Arnold Arbor. 57: 119-126.
- . 1978. Wood anatomy of Bruniaceae: correlations with ecology, phylogeny, and organography. Aliso 9: 323-364.
- . 1981a. Wood anatomy of Nepenthaceae. Bull. Torrey Bot. Club 108: 324-330.
- . 1981b. Wood anatomy of Pittosporaceae. Allertonia 2: 355-392.
- . 1982a. Wood anatomy of Buxaceae: correlations with ecology and phylogeny. Flora 172: 463-491.
- . 1982b. Wood anatomy of Daphniphyllaceae: ecological and phylogenetic considerations, review of pittosporalean families. Brittonia 34: 242-266.
- . 1984. Wood anatomy of Loasaceae with relation to systematics, habit, and ecology. Aliso 10: 583-602.
- . 1988. Comparative Wood Anatomy. Springer-Verlag, Berlin.
- . 1992. Wood anatomy of sympetalous dicotyledon families: a summary, with comments on systematic relationships and evolution of the woody habit. Ann. Missouri Bot. Gard. 79: 303-332.
- & D. A. HOEKMAN. 1985. Wood anatomy of Staphyleaceae: ecology, statistical correlations, and systematics. Flora 177: 195-216.
- , V. M. ECKHART & D. C. MICHENER. 1984. Wood anatomy of Polemoniaceae. Aliso 10: 547-572.
- CAVE, M. S., H. J. ARNOTT & S. C. COOK. 1961. Embryogeny in the California peonies with reference to their taxonomic position. Amer. J. Bot. 48: 397-404.
- CHALLICE, J. 1981. Chemotaxonomic studies in the family Rosaceae and the evolutionary origins of the subfamily Maloideae. Preslia 53: 289-304.
- CHAO, C.-Y. 1954. Comparative pollen morphology of the Cornaceae and allies. Taiwania 5: 93-106.
- CHAPMAN, M. 1953. The ovule and embryo sac of *Saxifraga virginicensis*. Amer. J. Bot. 20: 151-158.
- CORNER, E. J. H. 1946. Centrifugal stamens. J. Arnold Arbor. 27: 423-437.
- CRANE, P. R. & S. BLACKMORE. 1989. Evolution, Systematics, and Fossil History of the Hamamelidae. Clarendon Press, Oxford.
- CREPET, W. L. 1989. History and implications of the early North American fossil record of Fagaceae. Pp. 45-66 in P. R. Crane & S. Blackmore (editors), Evolution, Systematics, and Fossil History of the Hamamelidae, Volume 2. 'Higher' Hamamelidae. Clarendon Press, Oxford.
- CRONQUIST, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.
- . 1988. The Evolution and Classification of Flowering Plants. New York Bot. Gard., Bronx, New York.
- CROWDEN, R. K. 1969. Chemosystematics of the Umbelliferae—a general survey. Phytochemistry 8: 1963-1984.
- CUATRECASAS, J. 1970. Brunelliaceae. Flora Neotropica 2: 1-189.
- DAHLGREN, K. V. O. 1927. Über das Vorkommen von Stärke in den Embryosäcken der Angiospermen. Ber. Deutsch. Bot. Gesellsch. 45: 374-384.
- . 1930. Zur Embryologie der Saxifragoideen. Svensk Bot. Tidskr. 24: 429-448.
- DAHLGREN, R. 1975. The distribution of characters within an angiosperm system. I. Some embryological characters. Bot. Not. 128: 181-197.
- . 1977. A note on the taxonomy of the "Sympetalae" and related groups. Contr. Cairo Univ. Herb. 7 & 8: 83-102.
- . 1980. A revised system of classification of the angiosperms. Bot. J. Linn. Soc. 80: 91-124.
- . 1983. General aspects of angiosperm evolution and macrosystematics. Nordic J. Bot. 3: 119-149.
- , S. R. JENSEN & B. J. NIELSEN. 1976. Iridoid compounds in Fouquieriaceae and notes on its possible affinities. Bot. Not. 129: 207-212.
- , ——— & ———. 1981. A revised classification of the angiosperms with comments on correlation between chemical and other characters. Pp. 149-204 in D. A. Young & D. S. Sieglar (editors), Phytochemistry and Angiosperm Phylogeny. Praeger, New York.
- DAHLING, G. V. 1978. Systematics and evolution of *Garrya*. Contr. Gray Herb. 209: 1-104.
- DAUMANN, E. 1974. Zur Frage nach dem Vorkommen eines Septalnektariums bei Dicotyledonen. Zugleich ein Beitrag zur Blütenmorphologie und Bestäubungsökologie von *Buxus* L. and *Cneorum* L. Preslia 46: 97-109.
- DAVIS, G. L. 1966. Systematic Embryology of the Angiosperms. Wiley, New York.
- DAY, A. G. & R. MORAN. 1986. *Acanthogilia*, a new genus of Polemoniaceae from Baja California, Mexico. Proc. Calif. Acad. Sci. 44: 111-126.
- DEBUHR, L. E. 1977. Wood anatomy of the Sarraceniacae; ecological and evolutionary implications. Pl. Syst. Evol. 128: 159-169.
- . 1978. Wood anatomy of *Forsellesia* (*Glossopetalon*) and *Crossosoma* (Crossosomataceae, Rosales). Aliso 9: 179-184.
- DECANDOLLE, A. 1873. Prodromus Systematis Naturalis Regni Vegetabilis, Volume 17. Paris.
- DICKISON, W. C. 1967a. Comparative morphological studies in Dilleniaceae, I. Wood anatomy. J. Arnold Arbor. 48: 1-23.
- . 1967b. Comparative morphological studies in Dilleniaceae, II. The pollen. J. Arnold Arbor. 48: 231-240.
- . 1968. Comparative morphological studies in Dilleniaceae, III. The carpels. J. Arnold Arbor. 49: 317-329.
- . 1970. Comparative morphological studies in Dilleniaceae, VI. Stamens and young stem. J. Arnold Arbor. 51: 403-418.



