RELATIONSHIPS AND MORPHOLOGICAL CHARACTER CHANGE AMONG GENERA OF CELASTRACEAE SENSU LATO (INCLUDING HIPPOCRATEACEAE)[1]

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ABSTRACT

A cladistic analysis of Celastraceae sensu lato (including Hippocrateaceae) was conducted using 69 informative morphological characters representing variation in gross morphology, seed anatomy, seedling development, leaf anatomy, wood anatomy, pollen morphology, and karyotype. The 82 taxa sampled included 31 genera of Celastraceae sensu stricto, 22 genera of Hippocrateaceae, 7 genera that have been associated with Celastraceae (*Brexia, Canotia, Forsellesia, Goupia, Lophopyxis, Plagiopteron,* and *Siphonodon*), and outgroups from Corynocarpaceae, Crossosomataceae, Euphorbiaceae, Geissolomataceae, Huaceae, Saxifragaceae, and Stackhousiaceae. Character state changes mapped onto the phylogenetic hypotheses were generated to infer patterns of evolution of characters, including the aril in Celastraceae s.l. Based on this analysis, the inclusion of *Bhesa* and *Goupia* within Celastraceae s.l. is ambiguous, and *Siphonodon* should be excluded from Celastraceae s.l. *Forsellesia* (= *Glossopetalon*) is supported as closely related to Crossosomataceae. *Lophopyxis* is supported as a member of Euphorbiaceae. *Canotia* is resolved as the sister group of *Acanthothamnus,* included within Celastraceae sensu stricto. *Brexia* is resolved as the sister group of Celastraceae s.l. Theodor Loesener's subfamilies and tribes of Celastraceae s. str. are generally not supported. The Hippocrateaceae are resolved as having a single origin, and as nested within a paraphyletic Celastraceae s. str. with *Brassiantha, Dicarpellum,* and *Sarawakodendron* as "transitional" genera between the groups. *Campylostemon* appears as a derived group within Hippocrateaceae, not as a "transitional" genus. Nicolas Hallé's subfamilies of Hippocrateaceae are supported, but his tribes generally are not, with Campylostemoneae and Helictonemateae nested within Hippocrateeae. *Plagiopteron* is resolved as nested within tribe Hipocrateeae.

The Celastraceae sensu lato (including Hippocrateaceae) are a primarily pantropical family of woody lianas, shrubs, and trees with several subtropical and fewer temperate members. Members of the family exhibit substantial variation in stamen, fruit, and seed characters, which have been used to subdivide the family taxonomically. Economically important taxa within Celastraceae include: "khat," *Catha edulis,* used socially as a stimulant in northeastern Africa, the Arabian Peninsula, and Madagascar (Krikorian, 1985); *Euonymus, Celastrus,* and *Paxistima,* which are widely cultivated as ornamentals; *Kokoona zeylandica,* as a source of oil; fruits of *Salacia* from which the pulp is eaten; and various species of *Euonymus,* used for latex, medicines, and dyes (Hou, 1962; Heywood, 1993). This large family (850 to 1300 species) has not been the subject of a comprehensive taxonomic treatment since Loesener's monograph (1942a, 1942b), and a phylogenetic analysis of intergeneric relationships in the family is not available.

The Celastraceae s.l. have been estimated to include about 55 genera and 850 species (Hallé, 1986; Thorne, 1992; Heywood, 1993), 60–70 genera (Robson et al., 1994), 78 genera and 1150 species (Scholz, 1964), 85 genera (Brummitt, 1992), 85–90 genera and 860 species (Takhtajan, 1997), 90 genera and over 1000 species (Hou, 1962), 1100 species (Cronquist, 1981), or up to 94 genera and 1300 species (Mabberley, 1993). Estimates vary in part because relatively little taxonomic work has been done on the family, and because of dis-

agreements regarding generic delimitations. Also, questions concerning the recognition of Celastraceae and Hippocrateaceae as distinct families have existed since the initial description of Celastraceae (as the order "Celastrinae") by Robert Brown in 1814. Brown (1814: 555) stated that Celastrinae "in many respects so nearly approaches to the Hippocraticeae of Jussieu, that it may be doubted whether they ought not to be united." Diagnostic characters that have been used to distinguish Hippocrateaceae from Celastraceae are: stamens 3 (rarely 2 or 5) versus 4 or 5 (rarely 10), filaments inserted inside the disk versus at or below the margin of the disk, filaments connate at the base and recurved versus distinct and often incurved, and seeds not albuminous versus albuminous (Bentham & Hooker, 1862; Cronquist, 1981).

