

CIRCUMSCRIPTION OF THE MALVALES AND RELATIONSHIPS TO OTHER ROSIDAE: EVIDENCE FROM *Rbcl* SEQUENCE DATA¹

WILLIAM S. ALVERSON,^{2,6,10} KENNETH G. KAROL,^{2,7} DAVID A.
BAUM,³ MARK W. CHASE,⁴ SUSAN M. SWENSEN,^{4,8} RICHARD
MCCOURT,^{5,9} AND KENNETH J. SYTSMA²

²Department of Botany, University of Wisconsin, 430 Lincoln Drive, Madison, Wisconsin 53706;

³Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts 02138;

⁴Molecular Systematics Section, Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3DS, UK; and

⁵De Paul University, Department of Biological Sciences, 2330 W. Kenmore Avenue, Chicago, Illinois 60614

The order Malvales remains poorly circumscribed, despite its seemingly indisputable core constituents: Bombacaceae, Malvaceae, Sterculiaceae, and Tiliaceae. We conducted a two-step parsimony analysis on 125 *rbcL* sequences to clarify the composition of Malvales, to determine the relationships of some controversial families, and to identify the placement of the Malvales within Rosidae. We sampled taxa that have been previously suggested to be within, or close to, Malvales (83 sequences), plus additional rosids (26 sequences) and nonrosid eudicots (16 sequences) to provide a broader framework for the analysis. The resulting trees strongly support the monophyly of the core malvacean families, listed above. In addition, these data serve to identify a broader group of taxa that are closely associated with the core families. This expanded malvacean clade is composed of four major subclades: (1) the core families (Bombacaceae, Malvaceae, Sterculiaceae, Tiliaceae); (2) Bixaceae, Cochlospermaceae, and Sphaerosepalaceae (Rhopalocarpaceae); (3) Thymelaeaceae sensu lato (s.l.); and (4) Cistaceae, Dipterocarpaceae s.l., Sarcocaulaceae (Chlaenaceae), and *Muntingia*. In addition, *Neurada* (Neuradaceae or Rosaceae) falls in the expanded malvacean clade but not clearly within any of the four major subclades. This expanded malvacean clade is sister to either the expanded capparalean clade of Rodman et al. or the sapindalean clade of Gadek et al. Members of Elaeocarpaceae, hypothesized by most authors as a sister group to the four core malvacean families, are shown to not fall close to these taxa. Also excluded as members of, or sister groups to, the expanded malvacean clade were the families Aextoxicaceae, Barbeyaceae, Cannabinaceae, Cecropiaceae, Dichapetalaceae, Elaeagnaceae, Euphorbiaceae s.l., Huaceae, Lecythidaceae, Moraceae s.l., Pandaceae, Plagiopteraceae, Rhamnaceae, Scytopetalaceae, Ulmaceae, and Urticaceae.

Key words: angiosperm phylogeny; Elaeocarpaceae; Malvales; *Muntingia*; *Neurada*; *rbcL*.

The order Malvales, as traditionally circumscribed, includes four core families, Bombacaceae (~250 spp.), Malvaceae (1500 spp.), Sterculiaceae (1000 spp.), and Tiliaceae (400 spp.), plus from one to eight other families depending upon author (Takhtajan, 1987, 1997; Cronquist, 1988; Dahlgren, 1989; Thorne, 1992). Considering only the core four families, the order comprises predominantly woody and tropical trees, including several economically important genera such as cotton (*Gossypium*

spp.), chocolate (*Theobroma cacao*), cola nuts (*Cola* spp.), durians (*Durio zibethinus*), balsa wood (*Ochroma pyramidale*), jutes (*Corchorus capsularis* and *C. olitorius*), and okra (*Abelmoschus esculentus*). The family Malvaceae includes herbaceous elements that have undergone extensive radiation in the temperate zones, perhaps being derived from within tropical Bombacaceae (Judd, Sanders, and Donoghue, 1994). Bombacaceae, Sterculiaceae, and Tiliaceae are important components of many tropical forest ecosystems (Terborgh, 1983; Gentry, 1993) and are often exploited for timber.

The core malvacean families have a good palynological record stretching back to the Maastrichtian, late Cretaceous (Wolfe, 1975; Muller, 1984; Nilsson and Robyns, 1986; Taylor, 1988) and are thought to belong to a lineage of Gondwanan origin (Raven and Axelrod, 1974; Taylor, 1988). Given this age, it is not surprising that the group shows a great deal of diversity in vegetative and floral morphology, especially in respect to the development of androphores and gynophores and the splitting and fusion of the stamens (Edlin, 1935; Venkata Rao, 1952, 1954; van Heel, 1966; Gibbs, Semir, and da Cruz, 1988). Additionally, the group displays a great diversity of chromosome numbers ($2n = 10$ to ~270; Baker and Baker, 1968; Krapovickas, 1969; Cristóbal, 1967; Bates and Blanchard, 1970; Bates, 1976; Fernández, 1981; Baum

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⁶ Current address: Harvard University Herbaria, 22 Divinity Avenue, Cambridge, MA 02138.

⁷ Current address: Laboratory of Molecular Systematics, MRC 534, MSC, Smithsonian Institution, Washington, DC. 20560.

⁸ Current address: Biology Department, Ithaca College, Ithaca, NY 14850.

⁹ Current address: Academy of Natural Sciences of Philadelphia, 1900 Benjamin Franklin Parkway, Philadelphia, PA 19103.

¹⁰ Author for correspondence: email: walverso@oeb.harvard.edu.

TABLE 1. Putative members of the Malvales according to four recent authors.

Putative Malvales	Takhtajan (1997)	Thorne (1992)	Dahlgren (1989)	Cronquist (1988)	Takhtajan (1987)	Exemplars ^a
Bixaceae	– (Cistales)	– (Violales)	+	– (Violales)	– (Bixales)	1
Bombacaceae	+	+	+	+	+	5
Cistaceae	– (Cistales)	– (Violales)	+	– (Violales)	– (Bixales)	2
Cochlospermaceae	– (Cistales)	– (Violales)	+	– (Violales)	– (Bixales)	1
Diegodendraceae	+	+	?	– (Theales)	– (Ochnales)	0
Dipterocarpaceae	+	+	+	– (Theales)	+	1
Dirachmaceae	+	– (Geraniales)	– (Geraniales)	– (Geraniales)	– (Geraniales)	0
Elaeocarpaceae	– (Elaeocarpaceae) ^b	+	– (Rhizophorales)	+	+	6
Huaceae	+	+	+	– (Violales)	+	2
Malvaceae	+	+	+	+	+	2
Monotaceae	+	+	+	– (Theales)	+	1
Plagiopteraceae	+	+	+	– (Violales)	+	1
Sarcolaenaceae	+	+	+	– (Theales)	+	1
Sphaerosepalaceae	+	+	+	– (Theales)	+	1
Sterculiaceae	+	+	+	+	+	4
Tiliaceae	+	+	+	+	+	1

^a The identities of the exemplars included in this study are listed by family in Appendix 1.

^b Elaeocarpaceae (Elaeocarpaceae) grouped with Cistales and Malvales in Superorder Malvaneae of Takhtajan (1997).

and Oginuma, 1994), and much variation in pollination and breeding systems, (e.g., Cope, 1958, 1962; Seavey and Bawa, 1986; Gibbs and Bianchi, 1993; Baum, 1995). Nonetheless, the four core families have certain typical features, such as fibrous bark, palmate venation, and valvate calyx aestivation that make them morphologically coherent (Cronquist, 1981). In recent decades, additional technical characters that may be diagnostic for the order have been highlighted, such as mucilage canals or ducts, tangentially stratified phloem, tile cells (specialized, upright cells) in xylem rays, and cyclopropanoid fatty acids (Cronquist, 1981, 1988). Indeed, the close relationship among these families has been recognized since the time of Linnaeus (e.g., Bentham, 1862). Beyond the core four families, however, there has been no agreement as to which other families or taxa should be included in the order nor has there been agreement as to the closest relatives of the Malvales (Table 1).