- . 1971. Anatomical studies in the Connaraceae. I. Carpels. *J. Elisha Mitchell Sci. Soc.* 87: 77–86.
- . 1972a. Anatomical studies in the Connaraceae. II. Wood Anatomy. *J. Elisha Mitchell Sci. Soc.* 88: 120–136.
- . 1972b. Observations on the floral morphology of some species of *Saurauia*, *Actinidia*, and *Clematoclethra*. *J. Elisha Mitchell Sci. Soc.* 88: 43–54.
- . 1975a. Floral morphology and anatomy of *Bauera*. *Phytomorphology* 25: 69–76.
- . 1975b. Leaf anatomy of Cunoniaceae. *Bot. J. Linn. Soc.* 71: 275–293 + 7 pls.
- . 1975c. Studies of the floral anatomy of the Cunoniaceae. *Amer. J. Bot.* 62: 433–447.
- . 1978. Comparative anatomy of Eucryphiaceae. *Amer. J. Bot.* 65: 722–735.
- . 1979. A survey of pollen morphology of the Connaraceae. *Pollen & Spores* 21: 31–79.
- . 1980. Comparative wood anatomy and evolution of the Cunoniaceae. *Allertonia* 2: 281–321.
- . 1984. Fruits and seeds of the Cunoniaceae. *J. Arnold Arbor.* 65: 149–190.
- . 1986a. Floral morphology and anatomy of Staphyleaceae. *Bot. Gaz. (Crawfordsville)* 147: 312–326.
- . 1986c. Wood anatomy and affinities of the Alseuosmiaceae. *Syst. Bot.* 11: 214–221.
- . 1987a. A palynological study of the Staphyleaceae. *Grana* 26: 1–24.
- . 1987b. Leaf and nodal anatomy and systematics of Staphyleaceae. *Bot. Gaz. (Crawfordsville)* 148: 475–489.
- . 1989a. Comparisons of primitive Rosidae and Hamamelidae. Pp. 47–73 in P. R. Crane & S. Blackmore (editors), *Evolution, Systematics, and Fossil History of the Hamamelidae, Volume 1. Introduction and 'Lower' Hamamelidae*. Clarendon Press, Oxford.
- . 1989b. Stem and leaf anatomy of the Alseuosmiaceae. *Aliso* 12: 567–578.
- & P. BAAS. 1977. The morphology and relationships of *Paracryphia* (Paracryphiaceae). *Blumea* 23: 417–438.
- & R. RUTISHAUSER. 1990. Developmental morphology of stipules and systematics of the Cunoniaceae and presumed allies. II. Taxa without interpetiolar stipules and conclusions. *Bot. Helvetica* 100: 75–95.
- DNYANSAGAR, V. R. 1955. Embryological studies in the Leguminosae. XI. Embryological features and formula and taxonomy of the Mimosaceae. *J. Indian Bot. Soc.* 34: 362–374.
- DONOGHUE, M. J. 1985. Pollen diversity and exine evolution in *Viburnum* and the Caprifoliaceae *sensu lato*. *J. Arnold Arbor.* 66: 421–469.
- . 1992. Phylogenetic relationships of Dipsacales based on *rbcL* sequences. *Ann. Missouri Bot. Gard.* 79: 333–345.
- DOWNIE, S. R. & J. D. PALMER. 1992. Restriction site mapping of the chloroplast DNA inverted repeat: a molecular phylogeny of the Asteridae. *Ann. Missouri Bot. Gard.* 79: 266–283.
- DRINNAN, A. N., P. R. CRANE, E. M. FRIIS & K. R. PEDERSEN. 1991. Angiosperm flowers and tricolpate pollen of buxaceous affinity from the Potomac Group (Mid-Cretaceous) of eastern North America. *Amer. J. Bot.* 78: 153–176.
- EHRENDORFER, F. 1989. The phylogenetic position of the Hamamelidae. Pp. 1–7 in P. R. Crane & S. Blackmore (editors), *Evolution, Systematics, and Fossil History of the Hamamelidae, Volume 1. Introduction and 'Lower' Hamamelidae*. Clarendon Press, Oxford.
- ELIAS, T. S. 1971. The genera of Fagaceae in the southeastern United States. *J. Arnold Arbor.* 52: 159–195.
- ELSWORTH, J. F. & K. R. MARTIN. 1971. Flavonoids of the Proteaceae, part 1. A chemical contribution to studies on the evolutionary relationships in the S. African Proteoideae. *J. S. African Bot.* 37: 199–212.
- ENDRESS, P. K. 1969. Gesichtspunkte zur systematischen Stellung der Eupteleaceen (Magnoliales). *Ber. Schweiz. Bot. Ges.* 79: 229–278 + 2 pl.
- . 1977. Evolutionary trends in the Hamamelidales–Fagales–group. *Pl. Syst. Evol., Suppl.* 1: 321–347.
- . 1986. Floral structure, systematics, and phylogeny in Trochodendrales. *Ann. Missouri Bot. Gard.* 73: 297–324.
- . 1989a. Aspects of evolutionary differentiation of the Hamamelidaceae and the lower Hamamelididae. *Pl. Syst. Evol.* 162: 193–211.
- . 1989b. Phylogenetic relationships in the Hamamelidoideae. Pp. 227–248 in P. R. Crane & S. Blackmore (editors), *Evolution, Systematics, and Fossil History of the Hamamelidae, Volume 1. Introduction and 'Lower' Hamamelidae*. Clarendon Press, Oxford.
- . 1989c. The systematic position of the Myrothamnaceae. Pp. 193–200 in P. R. Crane & S. Blackmore (editors), *Evolution, Systematics, and Fossil History of the Hamamelidae, Volume 1. Introduction and 'Lower' Hamamelidae*. Clarendon Press, Oxford.
- ENGLER, A. 1930. Saxifragaceae. Pp. 74–226 in A. Engler & K. Prantl (editors), *Die Natürlichen Pflanzenfamilien* 18a, 2nd edition. Engelmann, Leipzig.
- ERDTMAN, G. 1952. Pollen Morphology and Plant Taxonomy. *Chronica Botanica*, Waltham.
- EYDE, R. H. 1964. Inferior ovary and generic affinities of *Garrya*. *Amer. J. Bot.* 51: 1083–1092.
- . 1966. The Nyssaceae in the southeastern United States. *J. Arnold Arbor.* 47: 117–125.
- . 1968. Flowers, fruits, and phylogeny of Alangiaceae. *J. Arnold Arbor.* 49: 168–192.
- . 1988. Comprehending *Cornus*: puzzles and progress in the systematics of the dogwoods. *Bot. Rev. (Lancaster)* 54: 233–351.
- & C. C. TSENG. 1971. What is the primitive floral structure of Araliaceae? *J. Arnold Arbor.* 52: 205–239.
- FLORES, E. M. & M. F. MOSELEY. 1982. The anatomy of the pistillate inflorescence and flower of *Casuarina verticillata* Lamarck (Casuarinaceae). *Amer. J. Bot.* 69: 1673–1684.
- FRANKS, J. W. & L. WATSON. 1963. The pollen morphology of some Ericales. *Pollen & Spores* 5: 51–68.
- GARDNER, R. O. 1978. Systematic notes on the Alseuosmiaceae. *Blumea* 24: 138–142.
- GAUMANN, E. 1919. Studien über die Entwicklungsgeschichte einiger Saxifragales. *Recueil Trav. Bot. Néerl.* 16: 285–322.