Since the original family descriptions (de Jussieu, 1811; Brown, 1814), Hippocrateaceae and Celastraceae have been recognized either as two distinct families (de Candolle, 1825; Lindley, 1853; Miers, 1872; Loesener, 1892a, 1892b, 1942a, 1942b; Smith, 1940; Perrier de la Bâthie, 1946; Hallé, 1962; Hutchinson, 1969; Cronquist, 1981) or as a single family (Bentham & Hooker, 1862 [as separate tribes of the order Celastrineae]; Baillon, 1880 [as 2 of 7 separate series of Celastraceae]; Hou, 1962, 1964; Robson, 1965; Hallé, 1978; Takhtajan, 1980, 1997; Dahlgren, 1983; Thorne, 1992; Robson et al., 1994). For the unified family, Celastraceae have been conserved over Hippocrateaceae (Bullock, 1958). Excellent taxonomic histories of Hippocrateaceae are provided by Miers (1872) and Smith (1940).

Miers (1872) cited 11 characters differentiating Hippocrateaceae from Celastraceae s. str. However, Hou (1964: 389) noted, "Many new genera and species have been described since 1873 [sic] which have obliterated many of Miers's arguments, and recent specialists agree that, if any, only few characters do hold." Lindley (1853) and Loesener (1942b) recognized Hippocrateaceae as distinct from Celastraceae s. str. based on one character—stamen number 4 or 5 in Celastraceae s. str., versus 3 (rarely 2) in Hippocrateaceae. This was the sole basis for Loesener's (1942a) transfer of two genera (*Campylostemon* and *Cheiloclinium*), which earlier workers included within Hippocrateaceae (Miers, 1872; Baillon, 1880; Loesener, 1892b; Smith, 1940), to Celastraceae s. str. Recently, on the basis of the very different fruits and seeds of *Hippocratea* s.l. relative to those of *Salacia* s.l., it has been suggested that taxa assigned to Hippocrateaceae have been derived from different parts of Celastraceae s.

str. such that the Hippocrateaceae are a polyphyletic group (Robson, 1965; Robson et al., 1994).

Hallé's taxonomic treatments of Hippocrateaceae. Hallé (1962) recognized Hippocrateaceae as a family, separate from Celastraceae. He described two subfamilies (Hippocrateoideae, Salacioideae) and three tribes (Campylostemonae [sic] and Hippocrateae [sic] of subfamily Hippocrateoideae; Salaciae [sic] of subfamily Salacioideae). In later publications, Hallé (1978, 1981, 1983, 1984) recognized Hippocrateaceae as a tribe ("Hippocrateae") of Celastraceae. In two later floras, Hallé (1986, 1990) cited Celastraceae as composed of two subfamilies—Celastroideae and Hippocrateoideae. Subfamily Hippocrateoideae was composed of four tribes—Salacieae (as "Salaciae" in 1986: 12), Helictonemeae [sic] ("Helictonemae" in 1986: 12), Hippocrateae, and Campylostemoneae. Following the *Code* (Greuter et al., 1994), Hallé's tribe "Helictonemeae" is properly Helictonemateae and Hallé's tribe "Hippocrateae" is properly Hippocrateeae (Richard Korf, pers. comm. 1998; note: we do not validly propose these names here).

In the classification of Hallé (1986, 1990), in which subfamily Hippocrateoideae is divided into four tribes, the hierarchical information of the classification of Hallé (1962), in which Hippocrateaceae are divided into subfamilies and tribes, is lost. It is unclear if this was intentional. In Hallé's most recent publication (Robson et al., 1994), in which he was a co-author, no subfamilial classification was provided.

