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PHYLOGENETIC  
RELATIONSHIPS OF *CORNUS*  
L. SENSU LATO AND  
PUTATIVE RELATIVES  
INFERRED FROM *rbcL*  
SEQUENCE DATA<sup>1</sup>

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Qiu-Yun Xiang, Douglas E. Soltis,  
David R. Morgan, and  
Pamela S. Soltis<sup>2</sup>

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ABSTRACT

A parsimony analysis of 46 *rbcL* sequences was performed to evaluate relationships among *Cornus* and putative relatives, as well as among subgroups within *Cornus*. Our results indicate that *Alangium*, nyssoids (*Nyssa*, *Davidia*, and *Camptotheca*), mastixioids (*Diplopanax* and *Mastixia*), *Curtisia*, and genera of Hydrangeaceae are the closest relatives of *Cornus*. These taxa, plus *Cornus*, constitute a "cornaceous clade," which differs from all previously proposed *Cornus* alliances. Within this cornaceous clade, four major lineages were identified; (i) *Cornus*-*Alangium*, (ii) nyssoids-mastixioids, (iii) *Curtisia*, and (iv) hydrangeoids. The relationships among the four major lineages within the cornaceous clade remain unresolved. Sequence data from *rbcL* also reveal that *Corokia*, *Helwingia*, *Aucuba*, *Garrya*, and *Griselinia*, previously placed in Cornaceae by some authors, are only distantly related to *Cornus* and other members of the cornaceous clade. Four major lineages were identified within *Cornus* by *rbcL* sequence data, but relationships among these groups are incompletely resolved.

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Relationships among members of the dogwood family (Cornaceae) have long been problematic due to the morphological diversity of the family. There is, for example, no consensus regarding the circumscription of the family; from 1 to 15 genera have been ascribed to Cornaceae by various authors. The troubled taxonomic history of Cornaceae is briefly reviewed below and summarized in Table 1.

Harms (1898) included 15 genera divided among seven subfamilies in his Cornaceae (Table 1), a treatment that largely followed Hooker (1867). Of these 15 genera, by far the largest and most widespread is *Cornus*, which comprises approximately 45–60 species. Many of the remaining 14 genera are small and/or localized in geographic distribution (Table 2). The considerable debate concerning the composition of Cornaceae is illustrated by the fact that 11 of the 15 genera included in Harms's (1898) Cornaceae have been treated as monotypic families by at least one author based on one or several distinctive morphological features (all orig-

inal references cited in Takhtajan, 1987, except Chen, 1988): *Davidia* (Li, 1955), *Camptotheca* (Chen, 1988), *Mastixia* (Calestani, 1905), *Aucuba* (Agardh, 1858), *Curtisia* (Takhtajan, 1987), *Garrya* (Lindley, 1834), *Alangium* (de Candolle, 1828), *Melanophylla* (Takhtajan ex Airy Shaw, 1972), *Griselinia* (Takhtajan, 1987), *Helwingia* (Decaisne, 1836), and *Toricellia* (Hu, 1934).

For brevity, we will review only the treatments of Takhtajan (1980, 1987), Cronquist (1981, 1988), and Eyde (1988), because they illustrate well the magnitude of the differences among proposed taxonomic schemes regarding the treatment of Cornaceae and putative relatives. Takhtajan (1980) retained only *Cornus*, *Curtisia*, and *Mastixia* in Cornaceae, placing them in three separate subfamilies (Table 1). Many of the genera originally placed in Cornaceae by Harms (1898) were treated as distinct families and considered to be only distantly related to *Cornus* (e.g., *Corokia*, *Griselinia*, *Helwingia*, *Melanophylla*, *Kaliphora*, and *Toricellia*) by Takhtajan (1980) (Table 1). More re-

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<sup>1</sup> We thank G. Plunkett and R. G. Olmstead for providing unpublished sequences; D. E. Boufford, E. Wood, I. Hay, S. Yankowski, P. Goldblatt, S. Brunsfeld, J. Wen, Y.-C. Tang, Z.-H. Ji, K.-Y. Pan, H.-N. Qin, E. K. Cameron, T. Edwards, E. G. H. Oliver, B. H. Macmillan, A. H. M. Jayasuriya, Arnold Arboretum, U. S. National Arboretum, Strybing Arboretum, Missouri Botanical Garden, and The Royal Botanical Gardens, Kew, England, for help in obtaining leaf material; and R. Olmstead and M. Chase for helpful comments regarding data analysis. This project was supported by NSF grant BSR 9007614, a WSU travel grant, and grants from Sigma Xi, the American Society of Plant Taxonomists, and the Northwest Scientific Association.

<sup>2</sup> Department of Botany, Washington State University, Pullman, Washington 99164-4238, U.S.A.

TABLE 1. Comparison of taxonomic treatments of *Cornus* and putative relatives. Genera are not listed under monotypic families and subfamilies. An asterisk (\*) indicates a family or an order that contains several genera or families, but only the genus or family listed has been considered a *Cornus* relative by some taxonomists. Hutchinson (1967) and Takhtajan (1987) divided *Cornus* into six segregate genera; for simplicity, only *Cornus* is listed below in their treatments.

Harms (1898)	Wangerin (1910)	Hutchinson (1967)	Takhtajan (1980)	Cronquist (1981)	Takhtajan (1987)	Eyde (1988)
Cornaceae		Araliales	Saxifragales*	Cornales	Hydrangeales*	Cornaceae
Garryoideae	Garryaceae	Cornaceae	Escalloniaceae*	Alangiaceae	Argophyllaceae*	Nyssoidae
Nyssoidae	Nyssa	<i>Aucuba</i>	<i>Corokia</i>	Nyssaceae	<i>Corokia</i>	<i>Nyssa</i>
	<i>Camptotheca</i>	<i>Cornus</i>		<i>Nyssa</i>	Griselinaceae	<i>Camptotheca</i>
<i>Camptotheca</i>	<i>Davidia</i>	<i>Corokia</i>	Cornales	<i>Camptotheca</i>	Melanophyllaceae	<i>Davidia</i>
Davidioideae	Alangiaceae	<i>Curtisia</i>	Davidiaceae	<i>Davidia</i>	<i>Melanophylla</i>	Mastixioideae
Alangoideae	Cornaceae	<i>Griselinia</i>	Nyssaceae	Cornaceae	<i>Kaliphora</i>	Cornoideae
Mastixioideae		<i>Kaliphora</i>	<i>Nyssa</i>	<i>Aralidium</i>		
Curtisioideae		<i>Melanophylla</i>	<i>Camptotheca</i>	<i>Aucuba</i>	Cornales	
Cornoideae		<i>Toricellia</i>	Alangiaceae	<i>Cornus</i>	Davidiaceae	
<i>Aucuba</i>		Alangiaceae	Cornaceae	<i>Corokia</i>	Nyssaceae	
<i>Cornus</i>		Garryaceae	Cornoideae	<i>Curisia</i>	<i>Nyssa</i>	
<i>Corokia</i>		Nyssaceae	Curtisioideae	<i>Griselinia</i>	<i>Camptotheca</i>	
<i>Griselinia</i>		<i>Nyssa</i>	Mastixioideae	<i>Helwingia</i>	Cornaceae	
<i>Helwingia</i>		<i>Camptotheca</i>	Aucubaceae	<i>Kaliphora</i>	Curtisiaceae	
<i>Kaliphora</i>		<i>Davidia</i>	Garryaceae	<i>Mastixia</i>	Mastixiaceae	
<i>Melanophylla</i>		Araliaceae*	Melanophyllaceae	<i>Melanophylla</i>	Aucubaceae	
<i>Toricellia</i>		<i>Helwingia</i>	<i>Kaliphora?</i>	<i>Toricellia</i>	Garryaceae	
		Caprifoliaceae	<i>Griselinia</i>	Garryaceae	Alangiaceae	
			Toricelliaceae		Toricelliales	
			Helwingiaceae		Apiales*	
					Helwingiaceae	

cently, Takhtajan (1987) removed *Curtisia* and *Mastixia* from Cornaceae and recognized them as monotypic families (Table 1). However, he still considered these two genera close allies of *Cornus* and members of his Cornales.

