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Circumscription of Malvaceae (Malvales) as determined by a preliminary cladistic analysis of morphological, anatomical, palynological, and chemical characters

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Judd, W. S. (Department of Botany, 220 Bartram Hall, University of Florida, Gainesville, FL 32611-8526, U.S.A.) & S. R. Manchester (Department of Natural Sciences, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, U.S.A.). Circumscription of Malvaceae (Malvales) as determined by a preliminary cladistic analysis of morphological, anatomical, palynological, and chemical characters. *Brittonia* 49: 384–405. 1997.—We report a phylogenetic analysis of “core” Malvales (Tiliaceae, Sterculiaceae, Bombacaceae, and Malvaceae) based on morphological, anatomical, palynological, and chemical features. The results of the analyses lead to the conclusion that Tiliaceae, Sterculiaceae, and Bombacaceae, as variously delimited, are paraphyletic; only the Malvaceae are likely monophyletic. The genera of “core” Malvales form a well-defined clade. Genera of “Tiliaceae” constitute the basal complex within “core” Malvales. The “Sterculiaceae” (most genera) + “Bombacaceae” + Malvaceae form a clade on the basis of a monadelphous androecium; “Bombacaceae” + Malvaceae also form a clade, which is diagnosable on the basis of monolocate anthers. It is clear that the traditional classification, with its arbitrarily delimited evolutionary grades, is unsatisfactory, especially if one seeks to reflect phylogeny accurately. Thus, Malvaceae is redefined to refer to the most recent common ancestor of plants previously considered to be “Tiliaceae,” “Sterculiaceae,” “Bombacaceae,” and Malvaceae, and all of the descendants of that ancestor. This broadly circumscribed Malvaceae can be diagnosed by several presumed synapomorphies, but we draw special attention to the unusual floral nectaries that are composed of densely packed, multicellular, glandular hairs on the sepals (or less commonly on the petals or androgynophore).

Key words: Tiliaceae, Sterculiaceae, Bombacaceae, Malvaceae, phylogeny, cladistics.

It has long been apparent to systematists that the delimitation of families within the “core” Malvales—i.e., Tiliaceae, Sterculiaceae, Bombacaceae, and Malvaceae (Cronquist, 1981; or suborder Malvaceae, see Schultze-Motel, 1964)—is problematic (Brizicky, 1965; Chang & Miao, 1989; Cronquist, 1981; Dorr, 1990; Edlin, 1935; Hutchinson, 1967; Judd et al., 1994; Manchester, 1992; Rendle, 1925; Zomlefer, 1994). Certain genera have been transferred back and forth between these families (see

Brizicky, 1965, 1966; Edlin, 1935; Erdtman, 1952; Fryxell, 1968; Kelman, 1991; Nilsson & Robyns, 1986; Robyns et al., 1977), and Edlin (1935: 122) argued “that the so-called families of the [core] Malvales, are not clear-cut families, as the term is generally applied, but are only representative of vague evolutionary trends.” Nearly all systematists have recognized the close relationship of these four families, placing them within a single order; only Hutchinson (1926, 1973) differed, placing Tiliaceae,

Sterculiaceae, and Bombacaceae in the Tiliales, and restricting the Malvales to Malvaceae alone. Thus, although the exact composition of Malvales has varied widely (see Cronquist, 1981, 1988; G. Dahlgren, 1989; R. Dahlgren, 1983; Edlin, 1935; Schultze-Motel, 1964; Takhtajan, 1980, 1987; Thorne, 1983, 1992), it has always included the core complex, composed of Tiliaceae, Sterculiaceae, Bombacaceae, and Malvaceae.

The core Malvales is a large group, containing ca. 2330 species of trees to herbs (Thorne, 1992), and is mainly tropical; but Malvaceae contains numerous temperate species. Most modern systematists hold the traditional view that these four families can be arranged from the most primitive to the most advanced, i.e., from Tiliaceae to Sterculiaceae to Bombacaceae to Malvaceae (Cronquist, 1981, 1988; Edlin, 1935; van Heel, 1966; Takhtajan, 1980, 1987). However, some—e.g., Warming (1895) and Rao (1952)—have considered the Sterculiaceae to be the most primitive. Questions of monophyly of core Malvales and of its included families have rarely been considered explicitly. The traditional taxonomic viewpoint suggests that these four families constitute a monophyletic group because they share numerous distinctive features, some of which may be synapomorphies. However, it also suggests that, of these four core families, only the Malvaceae are likely to be monophyletic. Bombacaceae usually have been allied with Malvaceae (see Bentham & Hooker, 1862/1867; Cronquist, 1981, 1988; Nilsson & Robyns, 1986; Rendle, 1925; Schumann, 1895; Thorne, 1992), although Hutchinson (1926, 1973) considered this family to be closer to Tiliaceae and Sterculiaceae. Thus, the traditional taxonomic scheme also supports the hypothesis that Malvaceae + Bombacaceae should constitute a monophyletic group.

In this preliminary cladistic analysis, our major goal was to clarify the circumscription of core Malvales, and especially to test the monophyly of Tiliaceae, Sterculiaceae, Bombacaceae, and Malvaceae. Beginning with the widely accepted view that these four families form a taxonomic progression—i.e., Tiliaceae > Sterculi-

aceae > Bombacaceae > Malvaceae—in which the familial boundaries are somewhat arbitrary (see Cronquist, 1981; Edlin, 1935; Judd et al., 1994; Zomlefer, 1994), we hypothesize that Tiliaceae, Sterculiaceae, and Bombacaceae are paraphyletic and that only Malvaceae is monophyletic. Furthermore, we predict that the clade Bombacaceae + Malvaceae is monophyletic, as is the clade Sterculiaceae + Bombacaceae + Malvaceae. In this paper we explicitly test these hypotheses through preliminary cladistic analyses of selected members of these families (and a few other presumably related genera). Additionally, we suggest that the phylogenetic structure within core Malvales supports the general conclusions of Judd et al. (1994)—namely, that within particular clades, a tropical, paraphyletic family (or families) often has been arbitrarily distinguished from a closely related and more temperate, monophyletic family (or families) as a result of traditional (i.e., evolutionary) taxonomic practice and a north-temperate bias.

This paper presents the results of a preliminary cladistic analysis of core Malvales. We make several taxonomic recommendations based on these results. Until the phylogenetic relationships within core Malvales are clarified, it is not possible to address other significant macroevolutionary, historical, or taxonomic questions.

Materials and Methods

Preliminary analyses of the phylogenetic relationships of 46 selected taxa of core Malvales, along with two representatives of Dipterocarpaceae and one of Elaeocarpaceae, were conducted using the Mhennig* algorithm (with bb*, extended branch-swapping) of Hennig86, version 1.5 (Farris, 1988), and the heuristic algorithm (with branch swapping by tree-bisection-reconnection and MULPARS applied on 100 random addition replicates, and with 100 random addition replicates applied [without MULPARS]) of PAUP, version 3.1.1 (Swofford, 1991). Clade robustness was assessed by decay analysis using AutoDecay 3.0 (Eriksson & Wikström, 1995) and by

reference to the number of synapomorphies supporting particular clades. MacClade, version 3.0 (Maddison & Maddison, 1992) was used to explore alternative tree topologies. Genera were used as terminal units, and we were careful to include sufficient taxa in the analysis to test the propositions that Tiliaceae, Sterculiaceae, and Bombacaceae are paraphyletic and that Malvaceae are monophyletic. Thus, a limited number of exemplar genera from these families was used (Table I). We tried to include at least one representative genus from each of the commonly recognized major infrafamilial taxa. Taxonomic groups suspected of being paraphyletic were sampled more intensively than those for which we had preliminary evidence of monophyly—thus our extensive sampling of Tiliaceae and Sterculiaceae and less complete sampling of Malvaceae. For example, molecular evidence strongly supports the monophyly of the very large tribe Malveae (La Duke & Doebley, 1995); therefore, detailed sampling of this group was deemed less important. These analyses should not be construed as detailed and definitive studies of core Malvales. Rather, we hope that this work will encourage more-detailed phylogenetic investigations of Malvales (including more taxa and molecular as well as additional morphological characters). The cladograms presented here should be considered tentative because only selected genera were included. They are, nevertheless, useful in providing a concrete starting point for future investigations.

We concentrated on morphological, anatomical, palynological, and chemical characters (see Tables II and III); DNA-based results, however, are discussed when available. Most of the 52 characters are based on the authors' observations of herbarium material (see Appendix) and, where possible, living material (especially plantings at Fairchild Tropical Garden), supplemented by various floras and revisionary studies (see Appendix). Some character scorings were taken from the literature; these are indicated in Table III, and the pertinent literature is referenced. The total variability of each genus was considered, and taxa varying in particular characters (indicated as

"variable" in Table III) were scored as "missing" in the Hennig86 analysis and polymorphic in the PAUP analyses, or were scored with the hypothesized ancestral state for that character (see Table III). Some workers have suggested that hypothesized ancestral state codings introduce an unacceptable degree of subjectivity. Thus, an additional analysis was conducted in which all variable characters were coded as polymorphic (see character codings in bold, Table III). Character states for two multistate characters were ordered in the initial analyses (see Tables II & III); all multistate characters were considered to be unordered in the additional analysis.

Elaeocarpaceae, as represented by *Elaeocarpus* and *Sloanea*, were employed as the outgroup (see Table III), and trees were rooted along the branch connecting the outgroup to the ingroup taxa. This rooting resulted in the character polarizations discussed herein (see Maddison et al., 1984; Stevens, 1980; Wheeler, 1981; Wiley, 1981). Elaeocarpaceae were chosen because the core Malvales are most often considered to be related to this family (Brizicky, 1965; Cronquist, 1968, 1981, 1988) or derived from Elaeocarpaceae-like or Violalean ancestors (Cronquist, 1968, 1988; Lawrence, 1951; Schumann, 1895; Takhtajan, 1969, 1980; Weibel, 1945). The family certainly shares several characters with members of core Malvales that are likely synapomorphic, e.g., stipulate leaves, frequent presence of a siphonostelic petiolar vascular system, and an androecium supplied by ten trunk bundles (although the stamens are numerous), but there are questions concerning the universality of these states. In addition, some members of Elaeocarpaceae have mucilage cells in the epidermis of their leaves. The group is phenotypically similar to Tiliaceae and often has been included in this family (Baillon, 1873; Bentham & Hooker, 1862/1867; Edlin, 1935; Hutchinson, 1926, 1973). We included two representatives of Dipterocarpaceae in the analyses following suggestions that it belongs within (Thorne, 1992; Takhtajan, 1980, 1987) or near (Cronquist, 1981) the Malvales. Recent molecular evidence suggests that Elaeocarpaceae may be more distantly related to Mal-