Cronquist's five "aberrant genera." Apart from the question of including Hippocrateaceae in Celastraceae, there is an additional set of problems in delimiting Celastraceae. Cronquist (1981: 714) stated, "[Celastraceae] is rather diversified and loosely knit," and he segregated "five of the more aberrant genera. . ." as separate families. These five genera are *Canotia*, *Chingithamnus*, *Goupia*, *Lophopyxis*, and *Siphonodon*. *Chingithamnus* has been recognized by Handel-Mazzetti (1933) and Merrill and Freeman (1940) as a member of *Microtropis* (Celastraceae). We know of no additional work on *Chingithamnus* other than the original description by Handel-Mazzetti (1932) and the later treatment of the species as a member of *Microtropis* by Handel-Mazzetti (1933) and Merrill and Freeman (1940). The remaining four genera are more problematic. Each genus has one or more character states that are unique within Celastraceae s.l. if considered a member of the family.

Canotia has been variously referred to Rutaceae (Gray 1877), Koeberliniaceae (Barnhart, 1910), and

Celastraceae (Hutchinson, 1969), as an anomalous genus (Loesener 1942a), or as closely related to *Acanthothamnus* (Johnston, 1975). Inclusion of *Canotia* within Celastraceae (and its close relation to *Acanthothamnus*) was later supported by Tobe and Raven (1993) on the basis of embryology. The unique character state of *Canotia* is its septicidally dehiscent capsules.

Goupia has been recognized as unusual relative to other members of Celastraceae by the vascular structure of its petiole (Metcalfe & Chalk, 1950), gross morphology (T. A. Sprague, in Metcalfe & Chalk, 1950), and wood anatomy (Loesener, 1942a), but not on the basis of leaf anatomy (Den Hartog née Van Ter Tholen & Baas, 1978). Hutchinson (1969: 357) discussed the taxonomic history of *Goupia*, which has also been assigned to Araliaceae and Rhamnaceae, and concluded, "If only on account of these diverse views it seems better to regard it as a separate family, following Miers (Contrib. Bot. 2, 134, t. 74 (1860–69))." *Goupia* has been suggested to be more closely related to Euphorbiaceae than to Celastraceae based on a chloroplast *rbc*L 5′ flanking sequence gene tree (Savolainen et al., 1997). Unique character states of *Goupia* are its umbellate inflorescences and bilobed extended anther connectives with brush-hairy tips.

Lophopyxis, when described by Hooker (1887–1888; 1888), was tentatively assigned to Euphorbiaceae. Pfeiffer (1951) recognized the genus as the only member of its own family, Lophopyxidaceae. This treatment was followed by Willis (1966), Dahlgren (1983), Thorne (1992), and Takhtajan (1997). Scholz (1964) included *Lophopyxis* within Celastraceae subfamily Tripterygioideae. The unique character states of *Lophopyxis* relative to Celastraceae s.l. are its tendrils, tomentose ovaries, and obturators.

Siphonodon has been recognized as unusual relative to other genera in Celastraceae based on structure of the gynoecium (Croizat, 1947), wood anatomy (Metcalfe & Chalk, 1950), and pollen morphology (Erdtman, 1952). *Siphonodon* has been retained in close relationship to Celastraceae s. str. (Loesener, 1892a, 1942a; Croizat, 1947), Hippocrateaceae (Bentham & Hooker, 1862; Hutchinson, 1969), or Celastraceae s.l. (Hou, 1963). This recognition of *Siphonodon* as unusual, but closely related to other members of Celastraceae s.l., was supported by an *rbc*L 5′ flanking sequence gene tree (Savolainen et al., 1997) in which *Siphonodon* was resolved as sister group of the five Celastraceae s.l. (including *Brexia*) sampled. A thorough summary of the varied taxonomic history of *Siphonodon* is given by Hou (1963). Unique character states of

Siphonodon are the presence of staminodes and stamens in a single flower (see Berkeley, 1953, in which the disk of Celastraceae is suggested to be composed of suppressed stamens), an apical hollow in the center of the ovary, and many irregularly superposed locules in the ovary.