The lack of a sound malvacean phylogeny is a major impediment to systematic and evolutionary studies of this order. For example, recent attempts to discuss historical phytogeography (Aubréville, 1975; Krutzsch, 1989) and the evolution of life history traits (Eriksson and Bremer, 1992) at familial and interfamilial levels depended heavily on tenuous assumptions about phylogenetic relationships inferred from traditional classification systems. At smaller taxonomic scales, attempts to determine intertribal relationships of Sterculiaceae (Kelman, 1991) and to determine generic limits of Bombacaceae using cladistic principles (Alverson, 1994) were thwarted by the lack of a resolved phylogeny at higher levels within this group. Manchester (1992) also noted that “. . . the need for modern systematic revision [of the Malvales] has impeded the understanding of paleobotanical data.” In sum, the determination of phylogeny at all taxonomic scales within the “Malvales” depends critically on the identification of a monophyletic malvacean clade and determination of its broader affinities.

In addition to the traditional, intuitive systems of classification, two recent studies have used cladistic methods to study the internal phylogeny of Malvales. La Duke and Doebley (1995) employed chloroplast restriction frag-

ment length polymorphism (RFLP) data to determine a phylogeny of the Malvaceae, using *Tilia* as an outgroup. Based on morphological data, Judd and Manchester (1997) inferred the relationships of the four core malvacean families, using representatives of Dipterocarpaceae and Elaeocarpaceae as outgroups. The latter study concluded that, of the core malvacean families, only Malvaceae appeared to be monophyletic. However, the analysis resulted in highly unresolved trees, and those clades that were obtained had weak internal support.

Five previous studies speak to the circumscription and placement of “Malvales”: the broad *rbcL* analysis of Chase et al. (1993), the more focused *rbcL* studies of Capparales (Rodman et al., 1993), Myrtales (Conti, Litt, and Sytsma, 1996) and Sapindales (Gadek et al., 1996), and the broad 18S rDNA studies of Soltis et al. (1997). In the *rbcL* studies, the malvacean exemplars formed a clade within Rosidae that was closely associated with the expanded Capparales, Sapindales, and Myrtales. The study of nuclear rDNA resulted in an equivocal placement of core malvacean taxa within rosids. However, these studies did not include many of the taxa that have at one time or another been associated with Malvales. Therefore, we undertook a study using *rbcL* data that directly addresses the phylogeny of Malvales.

MATERIALS AND METHODS

Taxon sampling—The total number of *rbcL* sequences used for phylogenetic analyses of Malvales was 125 (see Appendix 1 for a complete list of sequences and their provenance), of which 18 were generated for this study. All taxa that have been suggested as being within Malvales were sampled except for *Diegodendron* and *Dirachma*, which are being studied by Fay et al. (1998), and Thulin et al. (in press), respectively. In addition to 29 sequences from putative Malvales (see Table 1), 29 sequences were included to represent all the groups that have been suggested by recent authors (Cronquist, 1968, 1988; Dahlgren, 1983, 1989; Thorne, 1983) to be potential malvacean sister groups: Aextoxicaceae, Barbeyaceae, Cannabinaceae, Dichapetalaceae, Elaeagnaceae, Euphorbiaceae (subfamilies Acalyphoideae, Crotonoideae, Euphorbioideae, Oldfieldioideae, and Phyllanthoideae), Lecythidaceae, Pandaceae, Rhamnaceae, Scytopetalaceae, Simmondsiaceae, Thymelaeaceae (Aquilarioideae, Gonystyloideae, and Thymelaeoideae), Ulmaceae (Celtoid-

deae and Ulmoideae), and Urticaceae (Cecropioideae, Moroideae, and Urticoideae). A further 25 sequences represented taxa that have been linked to the core four families based on recent *rbcL* analyses; our selection of taxa was guided by the published *rbcL* phylogenies for these groups: expanded Capparales (Rodman et al., 1993), Sapindales (Gadek et al., 1996), and Myrtales (Conti, Litt, and Sytsma, 1996). Finally, an additional 42 sequences were included to represent the major clades of eudicots shown in trees produced by Search II of Chase et al. (1993): 13 from the rosoid I clade (in which the core Malvales families fell); four from each of the rosoid II and rosoid III clades; five from the rosoid IV clade; four from each of the asterid I and asterid III clades; three from the asterid II clade; two from the asterid IV clade; two placeholders from the ranunculid clade; and one from the hamamelid II clade (Appendix 1). We did not extensively sample the core malvalean families because our preliminary data showed little *rbcL* sequence divergence among members of these core families, and because our emphasis was on relationships at a broader scale. A concurrent and complementary study employs the more rapidly evolving chloroplast gene *ndhF* to examine phylogenetic structure at the tribal level within the core malvalean families (Alverson et al., unpublished data). Molecular studies of malvalean chloroplast *atpB* (M. Chase and C. Bayer) and single-copy nuclear gene sequences (F. Blattner, Johannes Gutenberg Universität Mainz, and M. Jenny, Palmengarten, Frankfurt) are also underway.

Laboratory methods—DNA extraction, *rbcL* amplification, and sequencing followed the general procedure described in Conti, Litt, and Sytsma (1996). Overlapping sequence fragments were obtained from both strands of the gene using a total of eight primers. Primer sequences, of length 26–34 nucleotides, were provided by G. Zurawski (Zurawski et al., 1981; Zurawski, Whitfield, and Bottomley, 1986). Sequences were easily aligned by visual inspection and no gaps were needed. Translation of the nucleotide sequences to the corresponding amino acid sequences with the TRANSLATE program of the Genetics Computer Group (GCG) package (<http://www.gcg.com/>) indicated no internal stop codons. A total of 1402 nucleotides, from positions 27 to 1428 of the *rbcL* exon were used.

Phylogenetic analyses—The analysis was carried out in two separate steps. The first step was designed to identify the membership of a broad clade, the “expanded Malvales,” comprising taxa closely associated with the core malvalean families. The second step was a focused study of the expanded malvalean clade plus its closest relatives. Unless otherwise stated, all parsimony searches used random addition sequences (RAS) and were run with tree bisection reconnection branch swapping (TBR), hold = 1, steepest descent off, and zero-length branches collapsed.

Identification of the malvalean clade—The first step of the analysis used all 125 taxa. The analysis used PAUP 4.0.0d versions 31 to 52 (Swofford, 1997) on five boxes: Power Macintosh models 7100/66 and 7100/80AV running Systems 7.5 and 7.5.3, a Macintosh PowerBook 5300/100 running System 7.5.2, a Macintosh Duo 2300/100 with System 7.5.5, and a Sun UltraSparc running Solaris OS 5.5, for a total of 50 complete, unconstrained RAS searches. The shortest trees from all 50 runs were condensed and then summarized by a single strict consensus tree. The phylogenetic signal present in the full *rbcL* data set was estimated using PAUP by analyzing the distribution of 1000000 random trees and calculating the skewness of their distribution (Hillis and Huelsenbeck, 1992; but see Källersjö et al., 1992 for shortcomings of this method). The inordinate amount of time required for these runs (average 39 h each) made standard bootstrap analysis impractical. Instead, the strength of support for 12 clades of particular interest (see Results) was assessed by decay analysis (“Bremer support”; Bremer, 1988) using inverse constraints and 100 RAS searches with MULPARS

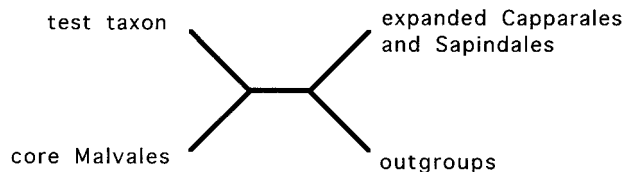


Fig. 1. Structure of backbone constraint trees used to test membership in expanded Malvales. The core malvalean clade was represented by exemplars of Bombacaceae, Malvaceae, Sterculiaceae, and Tiliaceae. Three exemplars of Papaveraceae, Ranunculaceae, and Trochodendra-ceae (Appendix 1) were used as outgroups.

off, and by a total of 100 bootstrap searches, each consisting of ten RAS searches without branch swapping.