Cronquist (1981), in contrast, retained a broader view of Cornaceae than Takhtajan (Table 1). Cronquist (1981) closely followed the treatment of Wangerin (1910) (Table 1), but added *Aralidium* to Cornaceae. Cronquist (1988) later added the nyssoids (*Nyssa*, *Davidia*, and *Camptotheca*) to Cornaceae following Eyde (1988) and included all of Harms's (1898) genera except *Alangium* and *Garrya* in his Cornaceae. He argued against dividing Cornaceae into a number of small or monotypic families as done by Takhtajan.

Attempting to synthesize all available evidence, Eyde (1988) considered the Cornaceae to consist of *Cornus*, nyssoids, and mastixioids (modern *Mastixia* and its fossil allies) (Table 1). Eyde also proposed that mastixioids may be the closest relatives of *Cornus* based primarily on a single shared trait: a two-armed surface hair formed from a single cell. The delimitation of Cornaceae became even less clear with the recent addition of *Diplopanax* to Cornaceae (Eyde & Xiang, 1990). *Diplopanax*, which consists of a single species (*D. stachyanthus* Hand.-Mazz.) occurring rarely in southern China and northern Vietnam, was previously placed in Araliaceae (Handel-Mazzetti, 1933).

Not only do concepts of Cornaceae vary greatly, but there is considerable disagreement regarding the closest relatives of *Cornus*. Different lines of evidence have suggested a wide array of closest relatives for *Cornus* (Table 3). Evidence from embryology, for example, suggests that *Alangium* is the closest ally of *Cornus* (Chopra & Kaur, 1965), whereas chromosome numbers suggest that *Nyssa*, *Davidia*, *Mastixia*, and *Garrya* are also close relatives of *Cornus* (Goldblatt, 1978). Seed structure (germination valves) provides a still different picture, suggesting a close relationship among *Cornus*, *Mastixia*, *Diplopanax*, *Nyssa*, and *Davidia* (Eyde, 1963, 1988; Eyde & Xiang, 1990). Evidence from palynology, wood anatomy, serology, secondary chemistry, and fatty acid chemistry each suggests a different suite of close relatives for *Cornus* (Table 3; Bate-Smith et al., 1975; Breuer et al., 1987; Fairbrothers & Johnson, 1964; Ferguson, 1977; Ferguson & Hideux, 1980; Li & Chao, 1954).

The taxonomic complexity of Cornaceae is further compounded by the extreme polymorphism of *Cornus*. Wangerin (1910) classified the genus into seven subgenera (Table 4) using primarily the morphology of the inflorescence, bracts, and fruits.

TABLE 2. Geographic distribution and species composition of *Cornus* and putatively related genera.

<i>Alangium</i>	ca. 20 spp., mostly in Asia, a few in Polynesia, New Guinea, subtropical Australia, tropical Africa, Madagascar, Comoro Islands.
<i>Aralidium</i>	3 spp., Malaya.
<i>Aucuba</i>	3-11 spp., eastern Himalayas to Japan.
<i>Camptotheca</i>	1 sp., southwestern and south-central China.
<i>Cornus</i>	ca. 45 to 60 spp., mostly in eastern Asia and North America, a few in Europe, 1 in Central America, 2 in South America, and 1 in tropical Africa.
<i>Corokia</i>	6 or 7 spp., South Pacific islands.
<i>Curtisia</i>	2 sp., southern Africa.
<i>Davidia</i>	1 sp., southwestern China and western Hupei of China.
<i>Diplopanax</i>	1 sp., southern China and northern Vietnam.
<i>Garrya</i>	14 spp., southwestern United States, Mexico, West Indies.
<i>Griselinia</i>	6 spp., New Zealand, Chile, and Brazil.
<i>Helwingia</i>	3 spp., Himalayas to Japan.
<i>Kaliphora</i>	1 sp., Madagascar.
<i>Mastixia</i>	13 spp., southeastern Asia and western Pacific.
<i>Melanophylla</i>	9 spp., Madagascar.
<i>Nyssa</i>	7 spp., eastern Asia, eastern North America, northern Mexico.
<i>Toricellia</i>	2 or 3 spp., eastern Himalayas and southwestern China.

Wangerin's view of *Cornus* has been largely followed by most modern investigators (Eyde, 1987; Ferguson, 1966; Xiang, 1987). In contrast, *Cornus* has been divided by some into as many as six genera (Table 5; Hutchinson, 1942, 1967; Pojarkova, 1950). The complex history of this problem and the nomenclatural changes involved have been reviewed by Eyde (1987) and Ferguson (1966).

Phylogenetic relationships among species groups within *Cornus* have also been debated. *Cornus* can be roughly divided into four groups: big-bracted dogwoods, dwarf dogwoods, cornelian cherries, and bractless dogwoods. Emphasizing the distribution of iridoids, Bate-Smith et al. (1975) proposed that the big-bracted dogwoods are the most primitive species of *Cornus* and the bractless dogwoods are the most advanced. This view is supported by evidence from wood anatomy (Adams, 1949; Li & Chao, 1954) and floral anatomy (Wilkinson, 1944). Dermen (1932) proposed that based on chromo-

TABLE 3. Close relatives of *Cornus* as suggested by eight different lines of morphological, anatomical, karyological, and chemical evidence.

Characters	Suggested close relatives
Cytology	<i>Nyssa</i> , <i>Davidia</i> , <i>Mastixia</i> , and <i>Garrya</i> (Goldblatt, 1978)
Pollen morphology	<i>Curtisia</i> , <i>Mastixia</i> , <i>Nyssa</i> , <i>Davidia</i> , and <i>Camptotheca</i> (Eramyan, 1971; Ferguson, 1977; Ferguson & Hideux, 1980; Eyde, 1988; Reitsma, 1970)
Floral anatomy	<i>Nyssa</i> , <i>Davidia</i> , <i>Mastixia</i> , and <i>Toricellia</i> (Eyde, 1967, 1988)
Fruit morphology	<i>Mastixia</i> , <i>Diplopanax</i> , <i>Nyssa</i> , and <i>Davidia</i> (Eyde, 1963, 1988)
Embryology	<i>Alangium</i> (Chopra & Kaur, 1965)
Wood anatomy	<i>Corokia</i> , <i>Helwingia</i> , <i>Schefflera</i> , <i>Nyssa</i> , <i>Garrya</i> , <i>Mastixia</i> , <i>Viburnum</i> , and <i>Griselinia</i> (Li & Chao, 1954)
Secondary metabolic products	<i>Mastixia</i> , <i>Curtisia</i> , and <i>Davidia</i> (Bate-Smith et al., 1975)
Fatty acid chemistry	<i>Curtisia</i> , <i>Mastixia</i> , and <i>Corokia</i> (Breuer et al., 1987)

some numbers and sizes, the cornelian cherry group is basal within *Cornus*. Eyde (1988), in contrast, proposed that the genus early diverged into two main lineages, a bracted (or red-fruited) line in which the inflorescence has basal bracts, and a bractless (or blue- or white-fruited) line in which the bracts are rudimentary or lacking. The bracted line includes the big-bracted dogwoods, dwarf dogwoods, and the cornelian cherries. Using morpho-

TABLE 4. Intrageneric treatment of *Cornus* proposed by Wangerin (1910): 50 species divided into seven subgenera. All species are woody and have bisexual flowers except those indicated.