- GERSHENZON, J. & T. J. MABRY. 1983. Secondary metabolites and the higher classification of angiosperms. *Nordic J. Bot.* 3: 5-34.
- GIANNASI, D. E. 1986. Phytochemical aspects of phylogeny in Hamamelidae. *Ann. Missouri Bot. Gard.* 73: 417-437.
- GIEBEL, K. P. & W. C. DICKISON. 1976. Wood anatomy of Clethraceae. *J. Elisha Mitchell Sci. Soc.* 92: 17-26.
- GILG, E. 1895a. Dilleniaceae. Pp. 100-128 in A. Engler & K. Prantl (editors), *Die Natürlichen Pflanzenfamilien III* (6). Engelmann, Leipzig.
- . 1895b. Ochnaceae. Pp. 131-153 in A. Engler & K. Prantl (editors), *Die Natürlichen Pflanzenfamilien III* (6). Engelmann, Leipzig.
- . 1925. Loasaceae. Pp. 522-543 in A. Engler & K. Prantl (editors), *Die Natürlichen Pflanzenfamilien*, 2nd edition. Engelmann, Leipzig.
- GORNALL, R. J., B. A. BOHM & R. DAHLGREN. 1979. The distribution of flavonoids in the angiosperms. *Bot. Not.* 132: 1-30.
- GRAHAM, A., J. W. NOWICKE, J. J. SKVARLA, S. A. GRAHAM, V. PATEL & S. LEE. 1987. Palynology and systematics of the Lythraceae. II. Genera *Haitia* through *Peplis*. *Amer. J. Bot.* 74: 829-850.
- GRUND, C. & U. JENSEN. 1981. Systematic relationships of the Saxifragales revealed by serological characteristics of seed proteins. *Pl. Syst. Evol.* 137: 1-22.
- GUSEJNOVA, N. A. 1976. On cytoembryology in Platanaeae. *Bjull. Glavn. Bot. Sada* 102: 67-71.
- HALL, J. W. 1952. The comparative anatomy and phylogeny of the Betulaceae. *Bot. Gaz. (Crawfordsville)* 113: 235-270.
- HALLIER, H. 1905. Provisional scheme of the natural (phylogenetic) system of flowering plants. *New Phytol.* 4: 151-162.
- HAM, R. VAN DER. 1988. Types harmomégathiques dans le pollen des Sapindaceae-Nephelieae. *Inst. Franç. Pondichéry, Trav. Sect. Sci. Tech.* 25: 355-358.
- & B. J. VAN HEUVEN. 1989. Evolutionary trends in the morphology and harmomegathy of the pollen of the genus *Guioa* (Sapindaceae-Cupanieae). *Blumea* 34: 21-60.
- HARDIN, J. W. & R. E. PILATOWSKI. 1981. Atlas of foliar surface features in woody plants, III. *Hydrangea* (Saxifragaceae) of the United States. *J. Elisha Mitchell Sci. Soc.* 97: 29-36.
- HARMS, H. 1930. Hamamelidaceae. Pp. 303-345 in A. Engler & K. Prantl (editors), *Die Natürlichen Pflanzenfamilien* 18a, 2nd edition. Engelmann, Leipzig.
- HART, H. 'T. & J. KOEK-NOORMAN. 1989. The origin of the woody Sedoideae (Crassulaceae). *Taxon* 38: 535-544.
- HASKINS, M. L. & W. J. HAYDEN. 1987. Anatomy and affinities of *Penthorum*. *Amer. J. Bot.* 74: 164-177.
- HEEL, W. A. VAN. 1987. Androecium development in *Actinidia chinensis* and *A. melandra* (Actinidiaceae). *Bot. Jahrb. Syst.* 109: 17-23.
- HEIMSCH, C. 1942. Comparative anatomy of the secondary xylem in the "Gruinales" and "Terebinthales," of Wettstein with reference to taxonomic grouping. *Lilloa* 8: 83-198 + 17 pls.
- & E. E. TSCHABOLD. 1972. Xylem studies in the Linaceae. *Bot. Gaz. (Crawfordsville)* 133: 242-253.
- & R. H. WETMORE. 1939. The significance of wood anatomy in the taxonomy of the Juglandaceae. *Amer. J. Bot.* 26: 651-660.
- HENRICKSON, J. 1967. Pollen morphology of the Fouquieriaceae. *Aliso* 6: 137-160.
- . 1972. A taxonomic revision of the Fouquieriaceae. *Aliso* 7: 439-537.
- HERR, J. M. & M. L. DOWD. 1968. Development of the ovule and megagametophyte in *Oxalis corniculata* L. *Phytomorphology* 18: 43-53.
- HICKEY, L. J. & J. A. DOYLE. 1977. Early Cretaceous fossil evidence for angiosperm evolution. *Bot. Rev. (Lancaster)* 43: 3-104.
- & J. A. WOLFE. 1975. The bases of angiosperm phylogeny: vegetative morphology. *Ann. Missouri Bot. Gard.* 62: 538-589.
- HIDEUX, M. J. & I. K. FERGUSON. 1976. The stereostructure of the exine and its evolutionary significance in Saxifragaceae *sensu lato*. Pp. 327-377 in I. K. Ferguson & J. Muller (editors), *The Evolutionary Significance of the Exine*. Academic Press, London.
- HIEPKO, P. 1965. Das zentrifugale Androeceum der Paeoniaceae. *Ber. Deutsch. Bot. Ges.* 77: 427-435.
- . 1966. Zur Morphologie, Anatomie und Funktion des Diskus der Paeoniaceae. *Ber. Deutsch. Bot. Ges.* 79: 233-245.
- HILS, M. H., W. C. DICKISON, T. W. LUCANSKY & W. L. STERN. 1988. Comparative anatomy and systematics of woody Saxifragaceae: *Tetracarpaea*. *Amer. J. Bot.* 75: 1687-1700.
- HJELMQUIST, H. 1948. Studies on the floral morphology and phylogeny of the Amentiferae. *Bot. Not., Suppl.* 2: 1-171.
- . 1957. Some notes on the endosperm and embryo development in Fagales and related orders. *Bot. Not.* 110: 173-195.
- HOOGLAND, R. D. 1952. A revision of the genus *Dillenia*. *Blumea* 7: 1-145.
- . 1979. Studies in the Cunoniaceae. II. The genera *Caldcluvia*, *Pullea*, *Acsmithia*, and *Spiraeanthemum*. *Blumea* 25: 481-505.
- HOWARD, R. A. 1970. Some observations on the nodes of woody plants with special reference to the problem of the 'split lateral' versus the 'common gap.' Pp. 195-214 in N. K. B. Robson, D. F. Cutler & M. Gregory (editors), *New Research in Plant Anatomy*. Academic Press, London.
- . 1979. The stem-node-leaf continuum of the Dicotyledoneae. Pp. 76-87 in C. R. Metcalfe & L. Chalk (editors), *Anatomy of the Dicotyledons* (2nd edition), Volume 1. Clarendon Press, Oxford.
- HUBER, H. 1963. Die Verwandtschaftsverhältnisse der Rosifloren. *Mitt. Bot. Staatssamml. München* 5: 1-48.
- HUFFORD, L. D. 1989. The structure and potential loasaceous affinities of *Schismocarpus*. *Nordic J. Bot.* 9: 217-227.
- . 1990. Androecial development and the problem of monophyly of Loasaceae. *Canad. J. Bot.* 68: 402-419.
- & P. R. CRANE. 1989. A preliminary phylogenetic analysis of the 'lower' Hamamelidae. Pp. 175-192 in P. R. Crane & S. Blackmore (editors), *Evolution, Systematics, and Fossil History of the Hamamelidae*, Volume 1. Introduction and 'Lower' Hamamelidae. Clarendon Press, Oxford.



- & W. C. DICKISON. 1992. A phylogenetic analysis of Cunoniaceae. *Syst. Bot.* (in press).
- & P. K. ENDRESS. 1989. The diversity of anther structures and dehiscence patterns among Hamamelididae. *Bot. J. Linn. Soc.* 99: 301–346.
- HUNTER, G. E. 1966. Revision of Mexican and Central American *Saurauia* (Dilleniaceae). *Ann. Missouri Bot. Gard.* 53: 47–89.
- HUTCHINSON, J. 1927. XIV.—Contributions towards a phylogenetic classification of flowering plants: VI. A. The genera of Hydrangeaceae. *Kew Bull.* 1927: 100–118.
- . 1959. *The Families of Flowering Plants. Volume 1. Dicotyledons.* Clarendon Press, Oxford.
- HUYNH, K.-L. 1969. Etude du pollen des Oxalidaceae, I. Morphologie générale—Palynotaxonomie des *Oxalis* américains. *Bot. Jahrb. Syst.* 89: 272–303.
- INGLE, H. D. & H. E. DADSWELL. 1986. The anatomy of the timbers of the south-west Pacific area, IV. Cunoniaceae, Davidsoniaceae, and Eucryphiaceae. *Austral. J. Bot.* 4: 125–151.
- JÄGER-ZÜRN, I. 1966. Infloreszenz- und blütenmorphologische, sowie embryologische Untersuchungen an *Myrothamnus* Welw. *Beitr. Biol. Pflanzen* 42: 241–271.
- JAY, M. 1967. Recherches chimiotaxinomiques sur les plantes vasculaires (1). Distribution des flavonoides chez les Saxifragacées. *Compt. Rend. Hebd. Séances Acad. Sci.* 264: 1754–1756.
- . 1968a. Distribution des flavonoides chez les Cunoniacées. *Taxon* 17: 489–495.
- . 1968b. Distribution des flavonoides chez les Hamamelidacées et familles affines. *Taxon* 17: 136–147.
- . 1969. Chemotaxonomic researches on vascular plants. XIX. Flavonoid distribution in the Pittosporaceae. *Bot. J. Linn. Soc.* 62: 423–429.
- . 1970. Quelques problèmes taxonomiques et phylogénétiques des Saxifragacées vus à la lumière de la biochimie flavonique. *Bull. Mus. Hist. Nat. (Paris) Ser. 2.* 42: 754–775.
- & P. LEBRETON. 1972. Recherches chimiotaxinomiques sur les plantes vasculaires, XXVI. Les flavonoïdes es Sarracéniacées, Népenthacées, Droseracées et Céphalotacées; étude critique de l'ordre des Sarracéniales. *Naturaliste Canad.* 99: 607–613.
- JENSEN, S. R. & B. J. NIELSEN. 1982. Iridoid glucosides in Fouquieriaceae. *Phytochemistry* 21: 1623–1629.
- , ——— & R. DAHLGREN. 1975. Iridoid compounds, their occurrence and systematic importance in the angiosperms. *Bot. Not.* 128: 148–180.
- JOHANSEN, D. A. 1936. Morphology and embryology of *Fouquieria*. *Amer. J. Bot.* 23: 95–99.
- JOHNSON, L. A. S. & K. L. WILSON. 1989. Casuarinaceae: a synopsis. Pp. 167–188 in P. R. Crane & S. Blackmore (editors), *Evolution, Systematics, and Fossil History of the Hamamelidae, Volume 2. 'Higher' Hamamelidae.* Clarendon Press, Oxford.
- JUNCOSA, A. M. & H. TOBE. 1988. Embryology of tribe Gynotrocheae (Rhizophoraceae) and its developmental and systematic implications. *Ann. Missouri Bot. Gard.* 75: 1410–1424.
- & P. B. TOMLINSON. 1988a. A history and taxonomic synopsis of Rhizophoraceae and Anisophylleaceae. *Ann. Missouri Bot. Gard.* 75: 1278–1295.
- & ———. 1988b. Systematic comparison and some biological characteristics of Rhizophoraceae and Anisophylleaceae. *Ann. Missouri Bot. Gard.* 75: 1296–1318.
- KAPIL, R. N. & R. S. VANI. 1963. Embryology and systematic position of *Crossosoma californicum* Nutt. *Curr. Sci.* 32: 493–495.
- KAUL, U. & R. N. KAPIL. 1974. *Exbucklandia populnea*—from flower to fruit. *Phytomorphology* 24: 217–228.
- KAVALJIAN, L. G. 1952. The floral morphology of *Clethra alnifolia* with some notes on *C. acuminata* and *C. arborea*. *Bot. Gaz. (Crawfordsville)* 113: 392–413.
- KEDVES, M. 1989. Evolution of the Normapolles complex. Pp. 1–8 in P. R. Crane & S. Blackmore (editors), *Evolution, Systematics, and Fossil History of the Hamamelidae, Volume 2. 'Higher' Hamamelidae.* Clarendon Press, Oxford.
- KEEFE, J. M. & M. F. MOSELEY. 1978. Wood anatomy and phylogeny of *Paeonia* section *Moutan*. *J. Arnold Arbor.* 59: 274–297.
- KENG, H. 1962. Comparative morphological studies in Theaceae. *Univ. Calif. Publ. Bot.* 33: 269–384.
- KLOPFER, K. 1973. Florale Morphogenese und Taxonomie der Saxifragaceae *sensu lato*. *Feddes Repert.* 84: 475–516.
- KOEK-NOORMAN, J. 1969. A contribution to the wood anatomy of South American (chiefly Suriname) Rubiaceae. I. *Acta Bot. Neerl.* 18: 108–123.
- KOHLER, E. 1980. Zur Pollenmorphologie und systematischen Stellung der Didymelaceae Leandri. *Feddes Repert* 91: 581–591.
- & P. BRUCKNER. 1989. The genus *Buxus* (Buxaceae): aspects of its differentiation in space and time. *Pl. Syst. Evol.* 162: 267–283.
- & ———. 1990. Considerations on the evolution and chorogenesis of the genus *Buxus* (Buxaceae). *Mem. New York Bot. Gard.* 55: 153–168.
- & C. SCHIRAREND. 1989. Zur Blattanatomie der neotropischen *Buxus*-Arten und ihre Bedeutung für die Systematik (Buxaceae). *Flora* 183: 1–38.
- LANGDON, L. M. 1939. Ontogenetic and anatomical studies of the flower and fruit of the Fagaceae and Juglandaceae. *Bot. Gaz. (Crawfordsville)* 101: 301–327.
- LAWRENCE, G. H. M. 1951. *Taxonomy of Vascular Plants.* Macmillan, New York.
- LEBRETON, P. & M.-P. BOUCHEZ. 1967. Recherches chimiotaxinomiques sur les plantes vasculaires—V. Distribution des composés polyphénoliques chez les Pariétales. *Phytochemistry* 6: 1601–1608.
- LEE, Y. S. & D. E. FAIRBROTHERS. 1978. Serological approaches to the systematics of the Rubiaceae and related families. *Taxon* 27: 159–185.
- LEEUWENBERG, A. J. M. 1969. Notes on American Loganiaceae, IV. Revision of *Desfontainia* Ruiz et Pav. *Acta Bot. Neerl.* 18: 669–679.
- & P. W. LEENHOUTS. 1980. Taxonomy. Pp. 8–96 in A. Engler & K. Prantl (editors), *Die Natürlichen Pflanzenfamilien* 28b, 2nd edition. Engelmann, Leipzig.
- LI, H.-L. & C.-Y. CHAO. 1954. Comparative anatomy of the woods of the Cornaceae and allies. *Quart. J. Taiwan Mus.* 7: 119–136.
- LINDLEY, J. 1847. *The Vegetable Kingdom; or Struc-*