TABLE I
MALVALEAN TAXA INCLUDED IN CLADISTIC ANALYSIS^a

Malvaceae s.str.^b	Helicteraceae
Malvaceae	<i>Pterospermum</i>
<i>Urena</i>	<i>Helicteres</i>
<i>Malvaviscus</i>	<i>Reevesia</i>
Malveae	Sterculiaceae
<i>Sida</i>	<i>Sterculia</i>
<i>Sphaeralcea</i>	<i>Firmiana</i>
<i>Abutilon</i>	Mansonieae
Hibisceae	<i>Nesogordonia</i>
<i>Hibiscus</i>	Fremontieae
Gossypieae	<i>Fremontodendron</i>
<i>Thespesia</i>	“Tiliaceae”^c
“Bombacaceae”^c	Brownlowieae
Durioneae	<i>Berrya</i> (see Table III)
<i>Durio</i>	<i>Brownlowia</i>
Matisiae	<i>Pentace</i>
<i>Quararibea</i> (but compare with Alverson, 1989)	Apeibeae
<i>Ochroma</i>	<i>Apeiba</i>
<i>Cavanillesia</i>	Tiliaceae
Adansonieae (incl. Ceibeae)	<i>Entelea</i>
<i>Huberodendron</i> (doubtfully distinct from	<i>Corchorus</i>
<i>Bernoullia</i>)	<i>Luehea</i>
<i>Spirotheca</i>	<i>Schoutenia</i>
<i>Ceiba</i> (see Table III)	<i>Tilia</i>
<i>Adansonia</i>	<i>Clappertonia</i>
<i>Pseudobombax</i>	Grewieae
<i>Pachira</i> (see Table III)	<i>Grewia</i>
“Sterculiaceae”^d	<i>Heliocarpus</i>
Dombeyaeae	<i>Triumfetta</i>
<i>Dombeya</i>	Incertae sedis
Hermannieae	<i>Craigia</i>
<i>Melochia</i>	Dipterocarpaceae
<i>Waltheria</i>	Dipterocarpoideae
Byttnerieae (incl. Theobromaeae)	<i>Dipterocarpus</i>
<i>Theobroma</i>	Monotoideae
<i>Guazuma</i>	<i>Monotes</i>
<i>Byttneria</i>	Elaeocarpaceae (outgroup)
Lasiopetaleae	<i>Elaeocarpus</i> and <i>Sloanea</i>
<i>Lasiopetalum</i>	
<i>Maxwellia</i>	

^a Family-level classification is that of Cronquist, 1981; Thorne's (1992) classification is similar except that *Monotes* is placed in Monotaceae.

^b Classification according to Fryxell, 1988.

^c Classification slightly modified from Schumann, 1895; see also Nilsson & Robyns, 1986. Hutchinson (1967) placed *Cavanillesia* in Hampeae and *Huberodendron* in Matisiae.

^d Tribal limits follow Edlin, 1935; *Maxwellia*, not treated by Edlin, is placed in Lasiopetaleae by Hutchinson (1967). Edlin (1935) placed Fremontieae in Bombacaceae. Hutchinson's (1967) classification is similar; he recognized Theobromieae as distinct from Byttnerieae.

^e Tribal limits slightly modified from Edlin's (1935), who placed *Craigia* in Byttnerieae; this genus also was placed in Sterculiaceae by Smith and Evans (1921); *Craigia* here is placed in Tiliaceae, as suggested by Ren (1989) and Chang and Miao (1989). Hutchinson's (1967) tribal delimitations are quite different. We note that he placed *Entelea* and *Corchorus* in Enteleae; *Clappertonia* in Sparrmanieae; *Luehea* in Lueheae; *Heliocarpus* and *Triumfetta* in Triumfetteae; and *Berrya* and *Pentace* in Berryeae; and *Craigia* in the Sterculiaceae.

vales than was previously suspected (D. Baum & W. Alverson, pers. comm.), and we note that the use of Dipterocarpaceae, a group showing many more core Malvalean

features than Elaeocarpaceae (see results), as a functional outgroup, resulted in no changes regarding ingroup structure. Molecular evidence also supports the use of

TABLE II

CHARACTERS USED IN CLADISTIC ANALYSIS OF CORE MALVALES. PRESUMED APOMORPHIC CHARACTER STATES ARE LISTED FIRST, FOLLOWED BY PLESIOMORPHIC ONES

1. Plants suffrutescent to herbaceous (1); plants trees or shrubs (0).
2. Phloem stratified into hard and soft layers, with wedge-shaped rays (1); stratified phloem lacking (0).
3. Tile-cells present in xylem rays (as seen in radial section) (1); tile-cells lacking (0).
4. Xylem parenchyma storied (1); unstoried (0).
5. Axile parenchyma aliform, confluent, or in bands (1); axial parenchyma reticulate or sparse, but not aliform, confluent, or in bands (0).
6. Axial parenchyma forming ground tissue of xylem with smaller amounts of fibers, and thus wood very low density (1); axial parenchyma not forming ground tissue of xylem, and thus wood heavier (0).
7. Mucilage cavities or canals present (1); mucilage cavities or canals lacking (0).
8. Gossypol glands present (1); such glands lacking (0).
9. Resin canals present (1); such canals lacking (0).
10. Indumentum of stellate hairs, stellate and simple hairs intermixed, or modified conditions, e.g., peltate scales (1); indumentum of only simple hairs (0).
11. Margin of lamina serrate to dentate and of a \pm malvoid type (Hickey & Wolfe, 1975) (1); margin of lamina entire (2); margin of lamina serrate, and non-malvoid (0). [unordered]
12. Leaf venation \pm palmate (actinodromous) (1); venation pinnate (craspedodromous to camptodromous; see Hickey 1973) (0).
13. Leaves palmately compound (1); leaves unifoliate (2); leaves simple (0). [ordered]
14. Leaves articulate, i.e., with clearly defined joint between lamina and petiole (1); leaves non-articulate, with or without an upper pulvinus (0).
15. Epicalyx clearly developed, as a whorl of bracts below calyx (2), epicalyx poorly developed, i.e., a few bracts attached along peduncle below calyx, and frequently quickly deciduous (1); epicalyx lacking (0). [unordered]
16. Staminate flowers produced (in conjunction with either perfect or carpellate flowers) (1); all flowers perfect (0).
17. Floral nectaries composed of densely packed, multicellular, glandular hairs on calyx, corolla, or androgynophore (1); nectaries lacking or not as above (0).
18. Sepals connate (1); sepals distinct (0).
19. Sepals imbricate (1); sepals valvate (0).
20. Sepals greatly expanded at maturity, forming 2-5 elongated wings (1); sepals not expanded, or if expanded, then not forming 2-5-lobate structure (0).
21. Petals imbricate, overlapping but not convolute (1); petals imbricate and convolute (= contorted) (2); petals valvate, or open (0). [ordered]
22. Petals absent (1); petals present (0).
23. Petals constricted and unusually shaped (1); petals \pm flat, not constricted (or lacking) (0).
24. Corolla adnate to base of androecium (1); corolla free from androecium (0).
25. Androecium developed exclusively from antipetalous whorl (1); androecium developed from two whorls (0).
26. Antipetalous androecium cluster lacking separate independent trace toward the staminodial apex of the staminal tube, an innermost median stamen, or several stamens (1); such a trace present (0).
27. Stamens 5 (1); stamens numerous to 10 (0).
28. Stamens connate into a distinct tube (1); stamens free or only slightly fascicled (0).
29. Elongate staminodia, five, antisepalous (1); elongate staminodia, five, alternisepalous (2); staminodia lacking, minute, or numerous and derived from members of fascicle (0). [unordered]
30. Staminal tube with 5 inner conspicuous teeth (1); staminal tube not present, or if present then lacking conspicuous teeth or merely 5-lobate (0).
31. Anther locules septate (1); anther locules non-septate (0).
32. Anthers monolocular, i.e., half-anthers (1); anthers bilocular (0).
33. Anther lacking conspicuous connective appendage (1); anther with conspicuous sterile appendage (0).
34. Half-anthers reasssociated, thus filaments with several vascular strands (1); normal 2-loculate anthers, or distinct half-anthers (0).
35. Flower with elongate androgynophore (1); androgynophore inconspicuous or lacking (0).
36. Pollen spiny (1); pollen non-spiny (0).
37. Pollen clearly pleurotreme, i.e., radially symmetrical grains with \pm strongly angular amb, having the apertures halfway between the clearly defined angles (1); pollen peritreme, goniotreme, or very slightly pleotreme, i.e., nearly circular, with poorly defined angles, e.g., as in *Tilia* (0).
38. Pollen globose (1); pollen oblate or prolate (0).
39. Pollen oblate (1); pollen globose to prolate (0).
40. Pollen polyaperturate, i.e., with 7-100+ apertures (1); pollen 2-4(-5)-aperturate (0).
41. Carpels more than 5 (1); carpels 5 or fewer (0).

TABLE II
CONTINUED

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42. Sterile carpels alternating with fertile carpels (1); all carpels fertile (0).
 43. Styles apically branched (1); styles \pm fused, with lobate or divided stigma (0).
 44. Ovules per locule 1-2 (1); ovules several to numerous (0).
 45. Ovules/seeds campylotropous in form (1); ovules/seeds anatropous to \pm hemitropous in form (0).
 46. Carpels separating at maturity, forming an aggregate of follicles (1); carpels remaining connate, fruits otherwise (0).
 47. Fruit schizocarpic (1); fruit various, but not schizocarpic (0).
 48. Fruit indehiscent, a nut or nut-like (1); fruits variously dehiscent, or indehiscent and samaroid, large \pm dry pods, or berry-like (0).
 49. Fruits with projections, usually hairy or barbed (1); fruits lacking such structures (0).
 50. Seeds associated with copious hairs, i.e., kapok (1); seeds not associated with elongate hairs in fruit (0).
 51. Embryo with folded cotyledons (1); cotyledons \pm flat (0).
 52. Seed fatty acids with a cyclopropenyl group (1); cyclopropenyl fatty acids lacking (0).
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Dipterocarpaceae as an outgroup to genera of core Malvales (Chase et al., 1993).

Nearly all characters that we selected were readily divisible into discrete states, thus avoiding arbitrary decisions relating to state delimitation (Stevens, 1991). A few problems are noted in Table III. Some features could not be included in the analyses because they showed too much infrataxon variation, e.g., leaf size, size and shape of floral parts, and indumentum types, or could not be delimited into discrete states, e.g., anther size, extent of staminal connation, and inflorescence structure (Bayer, 1994). Autapomorphic characters were omitted except for character 8, presence of gossypol glands, and character 9, presence of resin canals. The first feature was included because it is synapomorphic for the distinctive tribe Gossypieae, which has often been considered transitional between Bombacaceae and Malvaceae, whereas the second character was included because it is synapomorphic for the large subfamily Dipteroocarpoideae (Cronquist, 1981). Of course, the deletion of these two characters would have no effect on the topology of the resulting cladograms.

Finally, characters 38 and 39, which could have been treated as a single multi-state character, were formulated as they are in Table II because it is not possible to code for character polymorphisms in Hennig86, and the treatment of this information in a single (3 state) character would have led to a loss of information.