<i>Thelycrania</i>	bractless dogwoods, 36 spp. with spreading cymes.
<i>Afrocrania</i>	African cornelian cherry, 1 dioecious species, with four small herbaceous bracts subtending an umbel-like cyme.
<i>Macrocarpium</i>	cornelian cherries, 4 spp. with four herbaceous bracts subtending an umbel-like cyme.
<i>Arctocrania</i>	dwarf dogwoods, 2 herbaceous spp. with four petaloid bracts subtending a condensed cyme.
<i>Discoocrania</i>	Mexican disciflorous dogwood, 2 spp. with four small, herbaceous, and early deciduous bracts subtending a capitate inflorescence.
<i>Benthamidia</i>	North American big-bracted dogwoods, 2 spp. with four large petaloid bracts subtending a capitate inflorescence.
<i>Benthamia</i>	Asian big-bracted dogwoods, 3 spp. with four large petaloid bracts subtending a capitate inflorescence which subsequently develops into a compound fruit.

logical characters and evidence from fossils and embryology, Eyde proposed that the bractless dogwoods are ancestral and connect *Cornus* to the nyssoids. He classified *Cornus* into four informal subgroups without giving these groups taxonomic rank: bractless dogwoods, cornelian cherries, big-bracted dogwoods (including the Mexican disciflorous dogwoods), and dwarf dogwoods.

From the above review it is apparent that another experimental approach is needed to help unravel the systematic problems posed by Cornaceae. We therefore employed comparative sequencing of *rbcL* with the following objectives: (1) clarify relationships among *Cornus* and putatively related genera, and (2) elucidate evolutionary relationships among the major subgroups within *Cornus*. The advantages of *rbcL* sequencing for addressing phylogenetic questions at this level have been well reviewed (e.g., Clegg & Zurawski, 1992; Palmer et al., 1988).

#### MATERIALS AND METHODS

Species included in this study represent the major subgroups of *Cornus* as well as taxa that previously have been considered closely allied with *Cornus* by at least some investigators (e.g., *Cornus alternifolia* L.f., *C. canadensis* L., *C. chinensis* Wangerin, *C. florida* L., *C. kousa* Hance, *C. mas* L., *C. obliqua* Raf., *C. oblonga* Wall., *C. officinalis* Siebold & Zucc., *C. walteri* Wangerin; *Alangium chinense* (Lour.) Harms, *Aucuba japonica* Thunb., *Camptotheca acuminata* Decne., *Corokia cotoneaster* Raoul, *Curtisia dentata* (Burm.f.) G.A.Sm., *Davidia involucreta* Baill., *Diplopanax stachyanthus* Hand.-Mazz., *Garrya elliptica* Douglas ex Lindl., *Griselinia lucida* J.G. Forst, *Helwingia japonica* (Thunb.) F. Dietr., *Mastixia caudatilimba* C.Y. Wu ex Soong, *Nyssa ogeche*

TABLE 5. Comparison of several taxonomic schemes proposed for *Cornus* sensu lato, depicting the magnitude of the discrepancies that exist.

Strict view		Broad view	
Pojarkova (1950) (6 genera)	Hutchinson (1967) (6 genera)	Wangerin (1910) (7 subgenera)	Ferguson (1966) (8 subgenera)
<i>Thelycrania</i>	<i>Svida</i>	<i>Thelycrania</i>	<i>Kraniopsis</i>
<i>Bothrocaryum</i>			<i>Mesomora</i>
<i>Afrocrania</i>	<i>Afrocrania</i>	<i>Afrocrania</i>	<i>Afrocrania</i>
<i>Cornus</i>	<i>Cornus</i>	<i>Macrocarpium</i>	<i>Cornus</i>
	<i>Cynoxylon</i>	<i>Arctocrania</i>	<i>Arctocrania</i>
<i>Cynoxylon</i>	<i>Dendrobenthamia</i>	<i>Discocrania</i>	<i>Discocrania</i>
			<i>Benthamidia</i>
<i>Chamaepericlymenum</i>	<i>Chamaepericlymenum</i>	<i>Benthamia</i>	<i>Benthamia</i>

Marsh; see Appendix of this issue). The sequence for *Cornus kousa* was provided by R. G. Olmstead (unpublished). These taxa represent the major cast of characters required for a molecular phylogenetic analysis of *Cornus* and putative relatives. It would have been desirable to include in this study several additional genera (*Kaliphora*, *Melanophylla*, *Toricellia*, and *Aralidium*) of which we could not obtain either living or recent herbarium collections due to their rarity and/or geographically restricted distributions (Table 2).

Total DNAs were isolated from leaf tissue following the method of Doyle & Doyle (1987) as modified by Soltis et al. (1991). Double-stranded *rbcL* was amplified using thermostable DNA polymerase provided by either Promega or Epicentre Technologies. Primers used for amplifications are synthetic oligonucleotides. The forward or 5' primer (Z1) is composed of the first 30 bases of *rbcL* of *Zea mays* L. Two different reverse primers were used. The one used most often (3'*rbcL*) is that of Olmstead et al. (1992), which consists of 34 bp beginning 103 base pairs outside of the terminus of the gene in *Nicotiana*. For *Diplopanax* and *Mastixia*, however, this Z1-3'*rbcL* primer combination did not yield a product so we used an internal reverse primer, a 30-mer beginning at position 1351 of *rbcL* in *Z. mays*.

The double-stranded products subsequently were used as templates, and the forward and reverse primers used individually for single-stranded DNA amplifications. Single-stranded products were precipitated with 20% PEG/2.5M NaCl. DNA pellets were washed once each with 70% and 95% EtOH, dried, and redissolved in TE. DNA sequencing followed the dideoxy method using Sequenase 2.0 enzyme and the Sequenase 3.1 kit (U.S. Biochemical Corp.). Sequencing primers were derived from the *rbcL* sequence of *Z. mays* and kindly provided by G. Zurawski (DNAX Research Institute). Both

the forward and reverse strands were sequenced for all taxa.

Twenty-one sequences were generated in this study for *Cornus* and putatively related genera. Twenty-five additional sequences from Saxifragales, Apiales, and Asteridae (Fig. 1, also see Appendix, this issue) were included in a phylogenetic analysis to determine possible alliances of *Cornus*. *Cercidiphyllum* and *Daphniphyllum* (representatives of Hamamelidae) and *Itea*, *Saxifraga*, and *Astilbe* (representatives of Rosidae) served as outgroups for this analysis because they are close to, yet basal to, the taxa included in this broad *rbcL* sequence analysis. The choice of taxa and outgroups for use in our analysis was based on the results of the large phylogenetic analysis of 499 *rbcL* sequences for seed plants (Chase et al., 1993).