Relationships of Celastraceae. Cronquist (1981) included Celastraceae s. str. and Hippocrateaceae as 2 of 11 families in the order Celastrales. The other families included were Aextoxicaceae, Aquifoliaceae, Cardiopteridaceae, Corynocarpaceae, Dichapetalaceae, Geissolomataceae, Icacinaceae, Salvadoraceae, and Stackhousiaceae. Cronquist recognized the Dichapetalaceae as anomalous and the inclusion of Aextoxicaceae, Cardiopteridaceae, Corynocarpaceae, and Geissolomataceae as debatable.

Dahlgren (1983) recognized the order Celastrales as including Celastraceae s.l., Lophopyxidaceae, Stackhousiaceae, Cardiopteridaceae, and Corynocarpaceae (the last two as "uncertain"). Thorne (1992) cited the order Celastrales as including all the families Dahlgren did, except Cardiopteridaceae and Corynocarpaceae. Takhtajan (1980) described the order Celastrales as including all the families included by Cronquist, Dahlgren, and Thorne (except Aextoxicaceae and Dichapetalaceae), plus Medusandraceae, Paracryphiaceae, and Sphenostemonaceae. Takhtajan (1997) narrowed his circumscription of Celastrales to include only Celastraceae s.l., Goupiaceae, Lophopyxidaceae, and Stackhousiaceae. *Siphonodon* has been treated as a separate family (Takhtajan, 1980; Cronquist, 1981) or included within Celastraceae (Dahlgren, 1983; Thorne, 1992; Takhtajan, 1997). Likewise, *Goupia* has been treated as a separate family (Takhtajan, 1980, 1997; Cronquist, 1981; Thorne, 1992) or included within Celastraceae (Dahlgren, 1983).

Recent evidence has suggested that the Celastrales, as defined by Cronquist, Dahlgren, Takhtajan, and Thorne, are an unnatural group. Aquifoliaceae and Icacinaceae have been recognized as not closely related to Celastraceae s.l. by Savolainen et al. (1994, 1997) and Spichiger et al. (1993), using cpDNA sequence from the 5′ flanking region of *rbc*L. Likewise, the gene tree presented by Savolainen et al. (1997) suggested that Aextoxicaceae, Corynocarpaceae, Dichapetalaceae, Salvadoraceae, and Stackhousiaceae are all more closely related to families not included in Cronquist's Celastrales than to Celastraceae. In the gene tree, only Geissolomataceae were resolved as closely related to Celastraceae s.l. Salvadoraceae have been shown to be included within the order Capparales based on

morphology (Rodman, 1991) and *rbcL* sequence data (Rodman et al., 1996).

In the *rbcL* gene trees presented by Chase et al. (1993) and Morgan and Soltis (1993), *Brexia* (Brexiaceae) was resolved as the sister group of *Euonymus* (Celastraceae). The sister group of this clade was *Lepuropetalon* and *Parnassia* (Saxifragaceae). The same resolution of these taxa was found in the 18S nrDNA gene tree presented by Soltis et al. (1997). In the combined analysis of *rbcL* and many non-molecular characters presented by Nandi et al. (1998), Huaceae were resolved as the sister group of Plagiopteraceae plus "Celastrales s. str." (= Goupiaceae, Celastraceae, Stackhousiaceae). Four taxa within Celastraceae s.l. (one species each of *Hippocratea* and *Salacia*, two species of *Euonymus*) were sampled by Savolainen et al. (1994) and Spichiger et al. (1993). In the 5′ flanking region of the *rbcL* gene tree, *Salacia* was resolved as the sister group of *Euonymus* and *Hippocratea*, and Euphorbiaceae were resolved as the sister group of Celastraceae s.l. Savolainen et al. (1997) sampled the Celastrales more extensively. In their gene tree, the two species of *Euonymus* were resolved as the sister group of the clade that consists of *Hippocratea* and *Salacia*. *Brexia* was resolved as most closely related to this clade, followed by *Siphonodon* (Celastraceae/Siphonodontaceae), *Parnassia*, and *Geissoloma* (Geissolomataceae) as more distantly related.

The purpose of this study is to investigate patterns of structural character change and phylogenetic relationships within Celastraceae s.l. Based on these patterns, we attempt to: determine relationships among genera placed within Celastraceae s.l., determine if Cronquist's "aberrant genera" should be recognized as separate families or included within Celastraceae s.l., determine if Loesener's (1942a) subfamilies and tribes of Celastraceae s. str. are natural groups, and determine if Hallé's (1962, 1986, 1990) subfamilies and tribes are natural groups.