We wished to avoid excluding any taxa from the second step of the analysis that are actually members of the expanded Malvales. Therefore, for each putatively malvalean taxon that was excluded from the expanded Malvales in the consensus tree, we assessed the cost of forcing it into the expanded Malvales. This was achieved by conducting inverse backbone-constraint searches (Swofford, 1997). The backbone constraint was that the taxon in question was more closely related to the core Malvales than are the Capparales and Sapindales (Fig. 1). To orient the constraint tree, *Caltha*, *Papaver*, and *Trochodendron* were used as outgroups. For each taxon evaluated in this way (see Results), three RAS searches were conducted.

Structure of the malvalean clade—The second step of the analysis included 43 taxa representing the expanded malvalean clade plus the Capparales and Sapindales. This data set was subjected to 1000 unconstrained RAS searches with steepest descent on and members of the Sapindales used as an outgroup. To see the effect of the limited sampling within Capparales and Sapindales, an additional 1000 RAS/steepest descent searches were conducted with these two clades constrained to have the strict consensus topology obtained by Rodman et al. (1993) and Gadek et al. (1996), respectively. A total of 100 bootstraps, each consisting of ten RAS searches with TBR branch swapping, were conducted to estimate bootstrap support (Felsenstein, 1985). Decay indices were estimated for clades on the strict consensus tree. The phylogenetic signal present in this subset of *rbcL* data was also assessed by examining the skewness of 1000000 random trees, as discussed above.

RESULTS

Identification of the malvalean clade—The full data set included 506 potentially informative characters. Equally weighted parsimony analysis (Fitch, 1971) yielded 4616 trees of 4733 steps (including autapomorphies). These trees are distributed on one large island (4344 trees), which was found just once, and five small islands (16, 16, 40, 48, 48, and 168 trees) found 15 times. The 4616 trees have a consistency index (CI) of 0.240 (including all characters) and a retention index (RI) of 0.484. The data are significantly skewed as judged by a $g_1 = -0.280$ (Hillis and Huelsenbeck, 1992).

The portion of the consensus tree relevant to the Malvales exhibited robust phylogenetic structure (Fig. 2) in the form of seven major clades: (a) the four core malvalean families, (b) a bixalean clade, (c) a thymelaealean clade, (d) a dipterocarpacean clade, (e) the expanded Capparales, (f) the Sapindales, and (g) the Myrtales. The core malvalean, bixalean, and thymelaealean clades together form a clade to which either the dipterocarpacean clade or the expanded Capparales clade is a sister group. The Sapindales clade was sister to clades a–e and the Myrtales

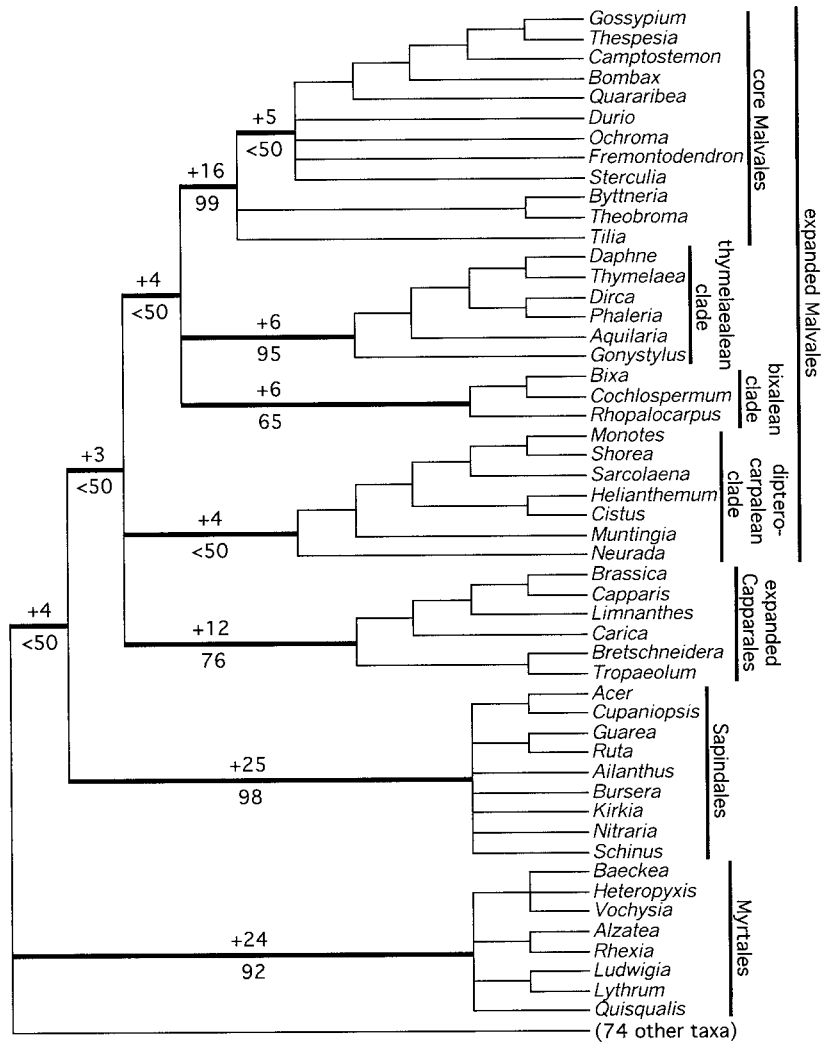


Fig. 2. Portion of the consensus tree, representing the consensus of 4616 trees at 4733 steps, resulting from step 1 of the analysis (including 125 taxa), in which core malvales taxa and their close relatives were found. Numbers above branches of the major clades of interest represent decay values derived from 100 TBR/RAS searches without MULPARS. Numbers below these branches are bootstrap values from 100 bootstrap searches, each consisting of ten RAS searches without branch swapping.

clade was sister to clades a–f. This result provides a specific criterion for selecting taxa to be included in the more focused analysis: namely all taxa falling within clades a–f.

Representative place-holders for 30 putative malvales taxa were not located in any of these seven major clades. Before rejecting a malvales placement of these taxa, we tested the strength of this exclusion using backbone constraint searches (see Materials and Methods). By using backbone rather than monophyly constraints, taxa other than those specified in the constraint tree were free to find their optimal position. For all 30 taxa, at least nine additional steps were required to satisfy the backbone constraint. In none of these cases did the test taxon fall into one of the clades of the expanded Malvales (clades a–d, above) but, rather, they were forced into a position between the expanded Malvales clade and the Capparales and Sapindales clades. This result justifies the exclusion of the following families from further consideration as members of the expanded malvales clade: Aextoxicaceae, Barbeyaceae, Cannabinaceae, Cecropiaceae, Di-

chapetalaceae, Elaeocarpaceae, Elaeagnaceae, Euphorbiaceae s.l., Huaceae, Lecythidaceae, Moraceae, Pandaceae, Plagiopteraceae, Rhamnaceae, Scytoperaceae, Simmondsiaceae, Ulmaceae, and Urticaceae. Concurrent work by Thulin, Bremer, and Chase (in press) also excludes *Dirachma* as a member of the expanded Malvales.

Structure of the malvales clade—The reduced data matrix of 43 taxa included 285 phylogenetically informative characters. The data are significantly skewed, as judged by a g_1 of -0.549 (Hillis and Huelsenbeck, 1992). An unconstrained, equally weighted search yielded two equally parsimonious trees of length 1213 (including all characters), with $CI = 0.472$ and $RI = 0.609$. These two trees, which only differed by their topologies within Sapindales, were located in a single island that was found in 663 of the 1000 RAS replicates.