For all taxa but *Diplopanax* and *Mastixia*, 1377 bp of *rbcL* sequence data were compared beginning at position 31 and ending at base pair 1407. Due to the amplification strategy required for *Diplopanax* and *Mastixia* (see above), we analyzed 1320 bp for these genera, from position 31 to 1350. All parsimony analyses were conducted with PAUP version 3.0s (Swofford, 1991) using MULPARS and TBR branch-swapping with characters specified as unordered and unweighted. To ensure that all "islands" of shortest trees were found (Maddison, 1991), 100 tree searches were performed each with a different order of taxa addition. A bootstrap analysis using 100 replicates was also conducted to obtain estimates of reliability for each monophyletic group.

## RESULTS

The phylogenetic analysis resulted in 690 most parsimonious trees that were 1,185 steps long, all in one island (Fig. 1). Two major groups can be identified in all of the most parsimonious trees. One

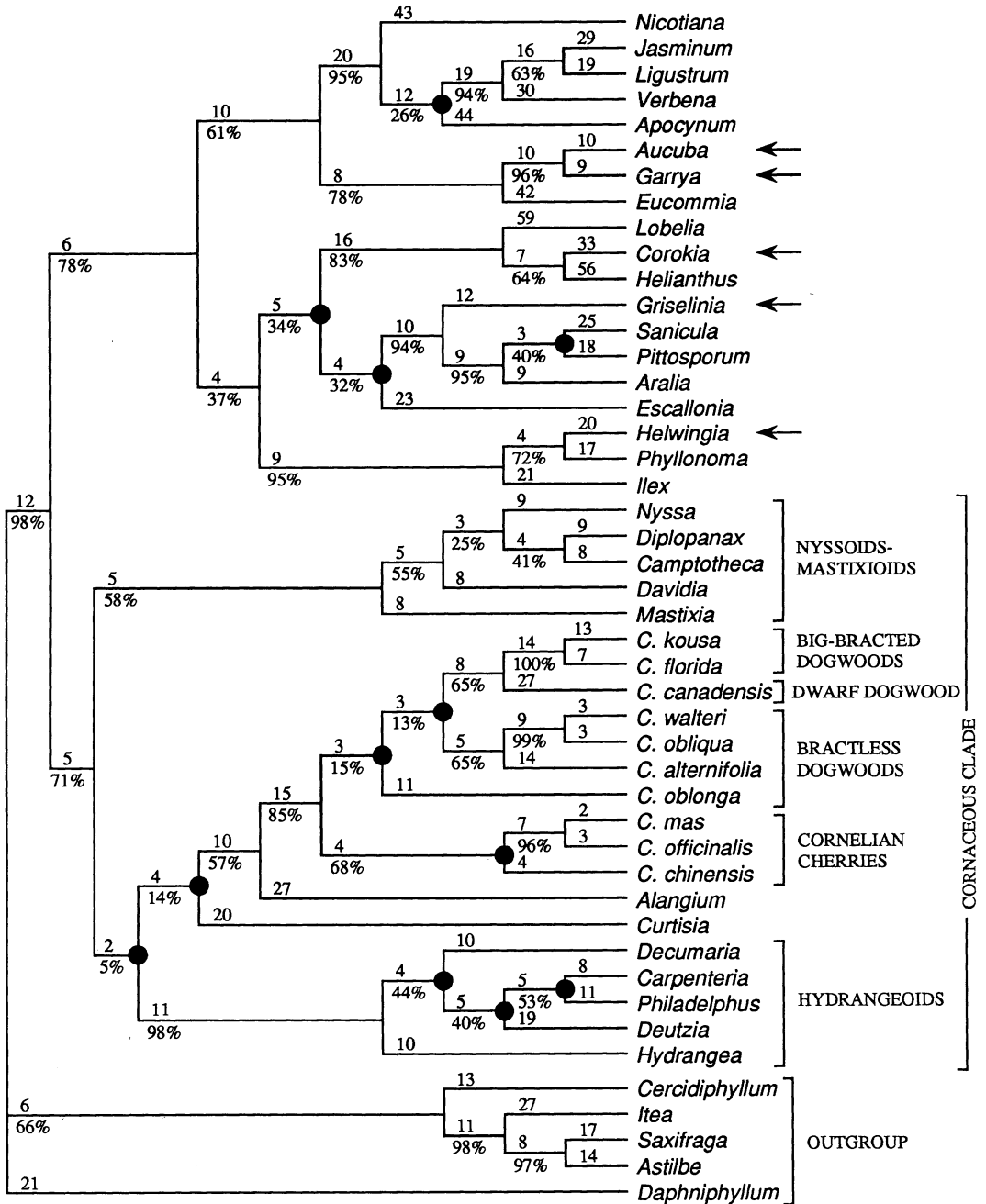


FIGURE 1. The majority-rule consensus tree including all compatible groupings constructed from 690 minimum length trees resulting from parsimony analysis of *rbcL* sequences of Cornaceae and additional taxa. This tree is one of the 690 shortest trees (length = 1,185 steps, consistency index = 0.470, retention index = 0.541). The tree is rooted using representatives from Hamamelidae (*Cercidiphyllum* and *Daphniphyllum*), and Rosidae (*Itea*, *Saxifraga*, and *Astilbe*). Numbers above lines indicate the number of nucleotide substitutions supporting each branch. Numbers below lines indicate the percentage of occurrence of each monophyletic group in the results of 100 bootstrap samples. Nodes that are not present in all 690 most parsimonious trees are indicated by black circles. Arrows indicate taxa outside the cornaceous clade that have been placed in Cornaceae by some investigators. Species of *Cornus* are abbreviated "C."

of these groups comprises *Cornus*, *Alangium*, *Curtisia*, *Nyssa*, *Camptotheca*, *Davidia*, *Diplopanax*, *Mastixia*, and genera from Hydrangeaceae (*Decumaria*, *Carpenteria*, *Deutzia*, *Philadelphus*, and *Hydrangea*) (Fig. 1). This group, hereafter referred to as the "cornaceous clade," has a bootstrap value of 71% (Fig. 1). The analysis of Chase et al. (1993) similarly indicates a monophyletic group identical to the cornaceous clade. Four major lineages can be recognized within the cornaceous clade, although the bootstrap values for some are not high: (1) nyssoids (*Nyssa*, *Camptotheca*, *Davidia*)–mastixioids (*Diplopanax* and *Mastixia*) (58%), (2) *Cornus*–*Alangium* (57%), (3) *Curtisia*, and (4) hydrangeoids (*Decumaria*, *Carpenteria*, *Deutzia*, *Philadelphus*, and *Hydrangea*) (98%) (Fig. 1). The second major group contains all of the remaining taxa analyzed, including those that have been considered close relatives of *Cornus* (*Aucuba*, *Garrya*, *Helwingia*, *Griselinia*, and *Corokia*). These five taxa are not closely allied with the cornaceous clade (Fig. 1). *Griselinia* is the sister of a well-supported (bootstrap value of 95%) araliaceous group. *Corokia* is allied with Asteraceae. *Helwingia* has as its closest relative *Phyllonoma*, a genus usually placed in Escalloniaceae or treated as a distinct subfamily of Saxifragaceae sensu lato (discussed in greater detail by Morgan & Soltis, 1993). *Aucuba* and *Garrya* are close allies; both appear in a clade with *Eucommia* (Eucommiaceae: Hamamelidae). The phylogenetic positions of these five genera traditionally allied with Cornaceae are congruent with those derived from the broad analysis of Chase et al. (1993), and a detailed analysis of sequences from the Asteridae (Olmstead, unpublished).