MATERIALS AND METHODS

Taxon sampling. The taxa included in the analysis are listed in Appendix 1. Members of Celastraceae s. str. are approximately arranged according to Loesener (1942a); members of Hippocrateaceae are arranged by the classification of Hallé (1986, 1990). Two modifications to Loesener's nomenclature are that tribe Eucassineae is recognized as tribe Cassineae, and tribe Eucelastreae is recognized as tribe Celastreae. The reason for this is that names of tribes are based on legitimate generic names (Greuter et al., 1994), and there are no gen-

era "*Eucassine*" or "*Eucelastrus*" (Loesener, 1942a; Royal Botanic Gardens, Kew, 1997). Therefore, Eucassineae and Eucelastreae are not valid tribes (Richard Korf, pers. comm. 1998).

Thirty-five (of about 65 currently recognized) genera of Celastraceae s. str. were sampled in addition to four genera that have been associated with Celastraceae (*Canotia*, *Goupia*, *Lophopyxis*, and *Siphonodon*), but recognized by Cronquist (1981) as separate families. *Chingithamnus*, the fifth genus that Cronquist (1981) recognized as a separate family, is not included in the analysis because Handel-Mazzetti (1933) and Merrill and Freeman (1940) have already reduced it to synonymy within *Microtropis* (Celastraceae). Twenty (of about 26 currently recognized) genera of Hippocrateaceae were sampled. *Brexia* was included in the analysis based on morphological (Perrier de la Bâthie, 1933), embryological (Kamelina, 1988; Tobe & Raven, 1993), and molecular (Chase et al., 1993; Morgan & Soltis, 1993; Savolainen et al., 1997; Soltis et al., 1997) studies that suggest it is closely related to Celastraceae. *Plagiopteron* was included in the analysis based on anatomical (Baas et al., 1979), embryological (Tang, 1994), and molecular (Nandi et al., 1998) studies that suggest it is closely related to Celastraceae.

Genera were selected for inclusion in the analysis based on four criteria. We wanted to include at least two representatives of every subfamily and tribe proposed by Loesener (1942a) and Hallé (1962, 1986, 1990) that include more than one genus, as well as those genera with unusual character states relative to other members of Celastraceae s.l. For character coding, we chose genera that are well described in the literature and/or represented by herbarium specimens at the herbaria visited (see below under "character coding"). Finally, we excluded "wildcard taxa" (terminals resolved in many different locations on most-parsimonious cladograms due to their many missing values; Nixon & Wheeler, 1991) in preliminary analyses. Missing values in these terminals were usually due to poorly detailed published descriptions, coupled with paucity of herbarium specimens available (e.g., many Australian endemics). Also omitted were genera that lack pertinent structures and which were therefore coded as inapplicable for those features (e.g., *Psammomoya*, in which the leaves are reduced to cataphylls).

The decision to use genera instead of representative species in the analysis was based on two factors. First, some publications do not list the individual species examined, only the genera (e.g., Metcalfe & Chalk, 1950). Other publications list

the species examined but describe only the genus, even when the genus is polymorphic for some of the characters described (e.g., Solereder, 1908). Furthermore, if only one species of a genus was selected, and a different species of that genus had been described for a given character, we would not have been able to include that information in our data matrix. This problem is magnified with each successive character scored from the literature as, for example, Erdtman (1952) in describing pollen morphology for a given genus probably did not look at the same species as Mennega (1997) in describing wood anatomy, or as Den Hartog née Van Ter Tholen and Baas (1978) in describing leaf anatomy. Second, many genera were represented by only a few sheets in the herbaria visited. In such cases, some species were only represented by flowering specimens, while other species were only represented by fruiting specimens. If only a single species was used, there would be that much more missing data for the flower or fruit characters, respectively. In our coding, flower characters may have been taken from one species and fruit characters taken from another. These compromises were made to avoid excessive missing values in the data matrix that would result in complete lack of resolution.