The strict consensus of the two most-parsimonious trees is shown in Fig. 3, with branch lengths, and bootstrap and decay values. The tree was rooted on the branch

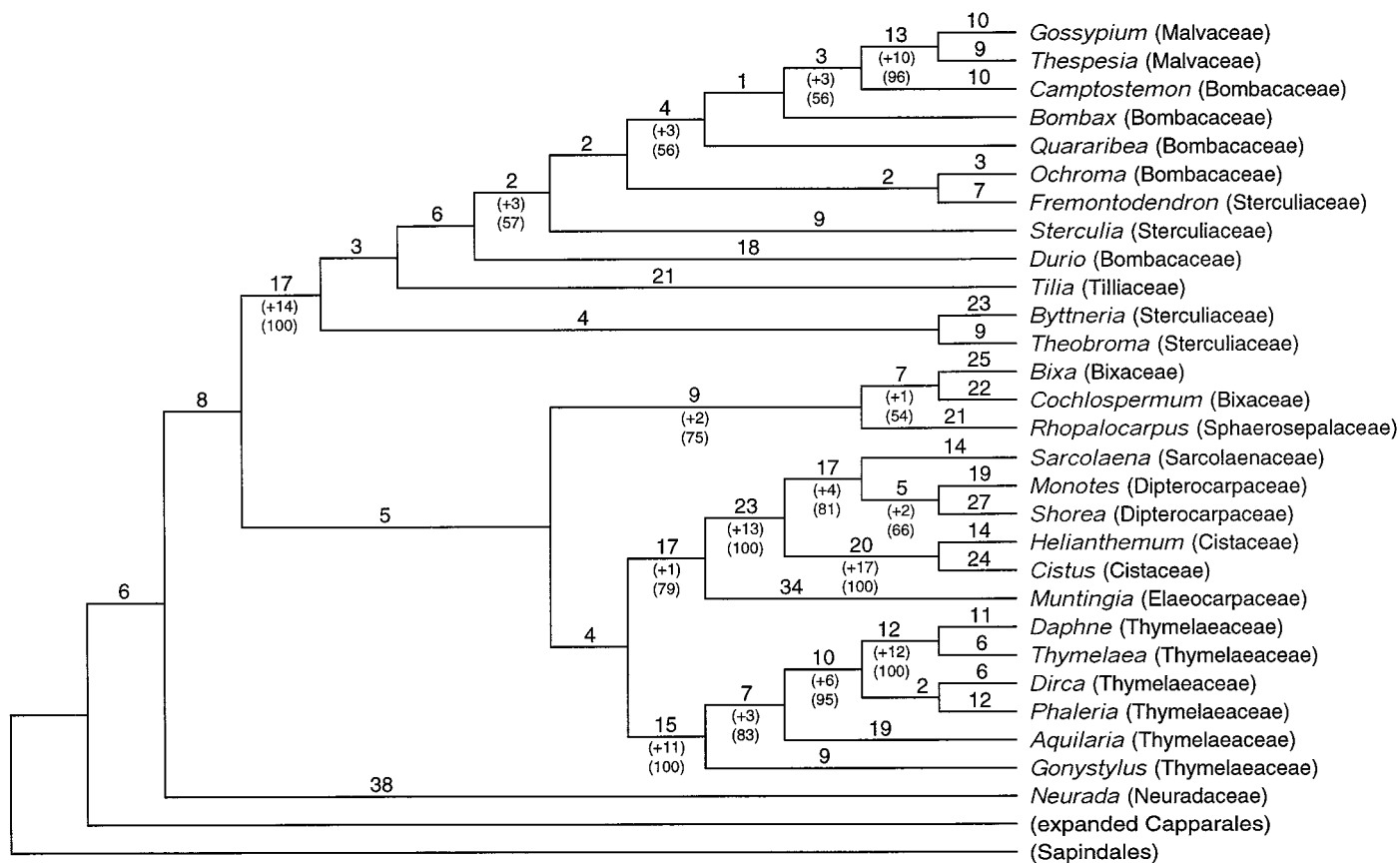


Fig. 3. Internal structure of the expanded malvalean clade. Shown is the strict consensus of the two most parsimonious trees with the set of 43 taxa used during the second step of the analysis, after 1000 unconstrained TBR/RAS searches with MULPARS. Numbers reported above the branches indicate branch lengths. Decay and bootstrap values are reported in parentheses below those branches with bootstrap values >50%. Family names follow Mabberley (1987).

between Sapindales and the remaining taxa, as suggested by the first step of the analysis, and was identical to the consensus tree from the first analysis with two exceptions: the bixalean, thymelaealean, and dipterocarpacean clades together form a weakly supported clade sister to the core malvalean clade; and *Neurada* is removed from the dipterocarpacean clade to become a sister group to all other members of the expanded Malvales.

A reanalysis of the same data matrix in which the Capparales and Sapindales were constrained to have the topology found in Rodman et al. (1993) and Gadek et al. (1996) found nine trees (not shown) of length 1218, CI = 0.740 (with autapomorphies), and RI = 0.606, distributed in a single island found in 1000 of the 1000 RAS replicates. The trees resulting from this constrained search showed a reduced resolution within the core malvalean clade and at its base, where there was an unresolved polytomy with the bixalean, thymelaealean, and dipterocarpacean clades.

DISCUSSION

Identification of the expanded Malvales—These analyses suggest the existence of a clade that we refer to as the expanded Malvales, here defined as all taxa that are more closely related to the core four families than they are to either Capparales or Sapindales. The expanded

Malvales clade comprises four major lineages (see above): (a) a core malvalean clade consisting of Bombacaceae, Malvaceae, Sterculiaceae, and Tiliaceae; (b) a bixalean clade that includes Bixaceae, Cochlospermaeae, and Sphaerosepalaceae; (c) a thymelaealean clade that includes Thymelaeaceae s.l. (i.e., including Aquilariaceae and Gonystylaceae); and (d) a dipterocarpacean clade that includes Cistaceae, Dipterocarpaceae s.l. (i.e., including Monotaceae), Sarcolaenaceae, and *Muntingia* (which has been variously placed in Elaeocarpaceae, Flacourtiaceae, or Tiliaceae). In addition, the monotypic *Neurada* (Neuradaceae or Rosaceae) falls within the expanded Malvales, but its exact placement is uncertain (see below).

Our analyses are equivocal as to the relationships among these four main clades. The first analysis, using all 125 taxa, indicated that either the bixalean or the thymelaealean clade was sister to the core malvalean clade (Fig. 2), but the second, more focused analysis placed these two lineages, together with the dipterocarpacean lineage, into a single clade that was sister to the core Malvales (Fig. 3). The reason for this disparity is apparent in the second analysis as the branch supporting the unified sister clade was weak (<50% bootstrap, decay at one additional step), as was the branch supporting the thymelaealean + dipterocarpacean clades.

To quantitatively assess the differences between the topologies resulting from the first and second analyses, we used the resulting consensus trees as reciprocal constraints. To impose the topology found by the first analysis onto the data set of 43 taxa used in the second analysis, we pruned 82 taxa from each of the 4616 shortest trees from the first analysis and then condensed the trees. This procedure yielded 26 trees. Two trees were 1214 steps long, one step longer than the shortest trees originally found by the second analysis. In these trees, either the bixalean or bixalean + thymelaealean clades were sister to the core Malvales. The other 24 trees were 1215 steps in length and showed the bixalean and/or thymelaealean clades as sister to the core Malvales. The topology found by the second analysis was imposed onto the full data set by using each of the two shortest trees from the second search as a strict constraint tree during five RAS searches of the full data set. These searches yielded 128 trees of 4736 steps, three steps longer than those originally found in the first analysis. Thus, there is a slight quantitative basis for choosing the consensus topology of the first analysis over that of the second.