The phylogenetic analysis of *rbcL* sequences reveals that *Cornus* is a well-supported monophyletic group (85%; Fig. 1). Four lineages can be recognized among the 10 species of *Cornus* sequenced, although these clades are not strongly supported in the bootstrap analysis: (1) big-bracted dogwoods–dwarf dogwoods (65%), (2) bractless dogwoods (65%), (3) cornelian cherries (68%), and (4) *C. oblonga*, a morphologically distinct bractless species (Fig. 1). Strongly supported lineages having bootstrap values of 96%–100% are further identified within three of these four lineages: the big-bracted dogwoods (*C. kousa* and *C. florida*), the opposite-leaved bractless species (*C. walteri* and *C. obliqua*), and two cornelian cherries (*C. mas* and *C. officinalis*) (Fig. 1). Sequence divergence among species of *Cornus* is very high. For example, *C. canadensis* differs from *C. kousa* by 54 base

substitutions and *C. mas* differs from *C. canadensis* by 54 base substitutions (Fig. 1).

## DISCUSSION

Numerous studies have demonstrated the great value of *rbcL* sequence data in reconstructing plant phylogenies (e.g., Doebley, 1990; Donoghue et al., 1992; Olmstead et al., 1992; Soltis et al., 1990; papers in this issue). The value of comparative *rbcL* sequencing for resolving phylogenetic questions in particularly troublesome groups is also illustrated by our analysis of Cornaceae. In this study, *rbcL* sequence data have (1) helped to identify an alliance composed of *Cornus* and related taxa (i.e., the cornaceous clade), (2) demonstrated that several genera traditionally allied with *Cornus* are only distantly related to this genus, and (3) suggested the presence of major lineages within the cornaceous clade and within *Cornus*.

### 1. THE CORNACEOUS CLADE

Our analysis reveals that *Cornus* is a well-supported lineage and suggests that nyssoids (*Nyssa*, *Davidia*, and *Camptotheca*), mastixioids (*Diplopanax* and *Mastixia*), *Alangium*, *Curtisia*, and hydrangeoids are the closest relatives of *Cornus* (Fig. 1). No suite of cornaceous relatives identical to those suggested by *rbcL* sequence data has been proposed previously, and only the proposals of Eyde (1988) and Takhtajan (1980, 1987) are somewhat close to the scheme suggested by our analysis of *rbcL* sequences.

*Alangium* has been widely recognized as a monotypic family (e.g., Cronquist, 1981, 1988; Hutchinson, 1967; Takhtajan, 1980, 1987; Wangerin, 1910). Our phylogenetic analysis of *rbcL* sequence data suggests that *Alangium* may be the sister group to *Cornus*. A close relationship between these two genera is also suggested by similarities in flowers, fruits, and embryology (Chopra & Kaur, 1965; Eyde, 1988), binucleate pollen (Brewbaker, 1967), and a base chromosome number of  $x = 11$ . In addition, one species of *Alangium* has the distinctive two-armed hairs (but with unequal arms) characteristic of *Cornus* (see Eyde, 1988). Eyde (1988) similarly concluded that *Alangium* was a close relative of *Cornus* using the above characters.

Nyssoids differ from *Cornus* primarily in having unisexual and polygamous flowers. However, nyssoids also share a number of important characters with *Cornus*: presence of iridoids (Bate-Smith et al., 1975), similar gynoecial vasculature (Eyde, 1967), germination valves on the fruit stone (Eyde,

1988), and H-shaped thinning of the pollen aperture (Eramyan, 1971; Ferguson, 1977; Ferguson & Hideux, 1980; Reitsma, 1970). Citing these features, Eyde (1988) proposed that nyssoids share a recent common ancestor with *Cornus*. Our sequence data, therefore, agree with these morphological, anatomical, and chemical similarities in suggesting that the nyssoids are closely related to *Cornus* (Fig. 1).

Relationships among nyssoids (*Nyssa*, *Davidia*, and *Camptotheca*) have long been controversial. The three genera of nyssoids are often placed in the family Nyssaceae (Cronquist, 1981; Hutchinson, 1967; Wangerin, 1910). Fruit and seed morphology, as well as evidence from wood anatomy and fatty acid chemistry (Breuer et al., 1987; Eyde, 1963, 1988; Hohn & Meinschein, 1976; Titman, 1949), suggests a close relationship among the nyssoids. However, *Davidia* has been recognized as a monotypic family by some authors (Takh-tajan, 1980, 1987). Using wood anatomy, Titman (1949) proposed that *Davidia* is the most primitive nyssoid, with *Camptotheca* derived from *Nyssa*. This proposal was supported by evidence from fatty acids (Breuer et al., 1987; Hohn & Meinschein, 1976), and data from morphological, palynological, and fossil studies (Eyde, 1963, 1988). Chen (1988) argued, however, that *Camptotheca* was only distantly related to *Nyssa* based on his embryological studies of *Camptotheca*, *Nyssa*, and *Davidia* and proposed a new monotypic family, Camptotheca-ceae (Chen, 1988). Serological data (Fairbrothers, 1977; Fairbrothers & Johnson, 1964), on the other hand, support the separation of *Davidia* from *Nyssa* and *Camptotheca*. Our analysis of *rbcL* sequence data suggests instead that these three genera, together with *Mastixia* and *Diplopanax*, form a monophyletic group.

*Diplopanax* was placed previously in Araliaceae by Handel-Mazzetti (1933) based on the resemblance of its flowers, without observation of fruits, to those of the araliaceous genus *Dendropanax*. This family assignment was questioned by Hoo & Tseng (1978) and Tseng (1983). They found important similarities between the fruits of *Diplopanax* and *Mastixia* and suggested that *Diplopanax* is better placed in Cornaceae. Eyde & Xiang (1990) made a direct comparison of *Diplopanax* fruits with fossil fruits of mastixioids and restated that *Diplopanax* is closely allied with *Mastixia* because both share distinctive fruitstones, two-armed hairs that are one-celled on the leaf midveins, and hooked petals. These structural features place *Diplopanax* in the genus *Mastixicarpum*,

part of a woody-fruited mastixioid complex that was thought to have gone extinct four million years ago. Although *Mastixicarpum* is the older name, nomenclatural rules require that the united group take the name of its modern component, *Diplopanax*.

Our *rbcL* sequence data place *Diplopanax* in the nyssoid group and support its removal from Araliaceae where it was initially placed (Handel-Mazzetti, 1933) and has since been classified (Hoo & Tseng, 1978; Hutchinson, 1967). Although *rbcL* sequence data indicate that *Diplopanax* is a close relative of *Mastixia*, whether *Diplopanax* is most closely related to *Mastixia* (as suggested by Eyde & Xiang, 1990) is still uncertain based on *rbcL* sequences. All of our analyses show *Diplopanax* to be closest to *Camptotheca*, but this relationship is not strongly supported by the bootstrap analysis (41%) (Fig. 1). *Diplopanax* and *Camptotheca* are similar in that both genera (as well as *Mastixia*) are diplostemonous. Further assessment of possible relationships between *Diplopanax* and the nyssoid genera are not presently possible because of the lack of embryological, chemical, and anatomical evidence for *Diplopanax*, a result of the geographic isolation and rarity of the genus.