Results

The Hennig86 analysis (in which variable characters were coded either as polymorphic or with a hypothesized ancestral condition; see Table III) resulted in the generation of 1925+ equally parsimonious trees of 153 steps (221 steps in MacClade, which counts steps on polymorphic terminals), a consistency index (CI) of 0.36, and a retention index (RI) of 0.72. The topologies represented in these trees, however, are all quite similar, especially with regard to position of genera of Malvaceae, Bombacaceae, and Sterculiaceae. For a representative cladogram and the strict consensus tree, see Figures 1 and 2, respectively. The initial PAUP analyses (with 100 random addition replicates) resulted in the production of 1000+ equally parsimonious trees that are a subset of those discovered by Hennig86; the strict consensus tree is identical to that of the Hennig86 analysis. A PAUP search with 100 random addition replicates and mulpars off failed to find any shorter trees or trees with differing topologies; i.e., all discovered trees belong to a single optimality peak. Support for most clades evident among the most parsimonious trees was relatively weak. All decayed in trees one step longer except for the following, which decayed in trees two steps longer: 1) the *Urena* + *Malaviscus* + *Sida* + *Sphaeralcea* + *Abutilon* clade, 2) the above-listed genera + *Hibiscus*, 3) the genera of Malvaceae s.str., 4) the *Guazuma* + *Byttneria* clade, 5) the *Sterculia* + *Firmiana* clade, 6)

TABLE III
CHARACTER VALUES FOR TAXA USED IN CLADISTIC ANALYSIS

Taxon ^c	Character ^{a, b}																											
	1					2					3					4					5							
	12345678901234567890123456789012345678901234567890123456789012																											
Urena	V	1	1	1	1	0	1	0	0	1	1	1	0	0	2	0	0	1	1	0	1	0	1	0	1	0	1	?
Malvavi	0	1	1	1	1	0	0	0	1	1	0	0	2	0	0	1	1	0	1	0	1	0	1	0	1	0	1	?
Sida	V	1	0	1	1	0	0	0	1	1	V	0	0	0	0	1	1	0	1	0	0	0	1	0	0	1	0	?
Sphaera	V	1	1	1	1	0	1	0	0	1	1	1	0	0	2	0	0	1	1	0	1	0	0	0	1	0	1	?
Abutilo	V	1	1	1	1	0	0	0	1	1	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0	1	0	?
Hibiscu	0	1	0	1	V	0	1	0	0	1	1	1	0	0	2	0	0	1	1	0	1	0	1	0	0	1	0	?
Thespes	0	1	1	0	0	1	1	0	2	0	0	1	1	0	0	2	0	0	1	1	0	1	0	1	0	0	0	?
Durio	0	1	1	0	0	1	0	0	1	2	0	0	0	1	1	0	0	2	0	0	1	1	0	0	0	0	0	?
Cavanil	0	1	0	1	0	1	0	0	1	2	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	?
Quarari	0	1	0	0	0	1	0	0	1	2	V	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	?
Ochroma	0	1	1	0	1	0	0	1	2	0	0	0	1	1	0	0	2	0	0	1	1	0	0	0	0	0	0	?
Huberod	0	1	0	1	0	0	1	2	1	1	0	1	0	0	2	0	0	1	0	0	1	1	0	0	0	0	0	?
Spiroth	0	1	0	1	0	0	1	2	1	1	0	1	0	0	2	0	0	1	1	0	0	1	0	0	0	0	0	?
Ceiba	0	1	0	1	V	0	1	0	0	1	1	1	1	0	1	0	0	2	0	0	1	1	0	0	0	0	0	?
Adanson	0	1	0	1	0	0	1	1	1	1	0	1	0	0	2	0	0	1	0	0	1	0	0	1	0	0	0	?
Pseudob	0	1	0	1	0	0	1	2	1	0	1	0	1	0	0	2	0	0	1	0	0	1	0	0	0	0	0	?
Pachira	0	1	0	1	0	0	1	2	1	1	0	1	0	0	2	0	0	1	0	0	0	0	1	V	0	0	0	?
Walther	V	1	0	0	1	0	0	1	1	0	0	1	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	?
Melochi	V	1	0	0	1	0	0	1	1	V	0	0	0	1	0	0	2	0	0	0	1	0	0	0	0	0	0	?
Dombeya	0	1	?1	1	0	0	1	1	0	0	2	0	1	0	0	2	0	0	0	0	1	0	0	0	0	0	0	?
Theobro	0	1	0	1	0	0	1	2	V	0	0	0	1	0	0	2	0	0	1	0	0	0	0	0	0	0	0	?
Guazuma	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	?	
Byttner	V	1	0	0	0	1	0	0	1	2	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	?
Lasiop	0	1	?1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	?	
Maxwell	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	
Nesogor	0	1	???	0	1	0	0	1	2	0	0	0	0	1	0	0	2	0	0	1	0	1	0	0	0	0	0	?
Reevesi	0	1	1	0	0	1	0	0	0	1	0	0	2	0	0	1	0	0	0	0	1	0	0	0	0	0	0	?
Helicte	0	1	0	0	V	0	1	0	0	1	1	0	0	1	0	0	2	0	0	1	0	1	0	0	0	0	0	?
Pterosp	0	1	1	V	0	0	1	0	0	1	1	0	0	1	0	0	2	0	0	1	0	1	0	1	0	0	0	?
Stercul	0	1	0	1	0	0	1	2	V	0	0	1	1	0	0	?1	0	?	0	0	0	0	0	0	0	0	0	?
Firmian	0	1	0	1	0	0	1	2	1	0	0	0	1	1	0	0	?1	0	?	0	0	0	0	0	0	0	?	
Fremont	0	1	?1	0	0	1	0	0	1	2	1	0	0	2	0	1	1	0	?	0	?	0	0	0	0	0	0	?
Apeiba	0	1	0	1	0	0	1	1	0	0	1	0	0	1	V	0	0	1	0	0	0	0	0	0	0	0	?	
Clapper	0	1	0	?0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	
Brownlo	0	1	0	1	0	0	1	2	1	0	0	0	1	0	0	2	0	0	1	0	0	0	0	0	0	0	?	
Entelea	0	1	?1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	
Corchor	V	1	?1	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	
Schoute	0	1	?1	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	
Tilia	0	1	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	
Luehea	0	1	1	0	0	1	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	
Triumfe	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	
Helioca	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	
Grewia	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	
Berrya	0	1	0	1	0	0	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	
Craigia	0	1	1	0	0	1	V	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	
Pentace	0	1	0	1	0	0	1	2	1	0	0	0	1	0	0	2	0	0	0	1	0	0	0	0	0	0	?	
Diptero	0	1	0	0	V	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	
Monotes	0	1	0	0	V	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	
Elaeoca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	

^a V = condition variable; ? = condition unknown. Bold character codings are coded as polymorphic (0/1) in second analysis except for the following: Scored (1/2) are *Durio* 21, *Ceiba* 11, *Adansonia* 11, *Pterospermum* 11, *Apebia* 11, and *Grewia* 11; scored (0/2) are *Tilia* 29 (see discussion in text).

^b Notes on characters: 1: Several genera, e.g., *Urena*, *Sida*, *Sphaeralcea*, are variable in development of woody tissue; these genera are indicated as variable in Table III, but are scored as "0" in the initial analyses because woodiness is assumed to be ancestral within each genus. 2: Scorings taken from Cronquist, 1981. 3-5: Scorings based on Chattaway, 1933; Kukatchka & Rees, 1944; Metcalfe & Chalk, 1950; and Manchester & Miller, 1978;

TABLE III
CONTINUED

supplemented by observations of wood from twigs of *Spirotheca*, *Pseudobombax*, *Byttneria*, *Lasiopetalum*, *Maxwellia*, *Fremontodendron*, *Entelia*, *Corchorus*, and *Craigia*. **6:** Data from Chattaway, 1933; we note that some species of *Pachira* have \pm low density wood. **7:** Mucilage canals or cavities are sometimes present in the cortex of members of Dipterocarpoideae; these not seen in *Dipterocarpus*. **8:** Gossypol glands are confined to and characteristic of the tribe Gossypieae, represented here by *Thespesia*. They are \pm spherical lysigenous glands that contain a mixture of pigments, of which gossypol, a sesquiterpene-like pigment, is the characteristic constituent (Fryxell, 1968, 1988). **9:** Characteristic, branched, intercellular resin-canals occur in the pith, wood, and bark of the Dipterocarpoideae (Cronquist, 1981). These are lacking in Monotoideae and Pakaraimoideae. **10:** Peltate scales occur in *Durio*, *Maxwellia*, and some species of *Apeiba* and *Pentace*; these are considered to be derived from stellate trichomes. In genera with species with stellate and simple hairs intermixed, or where some species have only simple hairs and others possess stellate hairs, the stellate condition is considered to be ancestral. **11:** Toothed as well as entire-margined leaves occur in *Ceiba*, *Adansonia*, *Pterospermum*, *Apeiba*, and *Grewia*; in all these groups the malvoid-toothed condition (see Hickey & Wolfe, 1975) is considered to be ancestral in initial analyses. **12:** Intermediates between pinnate and palmate venation sometimes occur, causing problems in state delimitation. Thus, the venation is scored as "V" in *Sida*, *Melochia*, *Craigia*, *Quararibea*, and *Theobroma*. The leaves of *Huberodendron* are scored as palmate, because the "leaf" of this genus is considered homologous to a leaflet of a palmately compound leaf of genera such as *Ceiba*, *Adansonia*, and *Pachira* (see char. 13). **13:** Leaves of *Durio* are scored as simple, although the presence of an upper pulvinus (as is characteristic of Bombacaceae) in this genus may be indicative of the unifoliolate condition; *Huberodendron*, however, is scored as unifoliolate because this interpretation is supported by the clear articulation at the base of the leaf blade, as in the palmately compound leaves of *Spirotheca*, *Ceiba*, *Adansonia*, and *Pachira*. **14:** Only leaves with a clearly defined joint, which is visible after drying as a impressed line between the blade and petiole, are considered to be articulate. Species with merely an upper pulvinus are scored as unarticulate, i.e., "0." **15:** Although some species of *Berrya* have a well-developed epicalyx, others lack this structure; the genus is coded as "0." **16:** Some species of *Berrya* have perfect flowers, e.g., *Berrya* s.str., while others are dioecious, e.g., *Carpodiptera* (Bornstein, 1989). Within this group, perfect flowers are considered to be ancestral in the initial analyses. **17:** See discussion of this character in Brown, 1938, and Cronquist, 1981; in Malvaceae, Bombacaceae, and Sterculiaceae, the nectar-producing glandular hairs are limited to the adaxial surface of the calyx, while in Tiliaceae their position is more variable and they may occur on the calyx, corolla, or androgynophore. Nectaries are poorly developed in *Lasiopetalum* and *Maxwellia*. In some Tiliaceae, e.g., *Tilia*, there is also a glandular nectary at the base of the sepals. **18:** Connation of sepals is only very slight in some taxa, e.g., *Dombeya* and *Monotes*. **20:** Wing-like sepals occur in *Schoutenia*, but in this genus they are not lobate, and clearly are not homologous to the condition in Dipterocarpaceae (e.g., *Dipterocarpus*, *Monotes*). **21:** Petals are lost in *Sloanea*, but the condition in *Elaeocarpus*, i.e., present and usually valvate, is taken as ancestral. Petals are imbricate but not convolute in *Durio oxleyanus*, while they are convolute in others, e.g., *D. testudinarum*, *D. lanceolatus*, *D. graveolens*, *D. kutejensis* (see van Heel, 1966); the convolute condition is considered ancestral in the initial analyses because it occurs in most Sterculiaceae (probable outgroup to Bombacaceae + Malvaceae) as well as in all other genera of Bombacaceae and Malvaceae. **22:** The lack of petals in the carpellate flowers of *Heliocarpus* is taken as a specialization; the genus is scored as having petals because they occur in the perfect flowers. Some species of *Schoutenia* lack petals, whereas in others they are small, linear structures. The presence of petals is considered to be ancestral in this genus. In *Craigia* the petals often are referred to as "petaloid staminodia." As noted by van Heel (1966: 385), however, the homology of petals throughout the order is in need of critical reevaluation. He noted that his investigations presented "no serious difficulties" in applying the idea of Gazet du Chatelier (1940), that the petals of Dombeyae, Helicterae, and Hermannieae are really pseudopetals, "being branches belonging to the antisepalous stamen fascicles," to members of the core Malvales. Additionally, he noted that the petals and stamen groups are intimately related and "located with great variability in relation to the sepals," and that the "double flowers of *Althaea rosea* and *Hibiscus rosa-sinensis* strongly indicate the close connection between (additional) petals and axillary stamen groups." Finally, he pointed out that he could not find "any difference in structure between pseudopetals and real petals in the Malvales." **23:** The constricted and unusually shaped petals of *Ayenia*, *Theobroma*, *Byttneria*, and *Guazuma* are tentatively taken as homologous; see Leinfellner (1960). **25:** Character taken from van Heel, 1966; he stated that "in the families under consideration ["core" Malvales] the androecia are formed by five-or, in some Tiliaceae, ten-groups of stamens." The androecium of Dipterocarpaceae and Elaeocarpaceae is considered to be derived from ten stamen-groups (see Cronquist, 1981; van Heel, 1966). The numerous stamens of many Malvales (and related orders Theales, Violales), which develop centrifugally, likely have developed from an ancestral condition of only 10 stamens, as indicated by developmental studies (van Heel, 1966; Rao, 1952) and recent phylogenetic investigations (Hufford, 1992; Chase et al., 1993). This is in contradiction to the opinion of Edlin (1935). The seemingly annular arrangement of some Tiliaceae is considered derived following the detailed developmental studies of van Heel (1966). **26:** Character taken from van Heel, 1966; he noted that "the chief difference between Bombacaceae and Malvaceae in this matter is formed by the constant occurrence in the Bombacaceae and the absence in the Malvaceae of a separate independent trace towards an innermost median stamen (in *Pachira* spp.) or towards the staminodial