- ture, Classification, and Uses of Plants, Illustrated upon the Natural System. Bradbury & Evans, London.
- MADDISON, W. P. & D. R. MADDISON. 1989. MacClade, version 2.97 c<sup>+</sup>. (Distributed by the authors.)
- MAGUIRE, B. 1978. Sarraceniaceae. Mem. New York Bot. Gard. 29: 36-62.
- MANNING, W. E. 1978. The classification within the Juglandaceae. Ann. Missouri Bot. Gard. 65: 1058-1087.
- MARCO, H. F. 1935. Systematic anatomy of the woods of the Rhizophoraceae. Trop. Woods 44: 1-20.
- MARKGRAF, F. 1955. Über Laubblatt-Homologien und verwandtschaftliche Zusammenhänge bei Sarraceniales. Planta 46: 414-446.
- MASON, C. T. 1975. *Apacheria chiricahuensis*: a new genus and species from Arizona. Madroño 23: 105-108.
- MAURITZON, J. 1936. Zur Embryologie einiger Parietales Familien. Svensk Bot. Tidskr. 30: 79-113.
- . 1939. Contribution to the embryology of the orders Rosales and Myrtales. Acta Univ. Lund. 35 (2).
- METCALFE, C. R. & L. CHALK. 1950. Anatomy of the Dicotyledons. Clarendon Press, Oxford.
- MOHANA RAO, P. R. 1972a. Embryology of *Nyssa sylvatica*, and systematic consideration of the family Nyssaceae. Phytomorphology 22: 8-21.
- . 1972b. Morphology and embryology of *Tieghemopanax sambucifolius* with comments on the affinities of the family Araliaceae. Phytomorphology 22: 75-86.
- MOHRBUTTER, C. 1936. Embryologische studien an Loganiaceen. Planta 26: 64-80.
- MOORE, R. J. 1948. Cytotaxonomic studies in the Loganiaceae. II. Embryology of *Polypremum procumbens* L. Amer. J. Bot. 35: 404-409.
- MORF, E. 1950. Vergleichend-morphologische Untersuchungen am Gynoeceum der Saxifragaceen. Ber. Schweiz. Bot. Ges. 60: 516-590.
- MOSELEY, M. F. 1948. Comparative anatomy and phylogeny of the Casuarinaceae. Bot. Gaz. (Crawfordsville) 110: 231-260.
- & R. M. BEEKS. 1955. Studies of the Garryaceae—I. The comparative morphology and phylogeny. Phytomorphology 5: 314-346.
- MULLER, J. 1969. Pollen-morphological notes on Ochnaceae. Rev. Palaeobot. Palynol. 9: 149-173.
- MURGAI, P. 1959. The development of the embryo in *Paeonia*.—A reinvestigation. Phytomorphology 9: 275-277.
- NAGARAJA RAO, A. 1957. A contribution to the embryology of Dilleniaceae. Proc. Iowa Acad. Sci. 64: 172-176.
- NAIR, N. C. & V. ABRAHAM. 1962. Floral morphology of a few species of Euphorbiaceae. Proc. Indian Acad. Sci. 56: 1-12.
- & V. S. SARMA. 1961. Organography and floral anatomy of some members of the Rhamnaceae. J. Indian Bot. Soc. 40: 47-55.
- NARAYANA, L. L. 1975. A contribution to the floral anatomy and embryology of Ochnaceae. J. Jap. Bot. 50: 9-20.
- & M. RADHAKRISHNAIAH. 1976. Floral anatomy of the Pittosporaceae 1. J. Jap. Bot. 51: 278-282.
- & D. RAO. 1971. Contributions to the floral anatomy of Linaceae II. Phytomorphology 24: 64-67.
- & L. L. SUNDARI. 1972. Embryology of the Pittosporaceae (1). J. Jap. Bot. 52: 204-209.
- NASH, G. V. 1903. A revision of the family Fouquieriaceae. Bull. Torrey Bot. Club 30: 449-459.
- NAST, C. G. & I. W. BAILEY. 1945. Morphology and relationships of *Trochodendron* and *Tetracentron*, II. Inflorescence, flower, and fruit. J. Arnold Arbor. 26: 267-276.
- & ———. 1946. Morphology of *Euptelea* and comparison with *Trochodendron*. J. Arnold Arbor. 27: 186-192.
- NIEDENZU, F. 1895. Tamaricaceae. Pp. 289-297 in A. Engler & K. Prantl (editors), Die Natürlichen Pflanzenfamilien III (6). Engelmann, Leipzig.
- NIXON, K. C. 1989. Origins of Fagaceae. Pp. 23-44 in P. R. Crane & S. Blackmore (editors), Evolution, Systematics, and Fossil History of the Hamamelidae, Volume 2. 'Higher' Hamamelidae. Clarendon Press, Oxford.
- NOWICKE, J. W. 1966. Pollen morphology and classification of the Pyrolaceae and Monotropaceae. Ann. Missouri Bot. Gard. 53: 213-219.
- OLMSTEAD, R. G., H. J. MICHAELS, K. M. SCOTT & J. D. PALMER. 1992. Monophyly of the Asteridae and identification of their major lineages inferred from DNA sequences of *rbcL*. Ann. Missouri Bot. Gard. 79: 249-265.
- PALIWAL, G. S. & L. KAKKAR. 1970. Leaf anatomy of some *Garrya* species. J. Linn. Soc. Bot. 63: 81-90.
- PALSER, B. F., W. R. PHILIPSON & M. N. PHILIPSON. 1989. Development of ovule, megagametophyte and early endosperm in representative species of *Rhododendron* L. (Ericaceae). Bot. J. Linn. Soc. 101: 363-393.
- PATEL, R. N. 1973. Wood anatomy of the dicotyledons indigenous to New Zealand. New Zealand J. Bot. 11: 421-434.
- PHILIPSON, W. R. 1970. Constant and variable features of the Araliaceae. Pp. 87-100 in N. K. B. Robson, D. F. Cutler & M. Gregory (editors), New Research in Plant Anatomy. Academic Press, London.
- . 1974. Ovular morphology and the major classification of the dicotyledons. Bot. J. Linn. Soc. 68: 89-108.
- . 1975. Evolutionary lines within the dicotyledons. New Zealand J. Bot. 13: 73-91.
- . 1977. Ovular morphology and the classification of dicotyledons. Pl. Syst. Evol., Suppl. 1: 123-140.
- PILLANS, N. S. 1947. A revision of Bruniaceae. J. S. African Bot. 13: 121-206.
- POLLARD, C. J. & K. S. AMUTI. 1981. Fructose oligosaccharides: possible markers of phylogenetic relationships among dicotyledonous plant families. Biochem. Syst. Ecol. 9: 69-78.
- PRAKASH, N. & E. J. MCALISTER. 1977. An embryological study of *Bauera capitata* with comments on the systematic position of *Bauera*. Austral. J. Bot. 25: 615-622.
- PUFF, C. 1978a. The nodal anatomy of *Myrothamnus flabellifolius* (Myrothamnaceae): another example of a "split-lateral" condition. J. Arnold Arbor. 59: 192-196.