The two analyses also differed qualitatively. The first analysis, using all taxa, had the potential advantage of a better sample of plesiomorphic character states for the expanded malvalean clade, whereas the second analysis offered a much more thorough analysis of the data. For want of a more compelling basis to choose one topology over the other, however, the relationship among the four main clades within the expanded Malvales should be considered as unresolved.

Morphological data are consistent with the results of our analyses of molecular data. The occurrence of an exotegmic seed coat with a palisade layer, cyclopropenoid fatty acids in seeds, complex chalazal anatomy, dilated phloem rays, and stratified phloem are potential synapomorphies for the expanded Malvales clade (Comer, 1976; Cronquist, 1981). Other characters common within, but not unique to, the expanded Malvales clade include lysigenous mucilage canals, stellate hairs, peltate scales, strong phloem fibers ("bast"), valvate sepals, ellagic acid, and the presence of an epicalyx.

The core Malvales—It is perhaps no great surprise that our analyses of *rbcL* data strongly support the monophyly of the core four families consisting of exemplars of Bombacaceae, Malvaceae, Sterculiaceae, and Tiliaceae: these families have been at the heart of every modern classification of Malvales. Judd and Manchester (1997) noted that the best contenders for morphological synapomorphies for the four families may be the type of nectaries, composed of tightly packed, multicellular hairs and normally found on the adaxial surface of the sepals (Brown, 1938), and the distinctive upright "tile" cells in wood rays (Manchester and Miller, 1978). C. Bayer (1994; Bayer and Kubitaki, 1996) recently determined that inflorescences of all members of these core families are composed of specialized modules, called "bicolor units," that also appear to provide a synapomorphy for the core Malvales.

Due to the low bootstrap and decay values generated by this data set (Fig. 3), little can be said at this time about the relationships within the core Malvales. How-

ever, two features warrant some comment. The fact that among the traditional families, only the family Malvaceae appears to be monophyletic is not surprising. Previous systematic analyses have usually placed the Malvaceae as the most "advanced" group derived from Bombacaceae, which in turn is derived from within Sterculiaceae or Tiliaceae (Edlin, 1935; Venkata Rao, 1952; Cronquist, 1981, 1988). Hence, we expected paraphyly of the latter three families, a result also obtained in the morphological cladistic analysis of Judd and Manchester (1997). Secondly, the separation of *Byttneria* and *Theobroma* (subfamily Byttnerioideae) from the rest of Sterculiaceae and their sister group position (along with some Tiliaceae) to the other core Malvales has also been found in our analyses of *ndhF* sequences (Whitlock, Alverson, and Baum, 1996; Alverson et al., unpublished data). Members of the Byttnerioideae have long been seen as distinct elements of Sterculiaceae, and the group has even been recognized at the familial rank as Byttneriaceae (Edlin, 1935; Cronquist, 1981, 1988). Further work is needed, however, to confirm and elaborate this unexpected but very plausible arrangement.

The bixalean clade—Bixaceae, Cochlospermaceae, and Sphaerosepalaceae formed a clade in all analyses (Figs. 2–3). These three families were linked with Cistaceae by Dahlgren (1983, 1989), in part because of the presence of an exotegmic seed coat with a palisade layer. Takhtajan (1969, 1997) and Thorne (1992) also grouped Bixaceae and Cochlospermaceae together with Cistaceae but excluded Sphaerosepalaceae (Table 1). Notably, Thorne (1992) associated the monotypic Malagasy family Diegodendraceae with Sphaerosepalaceae, a placement supported by morphological data reported elsewhere (Dickison, 1988; J. Horn, University of North Carolina, personal communication). A recent molecular study also indicated the existence of a clade formed by Diegodendron, Bixaceae, and Cochlospermaceae, but was equivocal on the placement of Sphaerosepalaceae (Fay et al., 1998).

The taxa comprised in the bixalean clade possess many characteristics traditionally associated with malvalean taxa, e.g., mucilage cells and canals, wedge-shaped phloem rays, stratified phloem, fibrous bark, exotegmic seed coats with palisade layers (at least in *Bixa* and *Cochlospermum*; Corner, 1976; Dahlgren, 1983), but these likely are synapomorphies for a broader clade rather than the bixalean clade alone. Cronquist (1981: 394) excluded Bixaceae s.l. (including Cochlospermaceae) from Malvales because "Neither [*Bixa* nor *Cochlospermum*] have been reported to produce the characteristic cyclopropenoid fatty acids of the Malvales." However, to our knowledge, neither family has been examined for the presence of these chemical compounds. The homology of the discoid staminal nectaries of *Bixa* and *Cochlospermum* (as well as in Capparaeae, Cistaceae, Sarcocaulaceae, and Thymelaeaceae; Brown, 1938) with the nectariferous surfaces inside the sepals of core Malvales also warrants further attention.

The thymelaealean clade—Aquilariaceae, Gonystylaceae, and Thymelaeaceae have been grouped together by numerous authors and are sometimes combined in a sin-

gle family, Thymelaeaceae (e.g., Mabberley, 1997). Dahlgren and Thorne (1984) and Conti, Litt, and Sytsma (1996) discussed the placement of this lineage, which has been often associated with Myrtales because of the occasional presence of internal phloem and vested pits. However, neither character unambiguously groups Thymelaeaceae s.l. with Myrtales, since vested pits are also common in the dipterocarpacean clade, and both features are absent from Gonystylaceae. The presence of cyclopropenoid fatty acids (Vickery, 1980, 1981) and exotegmic seed coats with palisade layers (Corner, 1976; Dahlgren, 1983), mucilage cells, tough phloem fibers (Dahlgren and Thorne, 1984), broad phloem rays (Cronquist, 1981), and stratified phloem (at least in *Dirca*; Zahur, 1959) make for a comfortable placement of the Thymelaeaceae clade within the expanded Malvales.

The *rbcL* trees here, and in Conti, Litt, and Sytsma (1996), suggest that *Gonystylus* is sister to the rest of this clade, as first suggested by Dahlgren (1983: 129): "If [subfamily Gonystyloideae] can be convincingly shown to be Thymelaeaceae [then it] probably represents a primitive group, and the internal phloem and vested pits would have evolved within the family . . ." Further study is needed to identify morphological synapomorphies that might support the monophyly of the thymelaeacean clade.

The dipterocarpacean clade—This clade consists of representatives of Cistaceae, Dipterocarpaceae, and Sarcolaenaceae. These three families have been placed singly or collectively in Malvales by Dahlgren (1983, 1989) and Thorne (1992). Ashton (1982) also discussed the apparently close relationship between Dipterocarpaceae and Sarcolaenaceae. Traits linking these families with core Malvales include the presence of cyclopropenoid fatty acids (in several genera of Sarcolaenaceae; Gaydou and Ramanolena, 1983), exotegmic seed coats with a palisade layer (in Cistaceae and Dipterocarpaceae; Corner, 1976), mucilage cells or canals and stratified phloem (with uncertain occurrence in Cistaceae but known from both other families, including the dipterocarp subfamily Pakaraimaeoideae; de Zeeuw, 1977), and ellagic acid (with uncertain status in Sarcolaenaceae but, likewise, reported from Pakaraimaeoideae by Giannasi and Niklas, 1977).

The association of the members of this clade with one another is consistent with the presence of vested pits in all three families (including *Pakaraimaea*; de Zeeuw, 1977). Interestingly, de Zeeuw noted the presence of internal phloem in *Pakaraimaea*, a trait also found in Myrtaceae and Thymelaeaceae. Flavonoid spectra are reportedly consistent with a close association of these families as well (Gornall, Bohm, and Dahlgren, 1979; Thorne, 1981; Young, 1981).

Muntingia—The neotropical genus *Muntingia*, which has been historically placed in the Elaeocarpaceae, Flacourtiaceae, or Tiliaceae (Cronquist, 1981; Benn and Lemke, 1992), falls at the base of the dipterocarpacean clade. The fact that it falls within the expanded Malvales is not surprising, given that this monotypic genus has stellate hairs, mucilage cells, and wedge-shaped secondary phloem rays (Zahur, 1959). The seed coat is exotegmic but apparently without a palisade layer (Corner,

1976), and vested pits and stratified phloem are lacking (Metcalf and Chalk, 1950; Zahur, 1959).