TABLE III
CONTINUED

apex of the staminal tube As a result each staminal lobe is served by a middle inner single trace and by two lateral outer fascicle traces" (van Heel, 1966: 293). He also noted that in Sterculiaceae the median lobe traces "supply foliar staminodial lobe parts. In other plants, like, e.g., many Elaeocarpaceae, a number of *Sterculia* and *Tilia* spp., *Schoutenia* and *Pachira* spp., the apical parts of the lobes are occupied by a single stamen that is supplied by the median trace only" (van Heel, 1966: 381). Regarding Tiliaceae, he noted that "the median trace usually supplies more than one stamen" (van Heel, 1966: 383). **27:** In a few species of *Trumfetta* only 5 stamens are present; this condition is considered (in initial analyses) to represent a reduction from the condition of 10-60 stamens present in most species of this genus. **29:** As noted by van Heel (1966), the elongated staminodia found in several genera of Sterculiaceae are not homologous. The condition in *Tilia* is variable; some species have 5 conspicuous elongate antipetalous staminodia, whereas others lack these structures. The 5 antipetalous staminodia of *Craigia* are similar to those of *Tilia*. **30:** Van Heel (1966: 250) stated that "the alternipetalous apical staminal lobe parts [in Malvaceae] . . . may persist in some species . . . but generally [they] . . . are later completely outsize by the ultimate stretching of the stamens, although sometimes a rest may remain in the form of a tiny subulate tooth. However, it should be added that in Ureneae [= Malvaceae] and Hibisceae [incl. Gossypieae] the subapical staminodes may be subject to this ultimate stretching, so that subulate appendages may surmount the sterile mouth of the tube in line with the staminal rows." The elongation of these subapical, \pm triangular staminodes is considered to be apomorphic. **31:** See also Manchester, 1992. **32:** The monothecate anthers, which characterize Bombacaceae and Malvaceae, are interpreted as derived, on the basis of outgroup analysis, whether or not these unusual structures are considered to represent half-anthers (i.e., the products of developmental/phylogenetic splitting; see Brizicky, 1965, 1966; Cronquist, 1981; Goebel, 1923; Zomlefer, 1994) or as "congenitally fused products of a multiple division" (as proposed by van Heel, 1966: 292). We consider van Heel's arguments to be somewhat typological, and prefer the half-anther hypothesis on the basis of developmental and anatomical evidence, e.g., presence of forked vascular traces and position of anther primordia. The monothecate stamens of certain genera of Bombacaceae, e.g., *Ceiba* (see char. 34), have become reassocated. The bithecal anthers of *Fremontodendron* likely represent reassocated monothecate anthers. Van Heel (1966: 319, 320) noted that "in *Fremontia californica* [= *Fremontodendron californica*] the five stamens [each] . . . receive three traces, a middle inner trace going towards the apex chiefly unbranching and two outer lateral traces giving off a series of more or less forking branches Moreover, the primordial stages actually show that the stamens originate in the form of trapezoid lobes bearing a theca along each side. Therefore, the homology between the stamens and the groups of structures which may be formed by a staminal lobe in most other species cannot be denied *Fremontia* can be fully compared in this respect with the *Ceiba* spp. and with *Chorisia crispiflora* in Bombacaceae." Thus, the anthers of *Fremontodendron* are scored as monothecate (see also Edlin, 1935, who also considered the stamens of this genus to be monothecate). In *Tilia* the anther locules may be contiguous or separate at the tips of a shortly bifurcate filament; thus, this genus is coded as variable for this character. **34:** We agree with van Heel (1966: 295), who stated that "in *Ceiba* and *Chorisia* spp. the fanning vascular system is much more prominent, with forked branches, indicating that the stamens in these species are homologous to entire groups in *Pachira* and the other genera [of Bombacaceae]." *Chorisia* here is considered within *Ceiba* following Gibbs et al., (1988). The staminal condition in *Durio* is complex, with variation from monothecate to multithecate anthers. This variation is likely due to reassociation of monothecate stamens, as suggested by variation in anther form within a single flower as well as the presence of branching vascular strands within the "stamen" (van Heel, 1966). **35:** Very short gynophores are present (or sometimes present) in several genera of Tiliaceae, e.g., *Brownlowia*, *Corchorus*, *Schoutenia*, *Tilia*, *Trumfetta*, *Grewia*, *Berrya*; these are scored as "0." In *Heliocarpus* the pistillode of the staminate flowers has a very short gynophore, while the carpellate flower has a conspicuous gynophore. In the initial analyses this structure was not considered homologous to the elongate gynophore found in *Sterculia* and relatives. **36:** Length of exine spines varies, but all genera with at least slightly spiny pollen are scored as "1." Substantial intragenetic variation seen in *Pachira* (see Nilsson & Robyns, 1986; Alverson, 1994) and *Berrya* (Erdtman, 1952). In four distylous species of *Waltheria*, the pollen is spiny from the stamens of thrum flowers and smooth-reticulate in pin flowers (Saunders, 1993)! We assume that non-spiny pollen is ancestral within *Waltheria* in the initial analyses. **37:** Data from Nilsson & Robyns, 1986, for Bombacaceae; Christensen, 1986, for Malvaceae; Sharma, 1969, for Tiliaceae; and Erdtman, 1952, for Sterculiaceae and other families, supplemented by personal observations. The pollen grains of *Tilia* vary from round to very slightly pleurotreme; thus, they are scored as "0." The grains of *Lasiopetalum*, *Trumfetta*, and *Sterculia foetida* are subtriangular, with rounded angles. These are not considered to be homologous to the strongly pleurotreme grains of many Bombacaceae, because of their very different shape (as seen in polar view), and are therefore coded as "0." The large pleurotreme pollen grains of Bombacaceae are often fenestrate to clearly reticulate, but size of surface reticulum varies greatly, making state delimitation quite arbitrary. Thus, size of exine reticulum, i.e., fenestrate to micro-reticulate, was not used as an additional character. **38-39:** Data from Nilsson & Robyns, 1986, for Bombacaceae; Christensen, 1986, for Malvaceae; Sharma, 1969, for Tiliaceae; and Erdtman, 1952, for Sterculiaceae and other families, supplemented by personal observations. State delimitation is \pm arbitrary, leading to "variable" coding of some taxa. Colpus length is strongly correlated with pollen shape (see Sharma, 1969), and thus this feature is not considered

TABLE III
CONTINUED

independently. Variation in pollen shape could have been considered as a single multistate character but here has been divided into its binary factors to facilitate character coding in the Hennig86 analysis. **40:** Data from same sources as characters 38, 39. When only few colpi are present they tend to be arranged equatorially, but grains with numerous apertures tend to be pantoporate. **41:** Occasionally only 5 carpels are found in *Abutilon* and *Sida*, but most species have more than 5 carpels. This feature was coded as polymorphic for these genera in the additional analysis (see text). **42:** See van Heel, 1978, for detailed presentation of development of this distinctive feature, which characterizes the Malvaceae (Fryxell, 1988). **43:** The taxonomic significance of this character is discussed by Fryxell (1988). Styler form is variable in *Helicteres*, which is coded as variable. Variation in Eleocarpaceae makes polarization difficult. **44:** Infrataxon variability in number of ovules per locule occasionally causes problems in scoring, e.g., 1-6 ovules per ovule occur in *Berrya*. **45:** Data from Corner, 1976; Reeves, 1936; Fryxell, 1968; and Cronquist, 1981. **46:** Postgenital separation of carpels is considered to be apomorphic, a conclusion based on outgroup analysis and upon developmental data (see Jenny, 1985). **47:** Fruit of *Malvaviscus* varies from a fleshy schizocarp to a berry; the schizocarpic condition was considered to be ancestral within the group in the initial analyses. **49:** Condition variable in Elaeocarpaceae. **50:** Seeds associated with elongate hairs also occur in some Malvaceae, e.g., *Gossypium*. These hairs are derived from the seed, in contrast to those in Bombacaceae, which grow from the fruit wall. Derived species of *Pachira*, e.g., *P. aquatica*, lack kapok and possess large and specialized seeds; however, several other species (usually segregated as *Bombacopsis*; see Alverson, 1994) have smaller seeds and possess varying amounts of these hairs. **51:** There is much variation within Malvaceae in the type of cotyledon folding exhibited, e.g., conduplicate, spiral-convolute, plicate-corrugate, etc., especially in Sterculiaceae, and these may not all be homologous. In addition, the embryo itself may be straight to curved. Clearly, this feature needs more study; see also information presented in Corner, 1976; Fryxell, 1968; Martin & Barkley, 1961; and Gunn & Ritchie, 1988. The cotyledons of some taxa—e.g., *Brownlowia*, *Durio*, *Sterculia*, *Theobroma*—are quite fleshy. In some species of *Pachira* only a single cotyledon is fleshy. **52:** Presence or absence of cyclopropenyl fatty acids is taken from Gibbs, 1974. *Thespesia* (a member of the Gossypieae) is scored as “1” due to the occurrence of cyclopropenyl fatty acids in *Gossypium*. *Pseudobombax* is scored as “1” due to the presence of these fatty acids in seeds of the related genus *Bombax*.

^c Genera abbreviated by first seven letters of name.

the *Waltheria* + *Melochia* clade, 7) the core Malvaceae clade, and 8) the *Dipterocarpus* + *Monotes* clade.