- . 1978b. Zur Biologie von *Myrothamnus flabellifolius* Welw. (Myrothamnus). *Dinteria* 14: 1-20.
- & E. ROBBRECHT. 1989. A survey of the Knoxieae (Rubiaceae-Antirheoideae). *Bot. Jahrb. Syst.* 110: 511-558.
- PUNT, W. 1978. Evolutionary trends in the Potalieae (Loganiaceae). *Rev. Palaeobot. Palynol.* 26: 313-335.
- RECORD, S. J. 1938a. The American woods of the family Euphorbiaceae. *Trop. Woods.* 54: 7-40.
- . 1938b. The American woods of the orders Celastrales, Olacales, and Santalales. *Trop. Woods* 53: 11-38.
- . 1942. American woods of the family Theaceae. *Trop. Woods* 70: 23-33.
- REITSMA, T. 1966. Pollen morphology of some European Rosaceae. *Acta Bot. Neerl.* 15: 290-307.
- . 1970. Pollen morphology of the Alangiaceae. *Rev. Palaeobot. Palynol.* 10: 249-332.
- RICHARDSON, P. E. 1970. Morphology of the Crosso-somataceae. I. Leaf, stem and node. *Bull. Torrey Bot. Club* 97: 34-39.
- RIZZINI, C. T. & P. OCCHIONI. 1949. Dialypetalanthaceae. *Lilloa* 17: 243-286.
- ROBBRECHT, E. & C. PUFF. 1986. A survey of the Gardenieae and related tribes (Rubiaceae). *Bot. Jahrb. Syst.* 108: 63-137.
- ROBERTSON, K. R. 1972. The Malpighiaceae in the southeastern United States. *J. Arnold Arbor.* 53: 101-112.
- . 1974. The genera of Rosaceae in the southeastern United States. *J. Arnold Arbor.* 55: 303-332.
- ROMEIKE, A. 1978. Tropane alkaloids—occurrence and systematic importance in angiosperms. *Bot. Not.* 85-96.
- RUTISHAUSER, R. & W. C. DICKISON. 1989. Developmental morphology of stipules and systematics of the Cunoniaceae and presumed allies. I. Taxa with interpetiolar stipules. *Bot. Helvetica* 99: 147-169.
- SAAD, S. I. 1961. Pollen morphology and sporoderm stratification in *Linum*. *Grana Palynol.* 3: 109-129.
- . 1962. Palynological studies in the Linaceae. *Pollen & Spores* 4: 65-82.
- SAINTY, D., F. BAILLEUL, P. DELAVEAU & H. JACQUEMIN. 1981. Malpighiacées: Nouvelle famille à iridoides étude du *Stigmaphyllon sagittatum*. *J. Nat. Prod.* 44: 576-578.
- SASTRI, R. L. N. 1958. Floral morphology and embryology of some Dilleniaceae. *Bot. Not.* 111: 495-511.
- SAWADA, M. 1971. Floral vascularization of *Paeonia japonica* with some consideration on systematic position of the Paeoniaceae. *Bot. Mag. Tokyo* 84: 51-60.
- SCHLECHTER, R. 1920. Die Columelliaceae. *Notizbl. Bot. Gart. Berlin-Dahlem* 7: 352-358.
- SCHMID, R. 1978a. Actinidiaceae, Davidiaceae, and Paracryphiaceae: systematic considerations. *Bot. Jahrb. Syst.* 100: 196-204.
- . 1978b. Reproductive anatomy of *Actinidia chinensis* (Actinidiaceae). *Bot. Jahrb. Syst.* 100: 149-195.
- SCHOLZ, H. 1964. Reihe Celastrales. Pp. 289-300 in H. Melchior (editor), *A. Engler's Syllabus der Pflanzenfamilien*, Volume 2. Gebrüder Borntraeger, Berlin.
- SCOGIN, R. 1977. Anthocyanins of the Fouquieriaceae. *Biochem. Syst. Ecol.* 5: 265-267.
- . 1978. Leaf phenolics of the Fouquieriaceae. *Biochem. Syst. Ecol.* 6: 297-298.
- SHOUP, J. R. & C. C. TSENG. 1977. Pollen of *Klotzschia* (Umbelliferae): a possible link to Araliaceae. *Amer. J. Bot.* 64: 461-463.
- SHREVE, F. 1906. The development and anatomy of *Sarracenia purpurea*. *Bot. Gaz. (Crawfordsville)* 42: 107-126.
- SINGH, B. 1959. Studies in the family Malpighiaceae: I. Morphology of *Thryallis glauca* Kuntze. *Hort. Advances* 3: 1-19.
- . 1961. Studies in the family Malpighiaceae. II. Morphology of *Malpighia glabra* Linn. *Hort. Advances* 5: 83-95.
- SLEUMER, H. 1968. Die Gattung *Escallonia* (Saxifragaceae). *Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect.* 58: 1-146.
- SMALL, J. K. & P. A. RYDBERG. 1905. Hydrangeaceae. *North American Flora. I.* 22: 159-178.
- SMITH, D. M., C. W. GLENNIE, J. B. HARBORNE & C. A. WILLIAMS. 1977. Flavonoid diversification in the Polemoniaceae. *Biochem. Syst. Ecol.* 5: 107-115.
- SOHMA, K. 1963. Pollen morphology of the Nyssaceae. 1. *Nyssa* and *Camptotheca*. *Sci. Rep. Tôhoku Imp. Univ., Ser. 4, Biol.* 29: 389-392.
- . 1967. Pollen morphology of the Nyssaceae. 2. *Nyssa* and *Davidia*. *Sci. Rep. Tôhoku Imp. Univ., Ser. 4, Biol.* 33: 527-532.
- SOLTIS, D. E., P. S. SOLTIS, M. T. CLEGG & M. DURBIN. 1990. *rbcL* sequence divergence and phylogenetic relationships in Saxifragaceae sensu lato. *Proc. Natl. Acad. U.S.A.* 87: 4640-4644.
- SORENSEN, N. A. 1977. Polyacetylenes and conservatism of chemical characters in the Compositae. Pp. 385-409 in V. H. Heywood, J. B. Harborne & B. L. Turner (editors), *The Biology and Chemistry of the Compositae*. Academic Press, London.
- SOUÈGES, R. 1936. Les embryogeniques des Crassulacées, Saxifragacées et Hypericacées. *Bull. Soc. Bot. France* 83: 317-329.
- SPONGBERG, S. 1971. The Staphyleaceae in the southeastern United States. *J. Arnold Arbor.* 52: 196-203.
- . 1972. The genera of Saxifragaceae in the southeastern United States. *J. Arnold Arbor.* 53: 409-498.
- . 1978. The genera of Crassulaceae in the southeastern United States. *J. Arnold Arbor.* 59: 197-248.
- STERN, W. L. 1974. Comparative anatomy and systematics of woody Saxifragaceae: *Escallonia*. *J. Linn. Soc., Bot.* 68: 1-20.
- . 1978. Comparative anatomy and systematics of woody Saxifragaceae: *Hydrangea*. *J. Linn. Soc., Bot.* 76: 83-113.
- , G. K. BRIZICKY & R. H. EYDE. 1969. Comparative anatomy and relationships of Columelliaceae. *J. Arnold Arbor.* 50: 36-75.
- STONE, D. E. & C. R. BROOME. 1971. Pollen ultrastructure: evidence for relationship of the Juglandaceae and the Rhoipteleaceae. *Pollen & Spores* 13: 5-14.
- & ———. 1975. Juglandaceae A. *Risch. ex Kunth. World Pollen Spore Flora* 4: 1-35.
- STUHLIK, L. 1967. Pollen morphology and taxonomy