In corroboration of the molecular analysis here, Metcalfe and Chalk (1950: 265) note that, "*Dicraspidia* and *Muntingia* differ considerably from the other genera [of Elaeocarpaceae studied] in their wood anatomy. Except for these two genera, which have many points in common with Tiliaceae . . . wood anatomy supports the establishment of the Elaeocarpaceae as a separate family." *Dicraspidia* and *Neotessmannia*, genera with comparably peripatetic taxonomic histories, share many morphological and anatomical traits with *Muntingia*. Investigation of their molecular, morphological, and chemical traits may help to clarify the placement of *Muntingia*. Meanwhile, Bayer, Chase, and Fay (1998) recognize Muntingiaceae as a separate family, which includes *Dicraspidia* and *Muntingia*.

Neurada—The placement of *Neurada* on morphological and anatomical grounds has been somewhat controversial. All recent authors have included this and two closely associated genera (*Neuradopsis* and *Grielum*) in the Rosaceae or as a closely related segregate family, the Neuradaceae. Ronse Decraene and Smets (1995) also "confidently suggest" a relationship with the Rosaceae based on floral development. However, a recent review of the systematic position of *Neurada* by Huber (1993) provides convincing evidence that *Neurada* exhibits two potential synapomorphies for the expanded Malvales: an exotegmic seed coat with a palisade layer and the presence of cyclopropenoid fatty acids in seeds. *Neurada* also shares other characteristics common in, but not unique to, malvalean taxa, including valvate sepals, lysigenous mucilage canals, stellate hairs, and an epicalyx (Solereder, 1908; Murbeck, 1916, 1941; Willis, 1973; Huber, 1993).

The molecular data presented here argue for placement of *Neurada* at or near the base of the expanded Malvales (Figs. 2–3). It takes six additional steps to force the *Neurada* sequence out of the expanded Malvales (using a backbone constraint tree and three inverse RAS searches), and even then it appeared at the base of the combined Sapindales + Capparales + expanded Malvales rather than in the vicinity of Rosaceae. Three additional inverse RAS searches indicate that 12 additional steps are needed to force *Neurada* outside the combined Myrtales + Sapindales + Capparales + expanded Malvales clade. Thus, *rbcL* supports the idea that the true affinities of *Neurada* are with the Malvales rather than Rosales.

Families excluded from the expanded malvalean clade—With the possible exception of the Elaeocarpaceae, none of the rejected families (see Results) should prove particularly controversial because of the relatively weak evidence linking each to Malvales. Of these excluded taxa, the most notable are the five exemplars for Elaeocarpaceae, since they have been frequently and consistently associated with the core malvalean families.

Cronquist (1988: 342) noted that "The Elaeocarpaceae stand somewhat apart from the rest of the [order Malvales], but even so the relationship is so close that they have often been included in the Tiliaceae." Yet, Cronquist linked Elaeocarpaceae with Malvales on the basis

of a single shared morphological character: valvate sepals versus the (mostly) imbricate sepals of the putative thealean ancestors. He also considered Elaeocarpaceae to be the “most archaic” family in the order because of the absence of virtually all of the diagnostic characters shared by the core malvacean families. Other modern authors have agreed with Cronquist’s placement of the Elaeocarpaceae, with the notable exception of Dahlgren (1989), who moved the Elaeocarpaceae from Malvales to Rhizophorales but provided no explanation for this change. The molecular data examined here unequivocally support a placement of Elaeocarpaceae (*Aceratium*, *Elaeocarpus*, *Crinodendron*, *Sloanea*, and *Vallea*, but not *Muntingia*) at a considerable distance from the expanded Malvales, close to *Ceratopetalum* (Cunoniaceae).

Molecular results and changes in taxonomic nomenclature—Before this new phylogenetic information on Malvales is formalized taxonomically, our results should be further corroborated by other morphological and molecular data. Judd and Manchester (1997) assembled an extensive morphological data matrix for the core malvacean families that can serve as a starting point for further studies. Such an analysis might provide further resolution within the expanded Malvales and might serve to reinforce (or contradict) some of the unanticipated features of our analyses. Also, we hope that the circumscription and phylogenetic structure of the expanded Malvales suggested by *rbcL* will serve to focus attention on some interesting characters that have not yet been studied in all the taxa. For example, the presence of cyclopropenoid fatty acids, until recently thought to serve as a synapomorphy for the core four families (Cronquist, 1981, 1988), is now known to occur commonly throughout the expanded Malvales. This underscores the need for a comprehensive and thorough review of the occurrence of these compounds throughout this part of the Rosidae. Similarly, other characters often used to diagnose the core families (e.g., valvate sepals, lysigenous mucilage canals, stellate hairs, bast fibers, and epicalyces) are scattered throughout the malvacean, capparalean, and sapindalean clades, raising questions as to their path of evolution. Although by no means offering a definitive phylogeny of the Malvales, we hope that the *rbcL* data reported here will catalyze further phylogenetic studies of the order and its close relatives.

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APPENDIX 1. The 125 species included in the study, listed alphabetically by family names, which follow Mabberley (1987). Also given are memberships of these genera in trees found by Chase et al. (1993), GenBank numbers, literature citations for previously published sequences, and source and voucher information for unpublished sequences.