Tiliaceae, Sterculiaceae, and Bombacaceae, as typically delimited (see Cronquist, 1981, 1988), are paraphyletic (or polyphyletic) in every tree (Figs. 1 & 2). Hereafter, these names are used with quotation marks as an indication of their potential paraphyly (Wiley, 1981). In contrast, the monophyly of the Malvaceae was supported by several apomorphies: spiny pollen (char. 36), which is usually 7–100+ aperturate (char. 40), the presence of a staminal tube with 5 apical teeth (char. 30) that lacks a separate independent trace toward the staminodial apex (char. 26), and a well-developed epicalyx (char. 15-2). It should be stressed, however, that all of these characters show homoplasy (Fig. 1) except for that of the anatomy of the staminal column, which has been only incompletely surveyed (van Heel, 1966). Spiny pollen, which traditionally has been stressed as a defining feature of Malvaceae (e.g., Cronquist, 1981), is hypothesized to have evolved several times within core

Malvaceae. In addition to its presence in genera of Malvaceae, this feature occurs in *Adansonia* (“Bombacaceae”), *Dombeya*, *Pterospermum* and some species of *Waltheria* (“Sterculiaceae”), and *Schoutenia* (“Tiliaceae”) (see Fig. 1; Erdtman, 1952; Nilsson & Robyns, 1986; Rao, 1950; Sharma, 1969). Polyaperturate pollen, a staminal column with five apical teeth, and a well-developed epicalyx have been lost in some groups of Malvaceae (Fig. 1; see also Fryxell, 1988), and epicalyxes have evolved independently in other Malvacean groups, e.g., *Fremontodendron*, *Dombeya* (“Sterculiaceae”), and *Luehea* (“Tiliaceae”). We acknowledge that pollen aperture number is more variable than is evident in Figure 1 due to our limited sampling (see discussion in Fryxell, 1988). The Malvaceae, as traditionally circumscribed, are best recognized on a combination of characters; i.e., the group is polythetic.

Within Malvaceae, the commonly recognized tribes were very tentatively supported (except for Hibisceae, of which only a single genus was included in the analy-

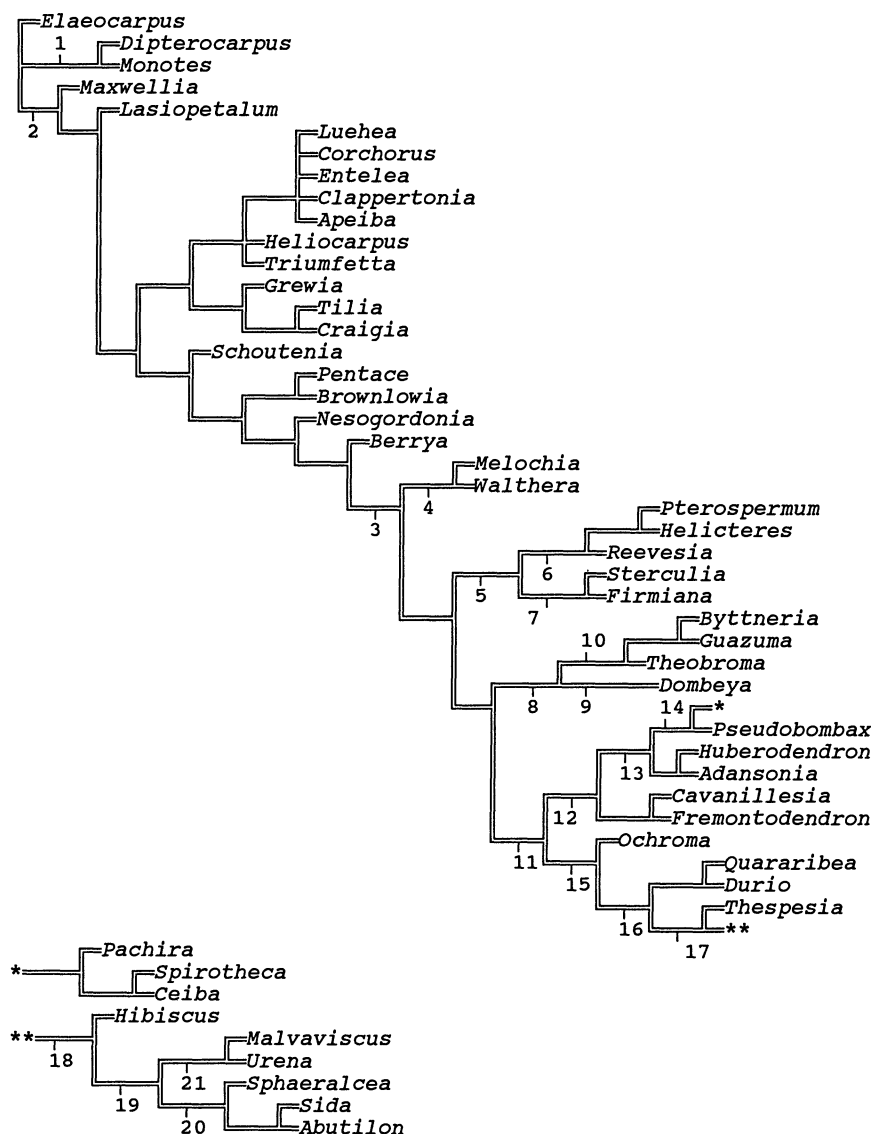


FIG. 1. Representative 153-step cladogram; CI = 0.36; RI = 0.72. Character states diagnosing major clades are indicated below (character numbers as in Table I): 1: 19, 20, 21, 48; 2: 17, 25, 33, 52; 3: 28; 4: 4(0), 11, 27; 5: 35, 46; 6: 3, 5(0); 7: 16, 22, 39; 8: 29; 9: 11, 15(2), 36; 10: 23; 11: 5(0), 15, 24, 32; 12: 37; 13: 13, 14; 14: 50; 15: 3; 16: 38, 39(0); 17: 15(2), 26, 30, 36, 40; 18: 5, 11, 43, 45; 19: 41, 44, 47; 20: 30(0); 21: 42.

ses). The synapomorphy of a loss of apical teeth on the staminal column (char. 30) diagnosed Malveae s.l. (Fryxell, 1988). The monophyly of the Malvavisceae (= Ureneeae) was supported by the presence of sterile carpels alternating with the fertile ones (char. 42; van Heel, 1978). These two tribes were united by the synapomorphy of schizocarpic fruits (char. 47), carpels fre-

quently greater than five (char. 44), and ovules only one or two per locule (char. 41). These tribes also show a tendency toward herbaceousness (char. 1). The genus *Hibiscus* (representative of Hibisceae) was positioned as the sister group to Malveae + Malvavisceae, sharing with these taxa several derived features, e.g., campylotropous ovules/seeds (char. 45) and apically

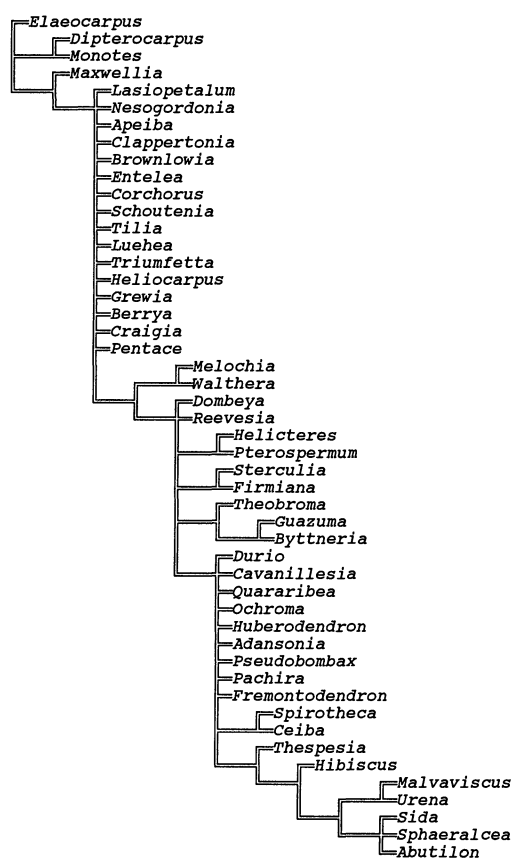


FIG. 2. Strict consensus of 1925+ trees discovered in Hennig86 analysis and 1000+ trees resulting from PAUP analysis.

branched styles (char. 43). Details of embryo form may constitute an additional synapomorphic feature (Fryxell, 1968). The monophyly of the Hibisceae cannot be determined without cladistic analyses including additional genera representative of this group. The Gossypieae was positioned basally in Malvaceae, and is probably monophyletic due to the presence of gossypol glands (char. 8; Fryxell, 1968).

The strict consensus tree from the Hennig86 and PAUP analyses contain little structure among the genera traditionally placed in "Bombacaceae" (Fig. 2). This is due, however, to the unstable placement of *Quararibea*, *Fremontodendron*, and *Cavanillesia*. When the analysis was rerun (in PAUP) with these genera omitted, more structure was apparent within this portion

of the cladogram; i.e., *Pseudobombax*, *Pachira*, *Ceiba*, and *Spirotheca* formed a clade, as did *Adansonia* and *Huberodendron*. *Durio* consistently formed a clade with Malvaceae in both Hennig86 and PAUP analyses on the basis of globose pollen grains (chars. 38, 39). *Ochroma* also linked with this clade due to the presence of tile cells; we note that this feature shows a high degree of homoplasy. In some trees, *Quararibea* or *Fremontodendron* also were members of this group.

The remaining genera of "Bombacaceae" formed either a monophyletic or a metaphyletic group in our trees. *Ceiba* (including *Chorisia*; see Table III, notes) and *Spirotheca* consistently formed a clade because they possess filaments with several vascular strands; i.e., they all show androecial reduction (char. 34). *Pseudobombax*, *Spirotheca*, *Ceiba*, and *Pachira* (incl. *Bombacopsis*; see Table III, notes) are linked by their seeds associated with kapok (char. 50). The Adansoniaceae (including Ceibeae), as represented by *Pseudobombax*, *Spirotheca*, *Ceiba*, *Pachira*, *Adansonia*, and *Huberodendron*, may be monophyletic, and are diagnosed by the presence of palmately compound, usually articulate leaves (chars. 13, 14). If Ceibeae are excluded, the Adansoniaceae become clearly paraphyletic (Fig. 1). In some trees, the above-listed genera, along with *Cavanillesia* and *Fremontodendron*, formed a clade, based on pleurotreme pollen grains (char. 37; see also Nilsson & Robyns, 1986). The high chromosome number characterizing this clade may also be synapomorphic (Baum & Oginuma, 1994; Fryxell, 1968). (We did not include chromosome number in the analyses because many inaccurate counts occur in the literature and because of the problem of state delimitation.) The clearest pattern in this portion of our cladograms is the separation of the paleotropical *Durio* from the mainly neotropical members of "Bombacaceae" (excepting *Ochroma*), in agreement with the conclusions of Baum and Oginuma (1994) based on chromosome number and other data. We note, however, that forcing the monophyly of Bombacaceae adds only three steps.

The Malvaceae and "Bombacaceae" to-

gether formed a clade (see Figs. 1 & 2) with several strong synapomorphies, including a poorly (to well-) developed epicalyx (char. 15), a slight adnation of androecium and corolla (char. 24), and monolocate anthers (char. 32). The latter feature is quite distinctive, although it is difficult to interpret in several “Bombacaceae” because of reassociation of half-anthers due to androecial reduction, e.g., *Ceiba* and *Fremontodendron* (see van Heel, 1966; Edlin, 1935; and Table III, notes).