- of the family Polemoniaceae. *Rev. Palaeobot. Palynol.* 4: 325-333.
- STYER, C. H. & W. L. STERN. 1979a. Comparative anatomy and systematics of woody Saxifragaceae: *Deutzia*. *J. Linn. Soc., Bot.* 79: 291-319.
- . 1979b. Comparative anatomy and systematics of woody Saxifragaceae: *Philadelphus*. *J. Linn. Soc., Bot.* 79: 267-289.
- SUBRA RAO, A. M. 1941. Studies in the Malpighiaceae. 2. Structure and development of the ovules and embryo sacs of *Malpighia coccifera* Linn. and *Tristellata australis* Linn. *Proc. Natl. Inst. Sci. India* 7: 393-404.
- SWAMY, B. G. L. 1948a. A contribution to the embryology of the Marcgraviaceae. *Amer. J. Bot.* 35: 628-633.
- . 1948b. A contribution to the life history of *Casuarina*. *Proc. Amer. Acad. Arts* 77: 1-32.
- . 1954. Morpho-taxonomical notes on the Escalloniaceae, part A. Nodal and petiolar vasculature. *J. Madras Univ., B.*, 24: 299-306.
- & I. W. BAILEY. 1949. The morphology and relationships of *Cercidiphyllum*. *J. Arnold Arbor.* 30: 187-210.
- SWOFFORD, D. L. 1989. Phylogenetic analysis using parsimony. Illinois Natural History Survey, Champaign.
- SZYSZYLOWICZ, I. 1895. Theaceae. Pp. 175-192 in A. Engler & K. Prantl (editors), *Die Natürlichen Pflanzenfamilien III* (6). Engelmann, Leipzig.
- TAKHTAJAN, A. L. 1969. Flowering Plants, Origin and Dispersal. (Translated by C. Jeffrey). Oliver & Boyd, Edinburgh.
- . 1980. Outline of the classification of flowering plants (Magnoliophyta). *Bot. Rev. (Lancaster)* 46: 225-359.
- . 1987. *Systema magnoliophytorum*. Nauka, Leningrad.
- TANDON, S. R. & J. M. HERR. 1971. Embryological features of taxonomic significance in the genus *Nyssa*. *Canad. J. Bot.* 49: 505-514.
- TANG, Y. 1932. Timber anatomy of Rhoipteleaceae. *Bull. Fan. Mem. Inst. Biol.* 3: 127-130.
- TATSUNO, A. & R. SCOGIN. 1978. Biochemical profile of Crossosomataceae. *Aliso* 9: 185-188.
- TAYLOR, T. N. & D. A. LEVIN. 1975. Pollen morphology of Polemoniaceae in relation to systematics and pollination systems: scanning electron microscopy. *Grana* 15: 91-112.
- THANIKAIMONI, G. & G. VASANTHY. 1972. Sarraceniaceae: palynology and systematics. *Pollen & Spores* 14: 143-155.
- THORNE, R. F. 1976. A phylogenetic classification of the Angiospermae. *Evol. Biol.* 9: 35-106.
- . 1977. Some realignments in the Angiospermae. *Plant Syst. Evol., Suppl.* 1: 299-319.
- . 1981. Phytochemistry and angiosperm phylogeny, a summary statement. Pp. 233-295 in D. A. Young & D. S. Sieglar (editors), *Phytochemistry and Angiosperm Phylogeny*. Praeger, New York.
- . 1983. Proposed new realignments in the angiosperms. *Nordic J. Bot.* 3: 85-117.
- TIEGHEM, M. P. VAN. 1903. Sur les Columelliacees. *Bull. Mus. Hist. Nat., Paris* 9: 233-239.
- TIPPO, O. 1938. Comparative anatomy of the Moraceae and their presumed allies. *Bot. Gaz. (Crawfordsville)* 100: 1-99.
- TITMAN, P. W. 1949. Studies in the woody anatomy of the family Nyssaceae. *J. Elisha Mitchell Sci. Soc.* 65: 245-261.
- TOBE, H. & P. H. RAVEN. 1983. An embryological analysis of Myrtales: its definition and characteristics. *Ann. Missouri Bot. Gard.* 70: 71-94.
- & ———. 1987. Systematic embryology of the Anisophylleaceae. *Ann. Missouri Bot. Gard.* 74: 1-26.
- & ———. 1988a. Floral morphology and evolution in Anisophylleaceae. *Bot. J. Linn. Soc.* 98: 1-25.
- & ———. 1988b. Seed morphology and anatomy of Rhizophoraceae, inter- and infrafamilial relationships. *Ann. Missouri Bot. Gard.* 75: 1319-1342.
- TSENG, C. C. & J. R. SHOUP. 1978. Pollen morphology of *Schefflera* (Araliaceae). *Amer. J. Bot.* 65: 384-394.
- UHL, C. H. 1964. Chromosomes and phylogeny of the Crassulaceae. *Cact. Succ. J.* 35: 80-84.
- URBAN, I. & E. GILG. 1900. *Monographia Loasacearum*. Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 76: 1-370.
- VARGHESE, T. M. 1969. A contribution on the foliar-venation of Scrophulariaceae. Pp. 253-266 in K. A. Chowdhury (editor), *Recent Advances in the Anatomy of Tropical Seed Plants*. Hindustan Publishing, Delhi.
- VENKATA RAO, C. 1965. Pollen grains of Proteaceae. *J. Palynol.* 1: 1-9.
- VEZEY, E. L., V. P. SHAH, J. L. SKVARLA & P. H. RAVEN. 1988. Morphology and phenetics of Rhizophoraceae pollen. *Ann. Missouri Bot. Gard.* 75: 1369-1386.
- VLIET, G. J. C. M. VAN. 1976. Wood anatomy of the Rhizophoraceae. *Leiden Bot. Ser.* 3: 20-75.
- WAKABAYASHI, M. 1970. On the affinity in Saxifragaceae *s. lato* with special reference to the pollen morphology. *Acta Phytotax. Geobot.* 24: 128-145.
- WALKER, J. W. 1976a. Comparative pollen morphology and phylogeny of the ranalean complex. Pp. 241-299 in C. B. Beck (editor), *Origin and Early Evolution of Angiosperms*. Columbia Univ. Press, New York.
- . 1976b. Evolutionary significance of the exine in the pollen of primitive angiosperms. Pp. 251-308 in I. K. Ferguson and J. Muller (editors), *The Evolutionary Significance of the Exine*. Academic Press, London.
- & J. A. DOYLE. 1975. The bases of angiosperm phylogeny: palynology. *Ann. Missouri Bot. Gard.* 62: 664-723.
- WEBERLING, F. 1976. Weitere Untersuchungen zur Morphologie des Unterblattes bei den Dikotylen. IX. Saxifragaceen *s. l.*, Brunelliaceae and Bruniaceae. *Beitr. Biol. Pflanzen* 52: 163-181.
- WEBSTER, G. L. 1987. The saga of the spurges: a review of classification and relationships in the Euphorbiales. *Bot. J. Linn. Soc.* 94: 3-46.
- WHITEHEAD, D. R. 1965. Pollen morphology in the Juglandaceae, II. Survey of the family. *J. Arnold Arbor.* 46: 369-410.
- WIGGINS, I. L. 1959. Development of the ovule and megagametophyte in *Saxifraga hieracifolia*. *Amer. J. Bot.* 46: 692-697.
- WILKINSON, A. M. 1944. Floral anatomy of some species of *Cornus*. *Bull. Torrey Bot. Club* 71: 276-301.