Species	Family ^a	Chase 93 ^b	GenBank	Citation, or source and voucher
<i>Acer saccharum</i> L.	Aceraceae	R2	L01881	Albert, Williams, and Chase, 1992
<i>Aextoxicon punctatum</i> Ruiz & Pavon	Aextoxicaceae	—	X83986	V. Savolainen; voucher unknown
<i>Amaranthus tricolor</i> L.	Amaranthaceae	R3 (Ca)	X53980	Rettig, Wilson, and Manhart, 1992
<i>Schinus molle</i> L.	Anacardiaceae	R2	U39270	Gadek et al., 1996
<i>Ilex vomitoria</i> Aiton	Aquifoliaceae	A2	M88583	Chase et al., 1993
<i>Achillea millefolium</i> L.	Asteraceae	A2	L13641	Kim et al., 1992
<i>Impatiens capensis</i> Meerb.	Balsaminaceae	A3	—	Chase et al., 1993
<i>Barbeya oleoides</i> Schweinf.	Barbeyaceae	Ca (R3)	—	M. Chase; <i>Collenette 1/93</i> , K
<i>Tabebuia heterophylla</i> (DC.) Britton	Bignoniaceae	—	L36451	Olmstead and Reeves, 1995
<i>Bixa orellana</i> L.	Bixaceae	—	AF022128	Alverson/Karol; <i>Alverson s.n.</i> , WIS
<i>Cochlospermum vitifolium</i> L.	Bixaceae	—	AF022129	Alverson/Karol; Fairchild Bot. Gard. FG X-19-3
<i>Bombax buonopozense</i> P. Beauv.	Bombacaceae	R2	AF022118	Alverson/Karol; <i>Alverson s.n.</i> , WIS
<i>Camptostemon schultzii</i> Mast.	Bombacaceae	—	AF022120	Alverson/Karol; <i>Dunlap s.n.</i> , WIS
<i>Durio zibethinus</i> Murr.	Bombacaceae	—	AF022119	Alverson/Karol; <i>Alverson 2180</i> , WIS
<i>Ochroma pyramidale</i> (Cav. ex Lam.) Urb.	Bombacaceae	—	AF022122	Alverson/Karol; <i>Alverson & Rubio 2246</i> , WIS
<i>Quararibea gomeziana</i> W.S. Alverson	Bombacaceae	—	AF022121	Alverson/Karol; <i>Alverson 2136</i> , WIS
<i>Brassica oleracea</i> L.	Brassicaceae	R2	M88342	Rodman et al., 1993
<i>Bretschneidera sinensis</i> Hemsl.	Bretschneideraceae	R2	M95753	Rodman et al., 1993
<i>Bursera augustis</i> Britton	Burseraceae	R2	L01890	Albert, Williams, and Chase, 1992
<i>Humulus lupulus</i> L.	Cannabidaceae	— (R1)	U02729	Chase et al., 1993
<i>Capparis hastata</i> Jacq.	Capparidaceae	R2	M95754	Rodman et al., 1993
<i>Viburnum acerifolium</i> L.	Caprifoliaceae	A2	L01959	Olmstead et al., 1993
<i>Carica papaya</i> L.	Caricaceae	R2	M95671	Rodman et al., 1993
<i>Cecropia palmata</i> Willd.	Cecropiaceae	—	—	Conti and Wiegrefe; Fairchild Bot. Gard. 3181
<i>Chrysobalanus icacao</i> L.	Chrysobalanaceae	R1	L11178	Morgan and Soltis, 1993
<i>Cistus revolinii</i> Coste & Soulie	Cistaceae	—	—	M. Chase; <i>Chase 524</i> , K
<i>Helianthemum grandiflorum</i> DC.	Cistaceae	—	—	M. Chase; <i>Chase 525</i> , K
<i>Quisqualis indica</i> L.	Combretaceae	R2 (R1)	L01948	Albert, Williams, and Chase, 1992
<i>Cornus canadensis</i> L.	Cornaceae	A4	L11213	Qiu et al., 1993
<i>Crossosoma californicum</i> Nutt.	Crossosomataceae	R2	L11179	Morgan and Soltis, 1993
<i>Alzatea verticillata</i> Ruiz & Pavon	Crypterionaceae	—	U26316	Conti, Litt, and Sytsma, 1996
<i>Ceratopetalum gummiferum</i> Small	Cunoniaceae	R1	L01895	Soltis et al., 1990
<i>Daphniphyllum</i> sp.	Daphniphyllaceae	R4 (R3)	L01901	Albert, Williams, and Chase, 1992
<i>Datisca cannabina</i> L.	Datisceae	R1	L21939	Chase et al., 1993
<i>Dichapetalum crassifolium</i> Chodat	Dichapetalaceae	—	X69733	Savolainen et al., 1994
<i>Dillenia indica</i> L.	Dilleniaceae	R3 (A5)	L01903	Albert, Williams, and Chase, 1992
<i>Monotes</i> sp.	Dipterocarpaceae	—	—	S. Dayanandan; <i>Harter 3134</i> , MO
<i>Shorea zeylanica</i> (Thwaites) Ashton	Dipterocarpaceae	— (R2)	—	Chase et al., 1993
<i>Diospyros virginiana</i> L.	Ebenaceae	A3	L12613	Kron and Chase, 1993
<i>Elaeagnus angustifolia</i> L.	Elaeagnaceae	—	U17038	Morgan and Soltis, 1993
<i>Aceratium ferrugineum</i> C.T. White	Elaeocarpaceae	—	L28947	P.G. Martin and J. Dowd; voucher unknown
<i>Crinodendron hookerianum</i> Gay	Elaeocarpaceae	—	—	M. Chase; <i>Chase 909</i> , K
<i>Elaeocarpus grandis</i> F. Muell.	Elaeocarpaceae	—	L28951	P.G. Martin and J. Dowd; voucher unknown
<i>Muntingia calabura</i> L.	Elaeocarpaceae ^c	—	—	M. Chase; <i>Chase 346</i> , NCU
<i>Sloanea latifolia</i> (Rich.) Schumann	Elaeocarpaceae	—	AF022131	Alverson/Karol; <i>Alverson 2211</i> , WIS
<i>Vallea stipularis</i> L.	Elaeocarpaceae	—	—	M. Chase; <i>Chase 654</i> , K
<i>Erica australis</i> L.	Ericaceae	A3	L12617	Kron and Chase, 1993
<i>Acalypha rhomboidea</i> Raf.	Euphorbiaceae	—	U00435	Gunter, Kochert, and Giannasi, 1994
<i>Croton alabamensis</i> Chapman	Euphorbiaceae	—	—	K. Wurdack; <i>Wurdack s.n.</i> , NCU
<i>Drypetes roxburghii</i> (Wall.) Hurus.	Euphorbiaceae	R1	M95757	Rodman et al., 1993
<i>Euphorbia polychroma</i> A. Kerner	Euphorbiaceae	R1	L13185	Chase et al., 1993
<i>Phyllanthus epiphyllanthus</i> L.	Euphorbiaceae	—	—	K. Wurdack; <i>Wurdack s.n.</i> , NCU
<i>Tetracoccus dioicus</i> Parry	Euphorbiaceae	—	—	K. Wurdack; <i>Levin 2202</i> , SD
<i>Pisum sativum</i> L.	Fabaceae	R1	X03853	Zurawski, Whitfield, and Bottomley, 1986
<i>Nothofagus balansae</i> (Baill.) Steenis	Fagaceae	— (R1)	L13344	Martin and Dowd, 1993
<i>Plagiopteron suaveolens</i> Griff.	Flacourtiaceae	—	—	M. Chase; <i>Chase 1335</i> , K
<i>Geranium cinereum</i> Cav.	Geraniaceae	R2	L14695	Price and Palmer, 1993
<i>Ribes aureum</i> Pursh	Grossulariaceae	R4 (R3)	L11204	Morgan and Soltis, 1993
<i>Hamamelis mollis</i> Oliv.	Hamamelidaceae	R4 (R3)	L01922	Albert, Williams, and Chase, 1992
<i>Afrostryax</i> sp.	Huaceae	—	—	M. Chase; <i>Cheek 5007</i> , K
<i>Hua gabonii</i> Pierre ex De Wilde	Huaceae	—	—	M. Chase; <i>Weiringa 3177</i> , WAG
<i>Hydrangea macrophylla</i> Torr.	Hydrangeaceae	A4	L11187	Morgan and Soltis, 1993
<i>Krameria lanceolata</i> Torr.	Krameriaceae	R1	—	Chase et al., 1993
<i>Asteranthos brasiliensis</i> Desf.	Lecythidaceae	—	AF022133	Alverson/Karol; <i>Mori 21856</i> , NY
<i>Couroupita guianensis</i> Aubl.	Lecythidaceae	—	AF022134	Alverson/Karol; <i>Alverson s.n.</i> , WIS
<i>Eschweilera odora</i> (Poepp.) Miers	Lecythidaceae	—	AF022135	Alverson/Karol; <i>de Granville 5086</i> , CAY

APPENDIX I. Continued.