“Sterculiaceae” did not constitute a clade (Figs. 1 & 2). However, the analyses suggest that most genera traditionally placed in this family may belong to one of three phylogenetically adjacent clades, i.e., a group (I) comprising Byttnerieae, including Theobromeae (as represented by *Byttneria*, *Guazuma*, and *Theobroma*) and Dombeyeae (represented by *Dombeya*); a group (II) comprising representatives of Helictereeae (represented by *Pterospermum*, *Helicteres*, and *Reevesia*) and Sterculieae (represented by *Sterculia* and *Firmiana*); and a group (III) comprising Hermannieae (as represented by *Melochia* and *Waltheria*) (Fig. 1). In contrast, *Lasiopetalum* and *Maxwellia* (of the Lasiopetaleae), along with *Nesogordonia* (of the Mansonieae), were placed more basally on the cladograms (Figs. 1 & 2). Forcing the monophyly of Sterculiaceae adds nine steps and is, therefore, much less parsimonious. However, linking only clades I and II is only one step longer, and linking clades I, II, and III is only two steps longer (based on the topology of other taxa shown in Fig. 1). Byttnerieae are hypothesized to be monophyletic on the basis of unusually constricted petals (char. 23; Leinfellner, 1960); and Dombeyeae, on the basis of their spiny pollen (see also Rao, 1950; Erdtman, 1952). The Byttnerieae + Dombeyeae (Group I) may be monophyletic due to the shared possession of five elongated antisepalous staminodia (char. 29–1), as suggested by many of the trees discovered by PAUP and Hennig86. Mistakenly, this feature often has been stressed as a defining character of Sterculiaceae. However, it is likely synapomorphic for Byttnerieae + Dombeyeae, and we believe that quite likely Byttnerieae

+ Dombeyeae do constitute a clade. The Helictereeae may be monophyletic due to the presence of reticulate or sparse axile parenchyma (reversal of char. 5); the monophyly of the Sterculieae is supported by the presence of staminate flowers (char. 16) and the loss of petals (char. 22; Edlin, 1935). Group II (Helictereeae + Sterculieae) is likely monophyletic due to the distinctive synapomorphies of flowers with an elongate gynophore (char. 35) and carpels that separate at maturity (Jenny, 1985), forming a cluster of follicles (char. 46). Group II was not present in all trees discovered by PAUP and Hennig86. However, we prefer the many trees showing this topology, because it is quite unlikely that these complex gynoecium and fruit characters could have evolved in parallel. Group III (Hermannieae) may be monophyletic on the basis of an androecium of only five stamens (char. 27) and unstored xylem parenchyma (reversal of char. 4). The group shows a tendency to herbaceousness; see also Brizicky (1966).

Our results support the existence of a large clade comprising Malvaceae + “Bombacaceae” (incl. *Fremontodendron*) + “Sterculiaceae” (excl. *Maxwellia* and *Lasiopetalum*, and possibly also *Nesogordonia*); the monophyly of this group is supported, however, only by a single character, i.e., a monadelphous androecium (char. 28) (see Figs. 1 & 2).

Relationships among genera traditionally placed in “Tiliaceae” are problematic, although in all discovered cladograms this assemblage is paraphyletic. Forcing the monophyly of “Tiliaceae” (with MacClade) is much less parsimonious, requiring five additional steps. We observed numerous different topologies in this portion of the generated cladograms, resulting in the collapse of all structure in the strict consensus trees (Fig. 2). This group forms a polytomy near the base of the cladogram (Figs. 1 & 2). In some trees, *Brownlowia* and *Pentace* formed a clade on the basis of five elongate alternisepalous staminodia (char. 29–2); both have been considered in the tribe Brownlowieae (Table I; Edlin, 1935). In addition, in some cladograms, *Triumfetta* and *Heliocarpus* formed a clade; both are members of the Triumfetteae, according to

Hutchinson (1967), or the Grewieae, according to Edlin (1935). In many cladograms, a large group of genera—i.e., *Luehea*, *Corchorus*, *Entelea*, *Clappertonia*, *Apeiba*, *Heliocarpus*, and *Triumfetta*—formed a clade; these genera often have fruits with stout projections (char. 49). Finally, *Tilia* sometimes formed a clade with *Craigia* on the basis of oblate, clearly pleurotreme pollen grains, flowers with five elongate alternisepalous staminodia, and embryo with \pm folded cotyledons (see also Manchester, 1994). Forcing *Craigia* into Sterculiaceae, where originally described, takes five additional steps (see also Ren, 1989). However, *Tilia* is linked with *Schoutenia* on the basis of the nut-like fruit (along with oblate pollen) in other trees. *Lasiopetalum* (usually placed in “Sterculiaceae”) likely is a member of this tiliaceous basal complex. *Maxwellia*, as suggested by Robyns et al. (1977) and Ren (1989), also belongs in “Tiliaceae.” Analyses including many more genera of “Tiliaceae” are necessary before any conclusions can be drawn regarding the monophyly of the variously recognized tribes within this complex. We are not at all confident in the monophyly of the broadly circumscribed tribes of Edlin (1935) or the more narrowly structured tribes of Hutchinson (1967).

The Dipterocarpaceae, which were included in our analysis as a transitional group between Elaeocarpaceae and core Malvales (as implied in Chase et al., 1993), are represented in our analyses by *Monotes* of the Monotoideae (Cronquist, 1981; or Monotaceae: Thorne, 1992) and *Dipterocarpus* of the Dipterocarpoideae (Cronquist, 1981; or Dipterocarpaceae: Thorne, 1992). These two genera formed a clade that is positioned, in all discovered cladograms (Figs. 1 & 2), as a sister group to core Malvales. However, we cannot infer from our results that dipterocarps constitute the clade most closely related to core Malvales, because a few possible malvoid groups, e.g., Bixaceae and Thymeliaceae, need to be included in a higher-level cladistic analysis of the order before a clear hypothesis can be developed relating core Malvales to the other families of the order. The Dipterocarpaceae s.l. (i.e., as circumscribed by Cronquist, 1981) may

be monophyletic on the basis of imbricate sepals (char. 19) that are greatly expanded at maturity (char. 20), imbricate petals (char. 21–1), and the indehiscent, nut fruit (char. 48). Dipterocarpoideae are monophyletic as evidenced by the presence of resin canals (char. 9), which seems to be associated with the reduction/loss of mucilage canals.

The monophyly of the core Malvales was supported by several features (see Fig. 1). Of these the most conspicuous is the unusual form of the floral nectaries (Brown, 1938; Cronquist, 1981): i.e., the nectaries are composed of densely packed, multicellular, glandular hairs on sepals and less commonly petals or androgynophore (char. 17). The stamens of this clade contrast strongly with those of Elaeocarpaceae and Dipterocarpaceae by their usual lack of a conspicuous connective appendage (char. 33). The presence of cyclopropenyl fatty acids (char. 52) may also be limited to this clade (Cronquist, 1981; Gibbs, 1974). Palmate leaf venation (char. 12) also may be a synapomorphy of this group, if the pinnate condition exhibited by *Maxwellia* and *Lasiopetalum* is due to reversals. It is also noteworthy that tile cells in the wood are not known to occur outside core Malvales. Tile cells are a special type of apparently empty upright (rarely square) ray cells occurring in intermediate horizontal series usually interspersed among the procumbent cells and are defined in such a way that they cannot occur in uniseriate rays. This may lead to an artificial distinction, i.e., uniseriate rays having the same kind of cells that in multiseriate rays would be classified as tile cells. This character coding problem may explain some of the apparent homoplasy seen in this feature in our analyses. Thus, it is possible that tile cells in a broader sense are an additional synapomorphy of core Malvalean taxa.

Members of Malvales (including Dipterocarpaceae) formed a monophyletic group, as evidenced by their stratified phloem with wedge-shaped rays (char. 2), mucilage cavities and/or canals in parenchymatous tissues (char. 7), indumentum of stellate hairs (char. 10), and connate sepals (char. 18). The analyses indicate that entire-margined

leaves (char. 11-2) may be an additional synapomorphy of malvacean taxa. We, however, think that it is more likely that the malvoid tooth type is ancestral in Malvales, with repeated evolution of entire-margined leaves in various lineages (see Hickey & Wolfe, 1975); this character is very homoplasious (Fig. 1). The hypothesized evolution of few ovules per locule at this point (Fig. 1) is also viewed with caution, as this is another very homoplasious feature. Although not included in this study, exotegmic seed coats (Dahlgren, 1983; Corner, 1976) and leaves with complex petiole anatomy (Cronquist, 1981) may represent other malvacean synapomorphies.

The PAUP analysis in which all variable characters were coded as polymorphic resulted in the generation of 1000+ trees of 232 steps; these trees are very similar to the cladograms described above, but their strict consensus is slightly less resolved. The trees resulting from this analysis are briefly compared with the trees resulting from the initial PAUP and Hennig86 analyses (see Figs. 1 & 2). A loss of resolution occurs within core Malvales. The half-anther clade (i.e., Bombacaceae + Malvaceae), which was consistently present in trees resulting from the initial analyses, is found in only 71% of the cladograms generated in the revised analysis. Thus, support for this clade is not as strong. Within the "Sterculiaceae" complex the position of *Helicteres* is altered; it forms a clade with *Melochia* and *Waltheria* instead of *Pterospermum*. Support for the monophyly of the Helicteraceae, therefore, is lessened. Within the complex of "Tiliaceae" genera, *Apeiba*, *Clappertonia*, *Entelia*, *Corchorus*, *Tilia*, *Luehea*, *Triumfetta*, *Heliocarpus*, *Grewia*, and *Craigia* consistently form a clade. This grouping also is present in many cladograms resulting from the initial analyses.

Bixaceae (including *Cochlospermum* and *Amoreuxia*; Cronquist, 1981) likely belongs within Malvales because the group is characterized by phloem tangentially stratified into hard and soft layers with wedge-shaped rays, leaf petioles often with complex anatomy, blades palmately veined, and androecia of numerous stamens that are associated with only 5–10 trunk bundles (Cronquist,

1981, 1988). Additionally, at least some members of this family possess mucilage canals. Also, the peltate scales of *Bixa* may have been derived from stellate hairs, as are the peltate scales of some Malveae, e.g., *Sphaeroclea leptophylla*. The group is distinctive due to its obviously parietal placentation (vs. "axile" in core Malvales, although the placental condition in these taxa has sometimes been interpreted as deeply intruded parietal). The Cistaceae also possess parietal placentation, and likely belong within Malvales. A few features of Thymeliaceae, e.g., fibrous phloem with wedge-shaped rays and mucilaginous epidermal cells, also may suggest a relationship with Malvales.