- . 1948a. Floral anatomy and morphology of some species of the genus *Viburnum* of the Caprifoliaceae. *Amer. J. Bot.* 35: 455-465.
- . 1948b. Floral anatomy and morphology of some species of the tribe Lonicereae of the Caprifoliaceae. *Amer. J. Bot.* 35: 261-271.
- . 1948c. Floral anatomy and morphology of some species of the tribes Linnaeae and Sumbuceae of the Caprifoliaceae. *Amer. J. Bot.* 35: 365-371.
- . 1949. Floral anatomy and morphology of *Triosteum* and of the Caprifoliaceae in general. *Amer. J. Bot.* 36: 481-489.
- WILSON, C. L. 1965. The floral anatomy of the Dilleniaceae. I. *Hibbertia* Andr. *Phytomorphology* 15: 248-274.
- . 1973. Floral anatomy of Dilleniaceae. II. Genera other than *Hibbertia*. *Phytomorphology* 23: 25-42.
- WITHNER, C. L. 1941. Stem anatomy and phylogeny of the Rhoipteleaceae. *Amer. J. Bot.* 28: 872-878.
- WOLFE, J. A. 1973. Fossil forms of Amentiferae. *Brittonia* 25: 334-355.
- . 1989. Leaf-architectural analysis of the Hamamelididae. Pp. 75-104 in P. R. Crane and S. Blackmore (editors), *Evolution, Systematics, and Fossil History of the Hamamelidae*, Volume 1. Introduction and 'Lower' Hamamelidae. Clarendon Press, Oxford.
- WORSDELL, W. C. 1908. The affinities of *Paeonia*. *J. Bot.* 46: 114-116.
- WUNDERLICH, R. 1959. Zur Frage der Phylogenie der Endospermtypen bei den Angiospermen. *Oesterr. Bot. Z.* 106: 203-293.
- YAKOVLEV, M. S. & M. D. YOFFE. 1957. On some peculiar features in the embryogeny of *Paeonia* L. *Phytomorphology* 7: 74-82.
- YANG, B.-Y. 1952. Pollen grain morphology in the Ericaceae. *Quart. J. Taiwan Mus.* 5: 1-24.
- ZAVADA, M. S. & D. L. DILCHER. 1986. Comparative pollen morphology and its relationship to phylogeny of pollen in the Hamamelididae. *Ann. Missouri Bot. Gard.* 73: 348-381.
- APPENDIX I. Characters and character states used in the cladistic analysis. Literature sources of data used in the analysis are indicated for each broad group of characters.
- Nodes and leaves (Bausch, 1938; Cronquist, 1981; Dahling, 1978; Dickison, 1975a, b, 1978, 1980, 1987b, 1989a, b; Dickison & Rutishauser, 1990; Elias, 1971; Endress, 1989c; Eyde, 1966; Haskins & Hayden, 1987; Henrickson, 1972; Hickey & Wolfe, 1975; Hils et al., 1988; Hoogland, 1979; Hufford, 1989; Hutchinson, 1959; Johnson & Wilson, 1989; Keng, 1962; Kohler & Bruckner, 1989; Kohler & Schirarend, 1989; Leeuwenberg & Leenhouts, 1980; Manning, 1978; Metcalfe & Chalk, 1950; Pillans, 1947; Puff, 1978a, b; Richardson, 1970; Robertson, 1972, 1974; Rutishauser & Dickison, 1989; Spongberg, 1972; Stern, 1974, 1978; Styer & Stern, 1979a, b; Swamy, 1954; Varghese, 1969; Weberling, 1976; Withner, 1941; Wolfe, 1973, 1989).
1. Nodes: trilacunar (0), unilacunar (1), multilacunar (2). *Myrothamnus* has the so-called "split lateral" nodal condition (Howard, 1970, 1979) in conjunction with its opposite leaves. In this analysis, the split lateral condition of *Myrothamnus* is homologized with the more conventional unilacunar, one-trace nodes.
  2. Leaf arrangement: alternate (0), opposite (1), whorls (2).
  3. Leaf morphology: simple (0), compound (1).
  4. Ascidiolate leaves: absent (0), present (1).
  5. Stipules: absent (0), present (1).
  6. Venation: pinnate (0), actinodromous (1), pinnate but with basal concentration of laterals (2).
  7. Secondary veins: brochidodromous (0), craspedodromous (1), semicraspedodromous (2), camptodromous (3).
  8. Stomates: anomocytic (0), laterocytic (1), paracytic (2), encyclocytic (3). Connaraceae and Platanaceae are coded as question marks because of stomatal variability.
  9. Reproductive short shoots with only a single leaf: absent (0), present (1).  
Wood (Baas & Zweypfennig, 1979; Bailey & Nast, 1945; Brush, 1917; Carlquist, 1964, 1966, 1969, 1976, 1978, 1981a, b, 1982a, b, 1984; Carlquist & Hoekman, 1985; Carlquist et al., 1984; Cronquist, 1981; DeBuhr, 1977, 1978; Dickison, 1967a, 1972a, 1978, 1980, 1986c; Dickison & Baas, 1977; Giebel & Dickison, 1976; Hall, 1952; Haskins & Hayden, 1987; Heimsch, 1942; Heimsch & Wetmore, 1939; Heimsch & Tschabold, 1972; Hils et al., 1988; Ingle & Dadswell, 1986; Keefe & Moseley, 1978; Keng, 1962; Koek-Noorman, 1969; Marco, 1935; Metcalfe & Chalk, 1950; Moseley, 1948; Moseley & Beeks, 1955; Nast & Bailey, 1946; Patel, 1973; Record, 1938a, b, 1942; Stern, 1974, 1978; Stern et al., 1969; Styer & Stern, 1979a, b; Swamy & Bailey, 1949; Tang, 1932; Tippo, 1938; Vliet, 1976).
  10. Conducting elements: only tracheids (0), vessels or vessels and tracheids (1).
  11. Vessel element perforations: all scalariform with many bars (>20) (0), all or most scalariform with few bars (<20) (1), all or most simple and those that are scalariform with few bars (2).
  12. Vessel element length: long (most >1,000  $\mu\text{m}$ ) (0), moderate (600-1,000  $\mu\text{m}$ ), (1), short (most <600  $\mu\text{m}$ ) (2).
  13. Vessel element diameter: narrow (most <60  $\mu\text{m}$ ) (0), moderate (60-100  $\mu\text{m}$ ) (1), wide (most >100  $\mu\text{m}$ ) (2).
  14. Intervessel pitting: scalariform (0), scalariform-opposite (1), opposite (2), opposite-alternate (3), alternate (4).
  15. Vessel distribution: solitary (0), mostly solitary with some clusters and some pairs and/or radial multiples (1), mostly radial multiples and clusters with few solitary (2).
  16. Imperforate elements: only true tracheids (0), true tracheids and fiber-tracheids (1), only fiber-tracheids (2).



fiber-tracheids and libriform fibers (3), only libriform fibers (4), variable with true tracheids, fiber-tracheids and libriform fibers (5). Character state definitions follow Carlquist (1988). Coding for *Alseuosmia* is based on Dickson's (1986c) characterization of the pits as "indistinctly bordered or simple" rather than on Carlquist (1988), who described the imperforate elements as true tracheids.

17. Imperforate element length: long (most >1,500  $\mu\text{m}$ ) (0), moderate (most 500–1,500  $\mu\text{m}$ ) (1), short (most <500  $\mu\text{m}$ ) (2).

18. Type of rays: heterogeneous type I (0), heterogeneous type IIA (1), heterogeneous type IIB (2), heterogeneous type III (3), paedomorphic type I (4), paedomorphic type II (5), paedomorphic type III (6), homogeneous type I (7). Character states based on definitions in Carlquist (1988). Linales, Celastrales, Rhamnales, and Myrtales are coded as question marks because of variability.