*Mastixia* has been assigned to a diverse array of families (e.g., Caprifoliaceae, Nyssaceae, Aquifoliaceae, Araliaceae, Icacinaceae, and Cornaceae; Matthew, 1976). Phylogenetic analysis of *rbcL* sequence data reveals that *Mastixia* is a member of the cornaceous clade. A number of lines of evidence (Table 3) suggest a close relationship between *Mastixia* and *Cornus*. However, based on *rbcL* sequences, *Mastixia* does not appear to be the sister of *Cornus* as suggested by Eyde (1988) but is more closely related to the nyssoids instead (Fig. 1). Thus, the two-armed surface hairs shared by *Mastixia*, *Diplopanax*, and *Cornus* (Eyde, 1988) may actually have evolved independently in each of these genera.

*Curtisia*, comprising two species endemic to South Africa, clearly is a member of the cornaceous clade in these analyses of *rbcL* sequences. Similar chemical patterns were observed in *Cornus* and *Curtisia* by Bate-Smith et al. (1975), adding further support for a close relationship between the two genera. *Curtisia* also has been linked with *Mastixia* based on chromosomal (Goldblatt, 1978) and palynological data (Ferguson, 1977; Ferguson & Hideux, 1980; Hideux & Ferguson, 1976). In contrast, Eyde (1988) did not consider *Curtisia* to be a close ally of *Cornus*, *Mastixia*, and nyssoids (his Cornaceae) because of its small pollen grains

and distinctive fruit-stone vascular bundles. *Curtisia* generally is placed in Cornaceae as a separate subfamily (Harms, 1898; Takhtajan, 1980; Thorne, 1983; Wangerin, 1910) or recognized as a monotypic family placed close to Cornaceae (Takhtajan, 1987; Thorne, 1992). Both of these views are concordant with *rbcL* sequence data.

The relationships of hydrangeoids have long been controversial (see review of this topic by Morgan & Soltis, 1993). Our analysis of *rbcL* sequences clearly supports their position as close relatives of *Cornus*, *Alangium*, *Curtisia*, nyssoids, and mastixioids, as suggested previously by Breuer et al. (1987), Takhtajan (1987), Philipson (1977), and Krach (1977) based on other lines of evidence. Hydrangeoids are similar to other members of the cornaceous clade in general flower structure: flowers 4–5-merous with an epigynous disk, calyx tube adnate to the ovary, petals free, ovary inferior (sometimes incompletely inferior as in *Hydrangea* or superior as in *Carpenteria*) with 2–5 locules, and ovules usually pendulous. In addition, both hydrangeoids and other members of the cornaceous clade produce iridoids. Several features, however, clearly separate the hydrangeoids from other members of the cornaceous clade. Hydrangeoids possess numerous ovules per locule, capsular fruits, and central bundles in the gynoecial vasculature. All other members of the cornaceous clade, in contrast, have a solitary ovule in each locule, typically bear drupes (*Camptotheca* has subsamaroid fruits), and lack central bundles in the gynoecial vasculature. Furthermore, hydrangeoids have unitegmic tenuinucellate ovules whereas nearly all the other members of the cornaceous clade (excluding *Curtisia* for which ovule type is unknown) have unitegmic crassinucellate ovules (Philipson, 1977). An exception is found in the bracted species of *Cornus*, which like the hydrangeoids have unitegmic tenuinucellate ovules (Erdelska, 1986; Eyde, 1988).

Although analysis of *rbcL* sequences has identified a well-supported cornaceous clade comprising four major lineages, relationships among these four major lineages are not resolved. To clarify more fully relationships within the cornaceous clade, sequences of more rapidly evolving nuclear or chloroplast genes will be required.

## 2. DISTANT RELATIVES OF CORNACEAE

Not only do *rbcL* sequence data indicate the presence of a cornaceous clade, these data also reveal that *Aucuba*, *Garrya*, *Corokia*, *Griselinia*, and *Helwingia*, all traditionally placed in Corna-

ceae, are not closely related to *Cornus* or to other members of the cornaceous clade (Fig. 1). Our findings are consistent with the broad phylogenetic analysis (Chase et al., 1993), which similarly indicates that these five genera are distantly related to the cornaceous clade. These genera have been placed in Cornaceae or Cornales by different taxonomists because of their tree or shrub form, vessel-segments usually with scalariform perforations, 3–5-merous and inconspicuous flowers, partially united sepals, separate petals, epigynous discs, inferior ovaries, solitary ovules per locule, and mostly drupaceous fruits. Each of these genera is discussed individually below.

*Aucuba* was placed in Cornaceae by Harms (1898), Wangerin (1910), and Cronquist (1981) and considered a close relative of Cornaceae by Takhtajan (1980, 1987). Our *rbcL* sequence analysis reveals, however, a distant relationship between *Aucuba* and the cornaceous clade. The distant relationship of *Aucuba* to the cornaceous clade is also supported by its distinctive wood structure and pollen morphology (Adams, 1949; Ferguson & Hideux, 1980). The closest relative of *Aucuba*, based on *rbcL* sequence data, is *Garrya*, a genus of 15 species in North America and the West Indies. *Garrya* has also been placed in Cornaceae (Harms, 1898) or recognized (as Garryaceae) as a close relative of Cornaceae (Cronquist, 1988; Hutchinson, 1967, 1969; Takhtajan, 1987; Thorne, 1983, 1992). The close affinity between *Aucuba* and *Garrya* suggested by sequence data is also supported by similarities in gynoecial vasculature (Eyde, 1964), phytochemistry (Bate-Smith et al., 1975), and fatty acids present in seed oils (Breuer et al., 1987).

*Corokia* is also far removed phylogenetically from *Cornus* in our analysis of *rbcL* sequences. Although *Corokia* traditionally has been placed in Cornaceae, more recently it has been considered closely related to *Argophyllum* (Escalloniaceae) based on pollen morphology and wood and floral anatomy (Eyde, 1988; Takhtajan, 1987). However, *rbcL* sequence data also reveal a distinct relationship between *Corokia* and *Escallonia*; an *rbcL* sequence is not available for *Argophyllum*.

Most treatments have placed *Griselinia* in Cornaceae (Cronquist, 1988; Harms, 1898; Hutchinson, 1967; Wangerin, 1910). It was, however, recognized as a monotypic family in Cornales by Takhtajan (1980), and later moved to his Hydrangeales (Takhtajan, 1987). Close affinities among *Griselinia*, *Aucuba*, and *Garrya* were proposed by Eyde (1964) based on gynoecial vascu-

lature. Phytochemical evidence also supports these relationships (Breuer et al., 1987). However, *rbcL* sequence data place *Griselinia* in a basal position in the araliaceous group, phylogenetically distant from *Aucuba* and *Garrya* (Fig. 1).

*Helwingia* was placed in Cornaceae by Harms (1898), Wangerin (1910) and Cronquist (1981). Our analysis of *rbcL* sequences reveals, however, that *Helwingia* is well outside the cornaceous clade. A distant relationship between *Helwingia* and *Cornus* is also supported by phytochemical data, as well as floral characters (Bate-Smith et al., 1975; Eyde, 1967), and both Adams (1949) and Eyde (1988) suggested that *Helwingia* be removed from Cornaceae. In our analyses, the genus is phylogenetically closest to *Phyllonoma*, a traditional member of Saxifragaceae sensu lato. *Phyllonoma* is similar to *Helwingia* in that both have flowers borne on the leaf blades. Although the two genera do share this rare characteristic, no previous authors have suggested a close relationship between *Helwingia* and *Phyllonoma* (see detailed discussion of this topic by Morgan & Soltis, 1993).