The results of these preliminary cladistic analyses are in agreement with our initial hypotheses, suggesting that "Tiliaceae," "Sterculiaceae," and "Bombacaceae" are non-monophyletic as currently circumscribed. All three are paraphyletic, if one ignores a few "misplaced" genera, i.e., *Lasiopetalum*, *Maxwellia*, *Fremontodendron*, and possibly *Nesogordonia*. [These genera are often placed in "Sterculiaceae," although Edlin (1935) considered *Fremontodendron* in "Bombacaceae" and Ren (1989) suggested that *Maxwellia* be placed in "Tiliaceae." Because *Fremontodendron* is placed with various genera of "Bombacaceae," and *Maxwellia* and *Lasiopetalum* with basal "Tiliaceae" in our cladograms (Figs. 1 & 2), the "Sterculiaceae" could be interpreted as polyphyletic.] Thus, "Tiliaceae," "Sterculiaceae," and "Bombacaceae" represent, at best, evolutionary grades, with "Tiliaceae" retaining numerous ancestral features of core Malvales and Malvaceae showing the most derived characters of the order. Malvaceae and "Bombacaceae" constitute a monophyletic group, best diagnosed by their monolocular anthers, while Malvaceae + "Bombacaceae" + "Sterculiaceae," excepting *Maxwellia*, *Lasiopetalum*, and possibly *Nesogordonia* (among analyzed taxa), form a more inclusive clade, diagnosed by the monadelphous androecium.

Discussion

How should our current family-level classification within Malvales be modified

TABLE IV
OUTLINE OF NOMENCLATURE FOR MALVACEAE S.L.^a

Malvaceae Juss., Gen. Pl. 271. 1789. Type: <i>Malva</i> L.
Tiliaceae Juss., Gen. Pl. 289. 1789. Type: <i>Tilia</i> L.
Byttneriaceae R. Br. in Flinders, Voy. Terra Austr. 2: 540. 1814. Type: <i>Byttneria</i> Loeffl., nom. cons.
Bombacaceae Kunth, Malvac., Byttner., Tiliac. 5. 1822. Type: <i>Bombax</i> L.
Sterculiaceae (DC.) Bartl., Ord. Nat. Pl.: 225, 340. 1830. (Tribe Sterculiace DC., Prodr. 1: 481. 1824.) Type: <i>Sterculia</i> L.

^a The names Malvaceae and Tiliaceae were published at the same time; the name Malvaceae here is chosen as the name for the combined family.

in order to be consistent with these results? It is clear that the current classification, with its arbitrarily delimited evolutionary grades, is unsatisfactory, especially if one seeks to reflect phylogeny accurately (Donoghue & Cantino, 1988; Judd et al., 1994; Hennig, 1966; Wiley, 1981; Wiley et al., 1991). One possibility would be to divide core Malvales into numerous small families (possibly as many as 15–20) in order to circumscribe monophyletic groups. We consider this alternative impractical because our knowledge of phylogenetic relationships among basal genera of core Malvales, i.e., the “Tiliaceae” grade, is not sufficient to delimit well-defined clades (which could then be considered at familial rank). In addition, the resulting families would be diagnosed, in most cases, only by a few homoplasious features. Instead, we propose that the core Malvales clade be recognized at the familial level, i.e., Malvaceae s.l. (see Table IV). International rules of botanical nomenclature specify that when two or more taxa are merged, the earliest published name has priority (Greuter, 1994). The names Malvaceae and Tiliaceae were published simultaneously (and both have priority over the names Bombacaceae and Sterculiaceae). We adopt the name Malvaceae, in preference to Tiliaceae, for this expanded familial concept of the core Malvales because the root “Malva-” has been used commonly already at the ordinal level. Thus, the Malvaceae is redefined to refer to the most recent common ancestor of plants

considered to be “Tiliaceae,” “Sterculiaceae,” “Bombacaceae,” and Malvaceae (see Cronquist, 1981) and to all of the descendants of that ancestor (a “node-based” phylogenetic definition; see de Queiroz & Gauthier, 1990, 1992). This broadly circumscribed Malvaceae can be diagnosed by several presumed synapomorphies (Fig. 1), but we draw special attention to the unusual floral nectaries (see also Brown, 1938; Cronquist, 1981) that are composed of densely packed, multicellular, glandular hairs on the sepals (and less commonly petals or androgynophore). This nectary form is unusual among angiosperms. The stamens of Malvaceae s.l. contrast strongly with those of Elaeocarpaceae and Dipterocarpaceae due to their lack of a conspicuous connective appendage. The presence of cyclopropenyl fatty acids, tile cells, and palmately veined leaves may also be diagnostic, but the first has been poorly sampled within the family, and the latter two are quite homoplasious. The monophyly of Malvaceae s.l. is also supported by preliminary cladistic analyses based on *rbcL* sequence data (Chase et al., 1993). Recognition of a broadly defined Malvaceae is also of practical benefit, as many members of the currently recognized “families” cannot be distinguished in vegetative condition. In this regard, it is of interest that Brown (1818) noted that the families of the Malvales were roughly equivalent to the tribes of the Rosaceae.

Although this conclusion runs counter to tradition, we believe that it best addresses the widely acknowledged problems regarding familial delimitation within core Malvales (see discussion in Cronquist, 1981; Edlin, 1935; Heywood, 1978; Judd et al., 1994; Manchester, 1992; Rendle, 1925; Takhtajan, 1969, 1980; Zomlefer, 1994). As mentioned above, our cladograms also support the widely held view that genera of core Malvales can be arranged from the most generalized “Tiliaceae,” through “Sterculiaceae” and “Bombacaceae,” to the most specialized, Malvaceae (see Cronquist, 1981; Edlin, 1935; Heywood, 1978; Hutchinson, 1926, 1973). The view of Warming (1859) and Rao (1952), that the “Sterculiaceae” are basal within core Mal-

vales, is not at all supported. The difficulty in diagnosing/recognizing these paraphyletic families is not at all surprising—this is simply a characteristic of paraphyletic groups (see Judd et al., 1994; Judd & Kron, 1993).

We emphasize that although we advocate an expanded circumscription of Malvaceae, this certainly does not mean the abandonment of familiar monophyletic taxa within Malvaceae s.l. For example, Malvaceae (sensu Cronquist, 1981; Fryxell, 1988; Fryxell & La Duke, 1994), Sterculiaceae (sensu Edlin, 1935), and possibly also Bombacaceae (excluding at least *Durio* and *Ochroma*) do appear to represent monophyletic groups, as do many currently recognized tribes (e.g., Malvaceae, Malveae, Gossypieae, Durioneae, Adansoniaceae, Byttneriaceae, Helicteraceae, and Sterculiaceae), and these groups should, therefore, be recognized at some infrafamilial level. This is not a task we have undertaken here; such decisions can be made only after a much more detailed phylogenetic study of Malvaceae s.l. However, care must be taken in this process not to create paraphyletic infrafamilial taxa inadvertently.

The placement of *Fremontodendron*, a genus traditionally considered to be discordant in “Sterculiaceae” (see Edlin, 1935; Erdtman, 1952; Kelman, 1991), in the Bombacaceae is supported by its pleurotreme pollen (char. 37), cryptically monolocate anthers (char. 32; at least as here interpreted, see Table III, notes), corolla adnate to base of androecium (char. 24), epicalyx (char. 15–1), and axile parenchyma not forming ground tissue of xylem (loss of char. 5). This placement is in agreement with the anatomical observations of the androecium of van Heel (1966), the observations and classification of Edlin (1935), and the palynological data of Erdtman (1952). The androecial anatomy of *Fremontodendron* is very similar to that of *Ceiba*, as has been pointed out by van Heel (1966) and Edlin (1935). The androecial structure of *Fremontodendron* is also similar to that of *Bernoullia*. The placement of this distinctive genus in “Sterculiaceae” likely has been due to the fact that the anthers appear to be bilocate. (However, it takes only

three steps to force *Fremontodendron* into “Sterculiaceae,” at the base of group I.)

Maxwellia and *Lasiopetalum* (and perhaps the entire Lasiopetaleae) are probably out of place in “Sterculiaceae.” Both of these genera are possibly quite basal within Malvaceae s.l. (Fig. 1), as evidenced by their pinnate venation, free stamens, and poorly developed nectaries.

Erdtman’s (1952) suggestion that Dombeyaceae be transferred to Malvaceae because of its spiny pollen is not supported, because the inclusion of these genera in Malvaceae (sensu Cronquist, 1981) would render this family polyphyletic. Likewise, Hutchinson’s (1967) transfer of *Huberodendron* from Adansoniaceae to Matisiaceae cannot be supported. The leaves of this genus have been derived from the palmately compound leaves characteristic of Adansoniaceae.

The Malvaceae, sensu Edlin (1935), i.e., species with schizocarpic fruits, are likely monophyletic, as is the traditional circumscription of this family, on the basis of spiny pollen (Cronquist, 1981; Thorne, 1992). However, the inclusion of Hibisceae and Gossypieae in “Bombacaceae,” as advocated by Edlin (1935), results in an even more paraphyletic “Bombacaceae.” Likewise, Edlin’s inclusion of Elaeocarpaceae within “Tiliaceae” makes this complex polyphyletic (and even less diagnosable). Edlin (1935) divided the tribes traditionally placed in “Sterculiaceae” into two families: Sterculiaceae s.str. (Sterculiaceae) and “Byttneriaceae” (remaining tribes). This renders Sterculiaceae s.str. monophyletic, based on the elongate gynophore and carpels separating at maturity, forming an aggregate of follicles—three very striking features (Jenny, 1985; Endress et al., 1983). However, the “Byttneriaceae” is still quite heterogeneous (in morphology, anatomy, and pollen features) and is paraphyletic/polyphyletic (see Fig. 2; discussion in Cronquist, 1981). Thus, the major effort of Edlin to restructure familial groupings within Malvales results in as much paraphyly (and thus arbitrarily delimited groups) as does the traditional and commonly recognized family groups (Cronquist, 1981, 1988; Dahlgren, 1983; Thorne, 1983, 1992; Takhtajan, 1980, 1987; Schumann, 1895). All other circum-

scriptions of families within core Malvales suffer from the same problem; see Bentham & Hooker, 1862/1867; Warming, 1895; and Hutchinson, 1973.

The continued recognition of families that are so poorly delimited is puzzling, but often fits a general pattern of arbitrary separation of temperate and tropical representatives of monophyletic groups. In each case studied (Judd et al., 1994), the possession of distinctive morphological features in the temperate to cosmopolitan family (as Malvaceae, sensu Cronquist, 1981; or Edlin, 1935), coupled with the fact that temperate taxa are relatively better known (Walters, 1961), has led to the segregation of monophyletic groups such as Malvaceae from tropical paraphyletic complexes such as "Bombacaceae." This has resulted from the application of traditional taxonomic procedures for grouping and ranking, which involve the weighting of certain features, e.g., pollen form and fruit type. Often these weighting decisions differ—thus the equally arbitrary use of spiny pollen (Cronquist, 1981) or schizocarpic fruits (Edlin, 1935) as "key" features of Malvaceae s.str. Edlin (1935: 4) commented on the fact that Malvales usually has been "inadequately" treated, and suggested that this is "due to the fact that only *Tilia* (Tiliaceae) and certain genera of Malvaceae, are common in the north temperate region." He also noted (1935: 4) that "some writers take *Sterculia* as being a typical genus of the family Sterculiaceae, but actually this genus and other Sterculieae are marked exceptions to the general type." Of course, Walters (1961) also pointed out the strong temperate bias on the part of many plant systematists!