Species	Family ^a	Chase 93 ^b	GenBank	Citation, or source and voucher
<i>Limnanthes douglasii</i> R. Br.	Limnanthaceae	R2	L14700	Rodman et al., 1993
<i>Lythrum hyssopifolia</i> L.	Lythraceae	R2 (R1)	L10218	Conti, Fischbach, and Sytsma, 1993
<i>Byrsonima crassifolia</i> (L.) Kunth.	Malpighiaceae	R1	L01892	Albert, Williams, and Chase, 1992
<i>Gossypium hirsutum</i> L.	Malvaceae	R2	M77700	Giannasi et al., 1991
<i>Thespesia populnea</i> (L.) Sol. ex Correa	Malvaceae	— (R2)	L01961	Albert, Williams, and Chase, 1992
<i>Rhexia virginiana</i> L.	Melastomataceae	—	U26334	Conti, Litt, and Sytsma, 1996
<i>Guarea glabra</i> Vahl.	Meliaceae	—	U39085	Gadek et al., 1996
<i>Morus alba</i> L.	Moraceae	R1	L01933	Soltis et al., 1990
<i>Myrica cerifera</i> L.	Myricaceae	R1	L01934	Albert, Williams, and Chase, 1992
<i>Baeckea ramosissima</i> A. Cunn.	Myrtaceae	—	U26319	Conti, Litt, and Sytsma, 1996
<i>Heteropyxis natalensis</i> Harv.	Myrtaceae	— (R1)	U26326	Conti, Litt, and Sytsma, 1996
<i>Neurada procumbens</i> L.	Neuradaceae	—	U06814	Morgan, Soltis, and Robertson, 1994
<i>Ochna serrulata</i> Walp.	Ochnaceae	R1	Z75273	Chase et al., 1993
<i>Ludwigia peruviana</i> (L.) Hara	Onagraceae	R2 (R1)	L10221	Conti, Fischbach, and Sytsma, 1993
<i>Hypseocharis</i> sp.	Oxalidaceae	— (R2)	L14699	Price and Palmer, 1993
<i>Oxalis dillenii</i> Jacq.	Oxalidaceae	R1	L01938	Albert, Williams, and Chase, 1992
<i>Microdesmis puberula</i> Hook. f.	Pandaceae	—	—	M. Chase; <i>Cheek</i> 5986, K
<i>Papaver orientale</i> L.	Papaveraceae	Ra	L08764	Chase et al., 1993
<i>Passiflora quadrangularis</i> L.	Passifloraceae	R1	L01940	Albert, Williams, and Chase, 1992
<i>Stegnosperma halimifolium</i> Benth.	Phytolaccaceae s.l.	R3 (Ca)	M62571	Rettig, Wilson, and Manhart, 1992
<i>Polygala cruciata</i> L.	Polygalaceae	R1	L01945	Albert, Williams, and Chase, 1992
<i>Plumbago capensis</i> Thunb.	Plumbaginaceae	R3 (Ca)	M77702 ^d	Giannasi et al., 1991
<i>Caltha palustris</i> L.	Ranunculaceae	Ra	L02431	Albert, Williams, and Chase, 1992
<i>Rhamnus catharticus</i> L.	Rhamnaceae	R1	L13189	Chase et al., 1993
<i>Rosa woodsii</i> Lindl.	Rosaceae	—	U06824	Soltis et al., 1993
<i>Rubia tinctorum</i> L.	Rubiaceae	—	X81104	Manen and Natali, 1995
<i>Ruta graveolens</i> L.	Rutaceae	—	U39281	Gadek et al., 1996
<i>Cupaniopsis anacardioides</i> Raklk.	Sapindaceae	R2	L13182	Chase et al., 1993
<i>Sarcolaena oblongifolia</i> F. Gérard	Sarcolaenaceae	—	U26337	Conti, Litt, and Sytsma, 1996
<i>Francoa sonchifolia</i> Cav.	Saxifragaceae	R2	L11184	Soltis et al., 1990
<i>Penthorum sedoides</i> L.	Saxifragaceae	R4 (R3)	L11197	Soltis et al., 1990
<i>Saxifraga integrifolia</i> Hook.	Saxifragaceae	R4 (R3)	L01953	Albert, Williams, and Chase, 1992
<i>Oubanguia alata</i> Baker f.	Scytotopetalaceae	—	—	M. Chase; <i>Gereau et al.</i> 5202, MO
<i>Ailanthus altissima</i> (Miller) Swingle	Simaroubaceae	R2	L12566	Gadek et al., 1992
<i>Kirkia wilmsii</i> Engl.	Simaroubaceae s.l.	—	—	Gadek et al., 1996
<i>Simmondsia chinensis</i> (Link.) S.K. Sch.	Simmondsiaceae	—	—	S. Hoot; <i>Hoot s.n.</i> , F
<i>Lycopersicon esculentum</i> Mill.	Solanaceae	A1	L14403	Olmstead et al., 1993
<i>Rhopalocarpus lucidus</i> Bojer	Sphaerosepalaceae ^e	—	AF022130	Alverson/Karol; <i>Miller and Schatz</i> 6275, MO
<i>Byttneria aculeata</i> (Jacq.) Jacq.	Sterculiaceae	—	AF022123	Alverson/Karol; <i>Alverson s.n.</i> , WIS
<i>Fremontodendron mexicanum</i> Davids.	Sterculiaceae	—	AF022124	Alverson/Karol; <i>Thorne</i> 54717, RSA
<i>Sterculia tragacantha</i> Lindl.	Sterculiaceae	—	AF022126	Alverson/Karol; FBG FG X.12-17
<i>Theobroma cacao</i> L.	Sterculiaceae	— (R2)	AF022125	Alverson/Karol; <i>Solheim BUF296</i> , WIS
<i>Camelia japonica</i> L.	Theaceae	A3	L12602	Kron and Chase, 1993
<i>Daphne mezereum</i> L.	Thymelaeaceae	—	AF022132	Conti/Karol; <i>Conti and Giordano</i> 46, WIS
<i>Aquilaria beccariana</i> Van Tiegh.	Thymelaeaceae	—	—	M. Chase; <i>Chase</i> 1380, K
<i>Dirca palustris</i> L.	Thymelaeaceae	—	U26322	Conti, Litt, and Sytsma, 1996
<i>Gonystylus macrophyllus</i> (Miq.) A. Shaw	Thymelaeaceae s.l.	—	—	M. Chase; <i>Chase</i> 1382, K
<i>Phaleria chermisideana</i> (Bailley) C. White	Thymelaeaceae	—	U26332	Conti, Litt, and Sytsma, 1996
<i>Thymelaea hirsuta</i> Endl.	Thymelaeaceae	—	—	M. Chase; <i>Chase</i> 1883, K
<i>Tilia americana</i> L.	Tiliaceae	— (R2)	AF022127	Alverson/Karol; <i>Alverson s.n.</i> , WIS
<i>Trochodendron aralioides</i> Sieb. & Zucc.	Trochodendraceae	H2	L01958	Albert, Williams, and Chase, 1992
<i>Tropaeolum majus</i> L.	Tropaeolaceae	R2	L14706	Price and Palmer, 1993
<i>Celtis yunnanensis</i> C.K. Schneid.	Ulmaceae	R1	L12638	Qiu et al., 1993
<i>Ulmus alata</i> Michx.	Ulmaceae	—	U00441	Gunter, Kochert, and Giannasi, 1994
<i>Boehmeria nivea</i> (L.) Gaudich.	Urticaceae	— (R1)	—	Chase et al., 1993
<i>Rinorea crenata</i> S.F. Blake	Violaceae	—	—	S. Hodges; <i>Ballard</i> 94-006, WIS
<i>Phoradendron serotinum</i> (Raf.) M.C. Johnst.	Viscaceae	A1/Ca	L11199	Morgan and Soltis, 1993
<i>Vochysia hondurensis</i> Sprague	Vochysiaceae	—	U26340	Conti, Litt, and Sytsma, 1996
<i>Nitraria retusa</i> (Forsskal) Asch.	Zygophyllaceae s.l.	—	U39278	Gadek et al., 1996

^a With the exception of *Muntingia* and *Rhopalocarpus* (see below), all family assignments are the same in Mabberley (1987) and Mabberley (1997).^b Clades occupied on trees found by Chase et al. (1993) are indicated by the following abbreviations: A1, A2, A3, A4 = asterid clades I, II, III, and IV; Ca = caryophyllid clade; H2 = hamamelid clade II; Ra = ranunculid clade; and R1, R2, R3, R4 = rosoid clades I, II, III, and IV. Citation of a second clade in parentheses indicates the clade membership of the genus in Search II of Chase et al. (1993) only when different from that of Search I.^c *Muntingia* was later moved to Tiliaceae by Mabberley (1997).^d Accession numbers M77701 (listed in GenBank as *Plumbago capensis*) and M77702 (listed as *Rheum × cultorum*) are reversed in GenBank, as evidenced by additional sequences for both genera (Lledó et al., unpublished, fide M. Chase).^e *Rhopalocarpus* was later moved to Ochnaceae (Diegodendraceae) by Mabberley (1997).