### 3. PHYLOGENETIC RELATIONSHIPS WITHIN *CORNUS*

The large amount of *rbcL* sequence divergence among species of *Cornus* is somewhat surprising given the conservative rate of evolution of *rbcL*. With this large amount of sequence divergence, our results demonstrate that *rbcL* sequence data can sometimes be used to study intrageneric relationships, as discussed below.

Varying schemes of intrageneric relationships have been proposed for *Cornus*, reflecting different hypotheses of morphological evolution and different emphases on available characters (Tables 4, 5). The major argument concerns the relative advancement within the genus of the bracted versus the bractless dogwoods. Our phylogenetic analysis of *rbcL* sequence data reveals four lineages: *C. oblonga*, big-bracted dogwoods—dwarf dogwoods, cornelian cherries, and bractless dogwoods. The latter three clades were also recognized in analyses of morphological characters (Eyde, 1988) and chloroplast DNA restriction site mutations (Brunsfeld et al., 1991; Xiang et al., 1991); insufficient material of *C. oblonga* was available for inclusion of this species in the cpDNA restriction site study. However, relationships among these four lineages are incompletely resolved by *rbcL* sequences (Fig. 1). The *rbcL* sequence analysis indicates that *C. oblonga*, a bractless species found in the eastern Himalayas and southwestern China, is a lineage distinct from cornelian cherries, the remaining

bractless species, and the big-bracted dogwoods—dwarf dogwoods (Fig. 1). Several morphological, embryological, and anatomical features similarly suggest the distinctiveness of *C. oblonga* (Adams, 1949; Chopra & Kaur, 1965; Zhu, 1984). This species commonly has been viewed as the most primitive species of *Cornus*, and the hypothetical ancestral dogwoods were reconstructed based largely on its morphological characters (Eyde, 1988; Rickett 1950). Although *rbcL* sequence data do not suggest a basal position for *C. oblonga* in *Cornus*, sequence data do agree with other evidence in suggesting an isolated phylogenetic position of this species in the genus. However, the exact phylogenetic position of *C. oblonga* awaits the sequence analysis of more rapidly evolving chloroplast genes, such as ORFK.

In summary, our analysis of *rbcL* sequences has (1) identified a cornaceous clade that includes *Cornus*, *Alangium*, *Curtisia*, *Nyssa*, *Camptotheca*, *Davidia*, *Diplopanax*, *Mastixia*, and genera from Hydrangeaceae (*Decumaria*, *Carpenteria*, *Deutzia*, *Philadelphus*, and *Hydrangea*); (2) revealed that several genera previously placed in Cornaceae (e.g., *Aucuba*, *Garrya*, *Corokia*, *Griselinia*, and *Helwingia*) are only distantly related to *Cornus*; (3) identified four major lineages within the cornaceous clade and suggested four major lineages within *Cornus*. Other putative relatives of *Cornus*, such as *Toricellia*, *Aralidium*, *Melanophylla*, and *Kaliphora*, may ultimately be considered part of the cornaceous clade if material becomes available for analysis of *rbcL*.

### LITERATURE CITED

- ADAMS, J. E. 1949. Studies in the comparative anatomy of the Cornaceae. *J. Elisha Mitchell Sci. Soc.* 65: 218–244.
- BATE-SMITH, E. C., I. K. FERGUSON, K. HUTSON, B. J. NIELSEN & T. SWAIN. 1975. Phytochemical interrelationships in the Cornaceae. *Biochem. Syst. Ecol.* 3: 79–89.
- BREUER, B., T. STUHLFAUTH, H. FOCK & H. HUBER. 1987. Fatty acids of some Cornaceae, Hydrangeaceae, Aquifoliaceae, Hamamelidaceae and Styracaceae. *Phytochemistry* 26: 1441–1445.
- BREWBAKER, J. L. 1967. The distribution and phylogenetic significance of binucleate and trinucleate pollen grains in the angiosperms. *Amer. J. Bot.* 54: 1069–1083.
- BRUNSFELD, S. J., D. E. SOLTIS & P. S. SOLTIS. 1991. Evolution of the big-bracted dogwood (*Cornus*). *Amer. J. Bot.* 78: 230.
- CHASE, M. W., D. E. SOLTIS, R. G. OLMSTEAD, D. MORGAN, D. H. LES, B. D. MISHLER, M. R. DUVALL, R. A. PRICE, H. G. HILLS, Y.-L. QIU, K. A. KRON, J. H. RETTIG, E. CONTI, J. D. PALMER, J. R. MANHART, K. J. SYTSMA, H. J. MICHAELS, W. J. KRESS, K. G. KAROL, W. D. CLARK, M. HEDREN, B. S. GAUT, R.