One controversy among systematists has been whether the multistaminate androecium of most core Malvales is an ancestral or a derived feature (see discussion in Cronquist, 1981; Edlin, 1935; Rao, 1952; van Heel, 1966; Warming, 1859). Our results suggest that an androecium composed of many stamens connected to five or ten trunk bundles is ancestral within the order, in agreement with the opinion of Cronquist (1981). Reduction has occurred, leading to androecia with only five stamens (e.g., *Waltheria*, *Melochia*, and the extinct *Flor-*

issantia) or, even more interestingly, androecia that seem to have only five stamens due to the reassociation of monothebate anthers (e.g., *Ceiba* and *Fremontodendron*) (see Table III, notes). Those who have argued (e.g., Rao, 1952; Warming, 1895), however, that numerous stamens have evolved from few stamens in a "primitive" malvacean ancestor may be partially correct. Recent phylogenetic analyses (Chase et al., 1993; Hufford, 1992) support the view that the centrifugally initiated numerous stamens of Malvales, Violales, and Theales are derived from two whorls of five stamens each through a secondary increase in number.

Documentation of the phylogenetic pattern discussed herein sets the stage for additional, more thorough analyses of Malvaceae s.l., especially those employing molecular characters.

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Appendix: List of Specimens Consulted in Cladistic Analysis

The list of items that follows is supplemented by the literature (see citations in the list below and references cited in text).

- Abutilon hulseanum* (Torr. & Gray) Torr. ex Chapman; Baltzell 2583 (FLAS); Shuey 2422 (FLAS).
- A. hypoleucum* Gray; Fryxell 788 (MO); Nelson 6111 (MO); Purpus 1261 (MO).
- Adansonia digitata* L.; Correia 1962 (MO); Greenway & Kanuri 14614 (MO); Judd 5540 (FLAS).
- A. za* Baill.; Phillipson 2630 (MO).
- Apeiba tibourbou* Aubl.; Stern et al. 601 (MO); Sullivan 251 (MO).
- Berrya ammonilla* Roxb.; Anderson 3981 (MO); Ibrahim 87608 (MO).
- B. cordifolia* (Rottb.) Pers.; Bernardi 15273 (MO).
- Brownlowia* sp.; Havel & Kairo NGF-17376 (MO).
- Byttneria catalpaefolia* Jacq.; Hinton et al. 12634 (MO); Purpus 7590 (MO); Ramirez 589 (MO); Skutch 2868 (MO).
- Carpodiptera africana* Mast.; Faden & Faden 74/1117 (MO); Harris 4028 (MO).
- Cavanillesia platanifolia* (Humb. & Bonpl.) H.B.K.; Croat 8421 (MO); Gentry 6737 (MO); Sousa 11081 (MO).
- Ceiba pentandra* (L.) Gaertn.; Covert s.n., 5 July 1972 (FLAS); Tucker s.n., 7 Feb 1962 (FLAS).
- Chorisia insignis* Kunth.; Gentry 53512A (MO); Gentry & Palaci 51732 (MO); West s.n., 11 Sept 1947 (FLAS).
- Chorisia speciosa* St. Hil.; Binacional 620 (MO); Norland s.n., 21 Oct 1966 (FLAS); Pérez 254 (MO); Schinini & Mereles 24663 (MO).
- Clappertonia ficifolia* (Willd.) Decne.; Bos 3162 (MO); Thomas 6230 (MO).
- Corchorus hirsutus* L.; Catino et al. 9 (FLAS); Roberto I-35 (FLAS).
- C. siliquosus* L.; D'Arcy 750C (FLAS); Proctor 11266 (FLAS).
- Dipterocarpus oblongifolius* Bl.; Chung 2636 (MO); Meijer & Duncan 13 (MO).
- Dombeya wallichii* (Lindl.) Benth. & Hook. ex Hook.f. & Jackson; Burch 6452 (FLAS); D'Arcy 1407 (FLAS).
- Durio crassipes* (Hassk.) Becc.; Othman et al. S.41337 (MO).
- D. zibethinus* L.; Gentry 4996 (MO).
- Elaeocarpus sphaericus* (Gaert.) Schumann; Huang et al. 10584 (MO).
- E. stipularis* Bl.; Maxwell 82-69 (MO).
- Entelea arborescens* R. Br.; Chapman CHR-258569 (MO); Gardner s.n., 12 Oct 1972 (FLAS).
- Firmiana simplex* (L.) W. F. Wight; Blum 2728 (FLAS); Reimer s.n., 3 June 1905 (FLAS); West 8702 (FLAS).
- Fremontodendron californicum* (Torr.) Cov.; Baker 4250 (MO); Dunn et al. 20822 (MO); Moran et al. 24246 (FLAS); Thorne & Munoz 38016 (MO).
- Grewia asiatica* L.; Gillis 10412 (MO); West s.n., 12 Sept 1947 (FLAS).
- G. coriacea* Mast.; Gentry & Pilz 32710 (MO); Jacques-Félix 2257 (MO).

- G. occidentalis* L.; Hough s.n., 28 Jan 1975 (FLAS); Kemp 978 (MO); Liebenberg 7772 (MO); West s.n., 16–21 June 1949 (FLAS).
- Guazuma ulmifolia* Lam.; Croat 6780 (MO); D'Arcy 723C (FLAS); Gonzales 302 (FLAS); Kennedy 2875 (MO); Rugel 207 (FLAS).
- Helicteres guazumaefolia* H.B.K.; Lazor 2196 (FLAS); Smith 2172 (FLAS); Stergios & Utrera 2312 (FLAS).
- H. jamaicensis* Jacq.; West & Arnold 544 (FLAS).
- H. lhotzkiana* (Schott & Endl.) Schumann; Palacios 1897 (MO).
- H. semitriloba* Bertero; Watson & Mejia 1058 (FLAS); West s.n., 10 Sept 1947 (FLAS).
- Heliocarpus attenuatus* Wats.; Templeton 7366 (FLAS).
- H. popayanensis* H.B.K.; Smith 4866 (FLAS).
- Hibiscus grandiflorus* Michx.; Orsenigo s.n., 28 June 1979 (FLAS).
- H. moscheutos* L. subsp. *incanus* (Wendl.) Ahles; Easterday & Judd 574 (FLAS).
- Huberodendron patinoi* Cuatr.; Monsalve 761 (MO).
- H. swietenoides* (Gleason) Ducke; Ducke 874 (MO).
- Lasiopetalum acutiflorum* Turcz.; Pritzl 701 (MO).
- L. baueri* Steetz.; Whibley 3713 (MO).
- Luehea candida* (DC.) Mart.; Neill 7424 (FLAS).
- L. ochrophylla* Mart.; Williams & Assis 8003 (FLAS).
- L. seemanii* Triana & Planch.; McDaniel 10317 (FLAS).
- L. speciosa* Willd.; Aymard et al. 1828 (MO); Gonzales 338 (FLAS); Solomon 9865 (MO); Valverde & Pena 7 (MO); Woytkowski 6839 (MO).
- Maxwellia lepidota* Baill.; McPherson 5281, 5290 (MO).
- Melochia tomentosa* (L.) Britt.; Fisher-Meerow 546 (FLAS); Hanley 5-120 (FLAS); Wilbur 8271 (FLAS).
- Monotes africanus* A. DC.; Mendes 801 (MO); Phillips 3350 (MO).
- M. discolor* R. E. Fr.; Strid 2620 (MO).
- Muntingia calabura* L.; Croat 43644 (FLAS); D'Arcy 2618 (FLAS); Zona 465 (FLAS).
- Nesogordonia kabingaensis* (Schumann) Capuron; Gentry & Pilz 32660 (MO); Testu 7909 (MO).
- Ochroma lagopus* Sw.; Breckon 3109 (FLAS); McDaniel 14772 (FLAS).
- Pachira aquatica* Aubl.; Beaman 591 (FLAS); Croat 5613, 9802 (MO); Judd & White s.n., 9 July 1982 (FLAS).
- Pentace borneensis* Pierre; Lee S.46487 (MO).
- Pseudobombax ellipticum* (H.B.K.) Dug.; Brumbach 7864 (FLAS); Whitty s.n., 13 July 1987 (FLAS).
- Pterospermum acerifolium* Willd.; MacCubbin s.n., 5 Apr 1976 (FLAS); Ohn s.n., 10 Mar 1926 (MO); West s.n., 27 Apr 1946 (FLAS).
- P. blumeianum* Kortte.??; Merrill 2011 (MO).
- P. heterophyllum* Hance; Wang 34757 (MO).
- Quararibea asterolepis* Pittier; Utley 5477 (MO); Wilbur 23370 (MO).
- Reevesia lofouensis* Chun; Wang 35967 (MO).
- R. siamensis* Craib; Maxwell 89-1528 (MO).
- R. thyrsoides* Lindl.; Chun 41043 (MO); Wang 36698 (MO).
- Schoutenia accrescens* (Mast.) Curtis; Maxwell 82-103 (MO).
- Sida acuta* Burm.; Godfrey 63464 (FLAS); Ward 4368 (FLAS).
- S. cordifolia* L.; Baltzell 11637 (FLAS); Wunderlin 5726 (FLAS).
- Sloanea* aff. *rufa* Planch. ex Benth.; Liesner 12480 (MO); Zaruma 555 (MO).
- S. fragrans* Rusby; Smith et al. 13719 (MO).
- Sphaeralcea ambigua* Gray; Curry s.n., 29 Apr 1979 (FLAS); Curry s.n., 9 May 1981 (FLAS).
- S. angustifolia* (Cav.) G. Don; Ward 5751 (FLAS).
- Spirotheca rhodostyla* Cuatr.; Smith 4477 (MO).
- S. rimbachii* Cuatr.; Dodson et al. 15194 (MO); Gentry et al. 14395 (MO).
- Sterculia apetala* (Jacq.) Karst.; Breckon 3165 (FLAS); Judd 2208 (FLAS); West s.n., 9 Apr 1953 (FLAS).
- S. ceramica* R. Br.; Beaman 593 (FLAS); Judd 2207 (FLAS).
- S. foetida* L.; Avery 335 (FLAS); Judd 2206 (FLAS).
- Theobroma grandiflora* (Willd. ex Spreng.) Schum.; Ayala 495 (MO); Cuadros 593 (MO).
- Thespesia populnea* (L.) Solander; Howard 11418 (FLAS); Laessle s.n., 3 Feb 1960 (FLAS); Perkins 73 (FLAS); West & Arnold 597 (FLAS).
- Tilia americana* L. var. *caroliniana* (Mill.) Castig.; West s.n., 9 July 1935, 1 June 1937 (FLAS).
- T. americana* L. var. *heterophylla* (Vent.) Loudon; Adams 19003 (FLAS); McQuilkin 8598 (FLAS).
- Triumfetta semitriloba* Jacq.; D'Arcy 413D (FLAS); Popenoe 10 (FLAS).
- Urena lobata* L.; Baltzell 8387 (FLAS); Feinsinger 194 (FLAS); Laessle s.n., 12 Oct 1940 (FLAS); Murrill s.n., 12 Oct 1941.
- Waltheria indica* L.; Anthone et al. 1-6 (FLAS); Snedaker E-175 (FLAS).

In addition, the following floras were consulted regarding variability of the above listed genera: Adams, 1972; Black, 1922–1929; Bornstein, 1989; Cheeseman, 1925; Corner, 1952; Correll & Correll, 1982; Dale & Greenway, 1961; Fawcett & Rendle, 1926; Fryxell, 1988, 1989; Gentry, 1993; Hutchinson & Dalziel, 1927–1928; Kearney, 1951; Keay et al., 1964; Oliver, 1868; Proctor, 1984; Ridley, 1922; Robyns, 1964a, 1964b, 1964c, 1965; Standley & Steyermark, 1949.