19. Rays with secretory canals: absent (0), present (1).

20. Ray cells with gum deposits: absent (0), present (1).

Flowers (Bange, 1952; Beamish & Lin, 1965; Benschel & Palser, 1975a, b, c; Bhandari, 1971; Bogle, 1986, 1989; Brizicky, 1961; Brouwer, 1924; Burkett, 1932; Chapman, 1953; Cronquist, 1981; Cuatrecasas, 1970; Dahlgren, 1975; Dahling, 1978; Daumann, 1974; Davis, 1966; Dickson, 1968, 1970, 1971, 1972b, 1975a, c, 1978, 1986a; Dnyansagar, 1955; Elias, 1971; Endress, 1969, 1977, 1986, 1989a, b, c; Eyde, 1964, 1968, 1988; Eyde & Tseng, 1971; Flores & Moseley, 1982; Gardner, 1978; Gaumann, 1919; Graham et al., 1987; Gusejnova, 1976; Harms, 1930; Heel, 1987; Herr & Dowd, 1968; Hils et al., 1988; Hjelmquist, 1948, 1957; Hufford & Endress, 1989; Hutchinson, 1927, 1959; Jäger-Zürn, 1966; Johansen, 1936; Juncosa & Tobe, 1988; Kapil & Vani, 1963; Kaul & Kapil, 1974; Kavaljian, 1952; Keng, 1962; Klopfer, 1973; Langdon, 1939; Lawrence, 1951; Leeuwenberg, 1969; Manning, 1978; Maguire, 1978; Mauritson, 1936; Mohana Rao, 1972a, b; Mohrbutter, 1936; Moore, 1948; Morf, 1950; Nagaraja Rao, 1957; Nair & Abraham, 1962; Nair & Sarma, 1961; Narayana, 1975; Narayana & Radhakrishnaiah, 1976; Narayana & Rao, 1971; Narayana & Sundari, 1972; Nast & Bailey, 1945; Palser et al., 1989; Philipson, 1970; Pillans, 1947; Prakash & McAlister, 1977; Puff & Robbrecht, 1989; Robertson, 1972, 1974; Sastri, 1958; Schlechter, 1920; Schmid, 1978b; Shreve, 1906; Singh, 1959, 1961; Sleumer, 1968; Small & Rydberg, 1905; Souèges, 1936; Spongberg, 1971, 1972, 1978; Stern et al., 1969; Subra Rao, 1941; Swamy, 1948b; Swamy & Bailey, 1949; Szyszylowicz, 1895; Tandon & Herr, 1971; Tieghem, 1903; Tobe & Raven, 1983, 1987, 1988a; Uhl, 1964; Wiggins, 1959; Wilkinson, 1944, 1948a, b, c, 1949; Wilson, 1965, 1973; Wunderlich, 1959).

21. Plant sex distribution: bisexual (0), monoecious (1), dioecious (2).

22. Floral phyllomes: unicyclic (0), bicyclic (1). *Euptelea*, *Cercidiphyllum*, Myricaceae, and Casuarinaceae are coded as question marks because floral phyllomes are absent. Hamamelidaceae subfamily Altingioideae and Asteraceae

are coded as question marks because of the ambiguous homology of the floral phyllomes.

23. Perianth merosity: numerous and helical (0), pentamerous (1), tetramerous (2), few and irregular (3).

24. Calyx connation: absent (0), present (1).

25. Corolla connation: absent (0), present (1).

26. Hypanthium: absent (0), present (1).

27. Nectary: absent (0), abaxial gynoecial surface (1), disc (2), perianth (3).

28. Androecial pattern and merosity: helical polyandry (0), haplostemony (1), complex polyandry with 11–20 stamens (2), complex polyandry with >20 stamens (3), diplostemony (4), centrifugal polyandry (5).

29. Epipetalous stamens: absent (0), present (1).

30. Anther insertion: basifixed (0), dorsifixed (1).

31. Stomial pattern: no bifurcations ("linear") (0), bifurcated proximally and/or distally (1). Pores are considered to be derived from unbifurcated stomia.

32. Carpel number: > five (0), five (1), four (2), three (3), two (4), one (5), variable one–five (6).

33. Carpel insertion: superior (0), only extreme base inferior (1), basal half inferior (2), mostly to completely inferior (3).

34. Carpel stipitation: absent (0), present (1).

35. Carpel connation: distinct (0), base of ovaries connate (1), ovaries completely connate and base of styles may be connate (2), ovaries and styles completely connate (3).

36. Style: eccentric peak of ovary (0), intercalated (1), absent (2).

37. Stigma position: decurrent (0), localized on stylar apex (1).

38. Placentation: marginal and/or axile (0), axile-apical (1), axile-basal (2), parietal (3).

39. Ovules per carpel: many (>10) (0), few and variable (1–10) (1), strictly one (2), strictly two (3), one per gynoecium (with more than one carpel) (4).

40. Orthotropous ovules: absent (0), present (1).

41. Integument number: two (0), one (1).

42. Nucellus: crassinucellate (0), tenuinucellate (1).

43. Entrance of pollen tube: porogamy (0), chalazallogamy (1).

44. Endosperm formation: ab initio cellular (0), nuclear (1).



45. Endosperm persistence: persists and copious (0), persists but scanty (1), does not persist (2).

Chemistry (Bate-Smith, 1973, 1977; Bohlmann et al., 1973; Challice, 1981; Cronquist, 1981; Crowden, 1969; Dahlgren et al., 1976; Elsworth & Martin, 1971; Gershenzon & Mabry, 1983; Giannasi, 1986; Gornall et al., 1979; Jay, 1967, 1968a, b, 1969; Jay & Lebreton, 1972; Jensen et al., 1975; Lebreton & Bouchez, 1967; Romeike, 1978; Sainty et al., 1981; Smith et al., 1977; Sorenson, 1977; Tatsuno & Scogin, 1978).

46. Iridoids: absent (0), present (1).

47. Polyacetylenes: absent (0), present (1).

48. Myricetin: absent (0), present (1).

49. Ellagic acid: absent (0), present (1).

50. Proanthocyanins: absent (0), present (1).

51. Oil cells: absent (0), present (1).

Pollen (Avetisian, 1975; Basak & Subramanyan, 1966; Bremer, 1987; Chao, 1954; Crepet, 1989; Cronquist, 1981; Dahling, 1978; Dickison, 1967b, 1979, 1987a; Dickison & Baas, 1977; Donoghue, 1985; Endress, 1986; Erdtman, 1952; Franks & Watson, 1963; Ham, 1988; Ham & Heuven, 1989; Henrickson, 1967; Hideux & Ferguson, 1976; Huynh, 1969; Kohler, 1980; Kohler & Bruckner, 1989, 1990; Maguire, 1978; Mason, 1975; Muller, 1969; Nixon, 1989; Nowicke, 1966; Puff & Robbrecht, 1989; Punt, 1978; Reitsma, 1966, 1970; Robertson, 1974; Robbrecht & Puff, 1986; Saad, 1961, 1962; Schmid, 1978a; Shoup & Tseng, 1977; Sohma, 1963, 1967; Stone & Broome, 1971, 1975; Stuchlik,

1967; Taylor & Levin, 1975; Thanikaimoni & Vasanthi, 1972; Tseng & Shoup, 1978; Venkata Rao, 1965; Vezey et al., 1988; Walker, 1976a, b; Whitehead, 1965; Yang, 1952; Zavada & Dilcher, 1986).

52. Pollen size: most 20–30  $\mu\text{m}$  or  $>30 \mu\text{m}$  (0), most  $<20 \mu\text{m}$  (1).

53. Aperture length : width ratio: 1 : 1 (0),  $\frac{2}{3}$  : 1 (1),  $>3$  : 1 (2). Apertures with a length : width ratio of 1 : 2 appear to be derived within Juglandaceae and Myricaceae.

54. Ectoaperture termini: rounded (0), pointed (1).

55. Endoaperture: absent (0), present (1).

56. Primary tectal sculpture: reticulate (0), striate (1), clavate (2), rugate (3), spinulose/scabrate (4), vermiform (5), psilate (6), verruculate (7), foveolate (8).

57. Secondary tectal sculpture: smooth (0), papillate (1).

58. Tectal structure: columellate (0), granular (poorly developed columellae) (1).

59. Tectal perforations: semitectate (0), tectate perforate (1), imperforate (2). The intectate *Myrothamnus* was coded as a question mark.

Fruit (Cronquist, 1981, 1988; Cuatrecasas, 1970; Dickison, 1984; Endress, 1989a; Gilg, 1895a, b; Hils et al., 1988; Hoogland, 1952; Hutchinson, 1959; Keng, 1962; Sleumer, 1968; Urban & Gilg, 1900).

60. Fruit type: follicle or septicidal capsule (0), loculicidal capsule (1), nut or samaroid nutlet (achene) (2), fleshy (berry) (3).