- K. JANSEN, K.-J. KIM, C. F. WIMPEE, J. F. SMITH, G. R. FURNIER, S. H. STRAUSS, Q.-Y. XIANG, G. M. PLUNKETT, P. S. SOLTIS, S. SWENSEN, S. E. WILLIAMS, P. A. GADEK, C. J. QUINN, L. E. EGUIARTE, E. GOLENBERG, G. H. LEARN, JR., S. W. GRAHAM, S. C. H. BARRETT, S. DAYANANDAN & V. A. ALBERT. 1993. Phylogenetics of seed plants: An analysis of nucleotide sequences from the plastid gene *rbcL*. *Ann. Missouri Bot. Gard.* 80: 528–580.
- CHEN, L. J. 1988. The Comparative Embryological Study and Proposed Affinity of *Camptotheca*, *Nyssa* and *Davidia*. Ph.D. Dissertation. Beijing Institute of Botany, Academia Sinica, Beijing, China.
- CHOPRA, R. N. & H. KAUR. 1965. Some aspects of the embryology of *Cornus*. *Phytomorphology* 15: 353–359.
- CLEGG, M. T. & G. ZURAWSKI. 1992. Chloroplast DNA and the study of plant phylogeny: Present status and future prospects. Pp. 1–13 in P. S. Soltis, D. E. Soltis & J. J. Doyle (editors), *Molecular Systematics of Plants*. Routledge, Chapman and Hall, London.
- CRONQUIST, A. 1981. *An Integrated System of Classification of Flowering Plants*. Columbia Univ. Press, New York.
- . 1988. *The Evolution and Classification of Flowering Plants*, 2nd ed. New York Botanical Garden, New York.
- DERMEN, H. 1932. Cytological studies of *Cornus*. *J. Arnold Arbor.* 13: 401–417.
- DOEBLEY, J. F. 1990. Molecular systematics of *Zea* (Gramineae). *Maydica* 35: 143–150.
- DONOGHUE, M. J., R. G. OLMSTEAD, J. F. SMITH & J. D. PALMER. 1992. Phylogenetic relationships of Dipsacales based on *rbcL* sequences. *Ann. Missouri Bot. Gard.* 79: 333–345.
- DOYLE, J. J. & J. L. DOYLE. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochem. Bull.* 19: 11–15.
- ERAMYAN, E. N. 1971. Palinologicheskie dannye k sistematike i filogenii Cornaceae Dumort. i rodstvennykh semeistv. Pp. 235–273 in L. A. Kupriyanova & M. S. Yakovlev (editors), *Morfologiya pyl'tsy: Cucurbitaceae, Thymelaeaceae, Cornaceae*. Izdatel'stvo "Nauka," Leningrad.
- ERDELSKA, O. 1986. Embryo development in the dogwood *Cornus mas*. *Phytomorphology* 36: 23–28.
- EYDE, R. H. 1963. Morphological and paleobotanical studies of the Nyssaceae. I. The modern species and their fruits. *J. Arnold Arbor.* 44: 1–59.
- . 1964. Inferior ovary and generic affinities of *Garrya*. *Amer. J. Bot.* 51: 1083–1092.
- . 1967. The peculiar gynoeical vasculature of Cornaceae and its systematic significance. *Phytomorphology* 17: 172–182.
- . 1987. The case for keeping *Cornus* in the broad Linnean sense. *Syst. Bot.* 12: 505–518.
- . 1988. Comprehending *Cornus*: Puzzles and progress in the systematics of the dogwoods. *Bot. Rev.* 54: 233–351.
- & Q.-Y. XIANG. 1990. Fossil mastixioid (Cornaceae) alive in eastern Asia. *Amer. J. Bot.* 77: 689–692.
- FAIRBROTHERS, D. E. 1977. Perspectives in plant serotaxonomy. *Ann. Missouri Bot. Gard.* 64: 147–160.
- & M. A. JOHNSON. 1964. Comparative serological studies within the families Cornaceae (dogwood) and Nyssaceae (sour gum). Pp. 305–318 in C. A. Leone (editor), *Taxonomic Biochemistry and Serology*. Ronald Press, New York.
- FERGUSON, I. K. 1966. Notes on the nomenclature of *Cornus*. *J. Arnold Arbor.* 47: 100–105.
- . 1977. World Pollen and Spore Flora 6: Cornaceae Dum. Almqvist & Wiksell, Stockholm.
- & M. J. HIDEUX. 1980. Some aspects of the pollen morphology and its taxonomic significance in Cornaceae *sens. lat.* *Proc. IV. Int. Palynol. Conf.*, Lucknow 1: 240–249.
- GOLDBLATT, P. 1978. A contribution of cytology in Cornales. *Ann. Missouri Bot. Gard.* 65: 650–655.
- HANDEL-MAZZETTI, H. F. V. 1933. *Plantae novae Chingianae*, III. *Sinensia* 3: 185–198.
- HARMS, H. 1898. Cornaceae. Pp. 250–270 in A. Engler & K. Prantl (editors), *Die Natürlichen Pflanzenfamilien*, Teil III, Abteilung 8. Engelmann, Leipzig.
- HIDEUX, M. & 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.
- HOHN, M. E. & W. G. MEINSCHNEIN. 1976. Seed oil fatty acids: Evolutionary significance in the Nyssaceae and Cornaceae. *Bioch. Syst. & Ecol.* 4: 193–199.
- HOO, J. & C. J. TSENG. 1978. Araliaceae. P. 135 in *Fl. Reip. Popul. Sin.*, Vol. 54. Academic Press, Beijing.
- HOOKE, J. D. 1867. Cornaceae. Pp. 947–952 in G. Bentham & J. D. Hooker (editors), *Genera Plantarum*, Vol. 1, part 3. Reeve & Co. and Williams & Norgate, London.
- HUTCHINSON, J. 1942. Neglected generic characteristics in the family Cornaceae. *Ann. Bot. n. s.* 6: 83–93.
- . 1967. *The Genera of Flowering Plants*, Vol. 2. Clarendon Press, Oxford.
- . 1969. *Evolution and Phylogeny of Flowering Plants—Dicotyledon: Facts and Theory*. Academic Press, London and New York.
- KRACH, J. E. 1977. Seed characters in and affinities among the Saxifragaceae. Pp. 141–153 in K. Kubitzki (editor), *Flowering Plants—Evolution of Higher Categories*. Springer-Verlag, Vienna, New York.
- LI, H.-L. & C.-Y. CHAO. 1954. Comparative anatomy of the woods of the Cornaceae and allies. *Quart. J. Taiwan Mus.* 7: 119–136.
- MADDISON, D. R. 1991. The discovery and importance of multiple islands of most-parsimonious trees. *Syst. Zool.* 40: 315–328.
- MATTHEW, K. M. 1976. A revision of the genus *Mastixia* (Cornaceae). *Blumea* 23: 51–93.
- MORGAN, D. R. & D. E. SOLTIS. 1993. Phylogenetic relationships among members of Saxifragaceae *sensu lato* based on *rbcL* sequence data. *Ann. Missouri Bot. Gard.* 80: 631–660.
- 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.
- PALMER, J. D., R. K. JANSEN, H. J. MICHAELS, M. W. CHASE & J. R. MANHART. 1988. Chloroplast DNA variation and plant phylogeny. *Ann. Missouri Bot. Gard.* 75: 1180–1206.

- PHILIPSON, W. R. 1977. Ovular morphology and the classification of dicotyledons. Pp. 123-140 in K. Kubitzki (editor), *Flowering Plants—Evolution of Higher Categories*. Springer-Verlag, Vienna, New York.
- POJARKOVA, A. 1950. De systemate generis Linneani *Cornus* L. Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk. SSSR 12: 164-180.
- REITSMA, T. 1970. Pollen morphology of the Alangiaceae. Rev. Paleobot. Palynol. 10: 249-332.
- RICKETT, H. W. 1950. *Cornus* in Mexico, with notes on the evolution of the genus. Anales Inst. Biol. Univ. Nac. Mexico 21: 83-94.
- 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.
- , ———, T. G. COLLIER & M. L. EDGERTON. 1991. Chloroplast DNA variation within and among genera of the *Heuchera* group (Saxifragaceae): Evidence for chloroplast transfer and parafyly. Amer. J. Bot. 78: 1091-1112.
- SWOFFORD, D. L. 1991. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.0s. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.
- TAKHTAJAN, A. L. 1980. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. 46: 225-359.
- . 1987. Sistema Magnoliifitov. Izdatel'stvo "Nauka," Leningrad.
- THORNE, R. F. 1983. Proposed new realignments in the angiosperms. Nordic J. Bot. 3: 85-117.
- . 1992. An updated phylogenetic classification of the flowering plants. Aliso 13: 365-389.
- TITMAN, P. W. 1949. Studies in the woody anatomy of the family Nyssaceae. J. Elisha Mitchell Sci. Soc. 65: 245-261.
- TSENG, C. J. 1983. The systematic position of *Diplopanax* Hand.-Mazz. Acta Phytotax. Sin. 21: 151-152.
- WANGERIN, W. 1910. Cornaceae. Pp. 1-101 in A. Engler (editor), *Das Pflanzenreich*. Series IV, family 229 (Heft 41). W. Engelmann, Leipzig.
- WILKINSON, A. M. 1944. Floral anatomy of some species of *Cornus*. Bull. Torrey Bot. Club 71: 276-301.
- XIANG, Q.-Y. 1987. A neglected character of *Cornus* L. s.l. with special reference to a new subgenus—*Sinocornus* Q. Y. Xiang. Acta Phytotax. Sin. 25: 125-131.
- , D. E. SOLTIS & P. S. SOLTIS. 1991. Molecular systematics of *Cornus* L. s.l. Amer. J. Bot. 78: 230.
- ZHU, Z.-Y. 1984. *Yinquania* Z. Y. Zhu—A new genus of Cornaceae from China. Bull. Bot. Res. (Harbin) 4(4): 121-128.