The problems with this approach to coding "composite terminals" have been discussed by Nixon and Davis (1991). These problems are: underestimating the cladogram length and overestimating the consistency indices, the most-parsimonious cladogram(s) using composite terminals may differ from the most-parsimonious cladogram(s) when the composite terminals are divided into all naturally occurring combinations of character states, and that the composite terminals are assumed to be monophyletic when they may not be. These factors should be taken into account in interpreting the cladograms presented.

Genera were initially planned to be the terminals in this analysis, but selected genera that were extremely variable in the characters scored were divided into subgenera (when available) or individual species (when subgenera were not available) to partition the variation into separate terminals. The division of *Celastrus* into subgenera follows Hou (1955). The division of *Cheiloclinium* into species groups follows Smith (1940). Note that the terminal "*Cheiloclinium* except species-group *Anomala*" represents members of Smith's other three species groups—*Cognata*, *Hippocrateoides*, and *Serrata*. The division of *Salacia* into subgenera follows Loesener (1942b). *Cassine* is recognized as distinct from *Elaeodendron* following Archer and van Wyk

(1997). The recognition of *Gymnosporia* as distinct from *Maytenus* follows Jordaan and van Wyk (in press). *Quetzalia* is recognized as distinct from *Microtropis* based on Lundell (1970). *Tricerma* is recognized as distinct from *Maytenus* following Lundell (1971). *Catha* is restricted to *Catha edulis* following Robson (1965) and the assertion by van Wyk and Prins (1987) that the other two species that have been assigned to *Catha* are not closely related to *Catha edulis*. When individual species were used as terminals (as in *Cassine, Elaeodendron, Euonymus,* and *Maytenus* s.l. [including *Gymnosporia* and *Tricerma*]), at least two representative species of each genus were included to represent some breadth of the character state variation and to test the monophyly of that genus. Individual species were selected based on how divergent they are relative to one another in terms of character states scored in this analysis (we tried to maximize the variation to test monophyly of the genus), and based on our ability to code character states for them (i.e., herbarium specimensand/or thorough literature descriptions available).

Outgroup selection. Outgroup terminals were selected from seven families: Corynocarpaceae, Crossosomataceae, Euphorbiaceae, Geissolomataceae, Huaceae, Saxifragaceae, and Stackhousiaceae. Morphological (Takhtajan, 1980, 1997; Cronquist, 1981; Dahlgren, 1983; Thorne, 1992) and molecular (Chase et al., 1993; Morgan & Soltis, 1993; Savolainen et al., 1994, 1997; Soltis et al., 1997; Nandi et al., 1998) studies have variously suggested that members of these outgroup families are closely related to Celastraceae s.l. Crossosomataceae were included because *Forsellesia* (= *Glossopetalon* A. Gray) has been transferred from Celastraceae to Crossosomataceae (Thorne & Scogin, 1978). Based on this transfer, *Crossosoma* and *Forsellesia* are expected to be resolved as sister groups. The specific genera of the seven outgroup families were chosen based on literature and/or herbarium specimens available describing character states in these genera, possession of structures that could be scored for the characters included in the analysis, and genera that were not too variable for the characters included in the analysis. We did not include *Euphorbia* (Euphorbiaceae) because of extreme reduction in its flowers. The cladogram was rooted with genera from Euphorbiaceae.

Character coding. Seventy-nine characters representing gross morphology, leaf and stem anatomy, pollen morphology, and karyotype characters were scored. Of these 79 characters, 10 are uninformative. These 10 uninformative characters were in-

Figure 1. "Basal" portion of strict consensus of 115 most-parsimonious cladograms (309 steps, CI = 0.36, RI = 0.72, excluding uninformative characters; 321 steps including uninformative characters) for 82 taxa of Celastraceae and related families, obtained by equal-weighted analysis of 69 informative characters (Appendices 1, 2). Bremer-support values (Bremer, 1988) greater than 1 are plotted above branches.

cluded in this paper (but not in cladogram searches or cladogram statistics) for their information content in delimiting genera. The "unique" character states are not autapomorphies (unless the genus is mono-

typic); they are synapomorphies for individual genera. Characters were initially taken from original taxon descriptions, monographs of individual genera and entire families, e.g., Loesener (1942a,
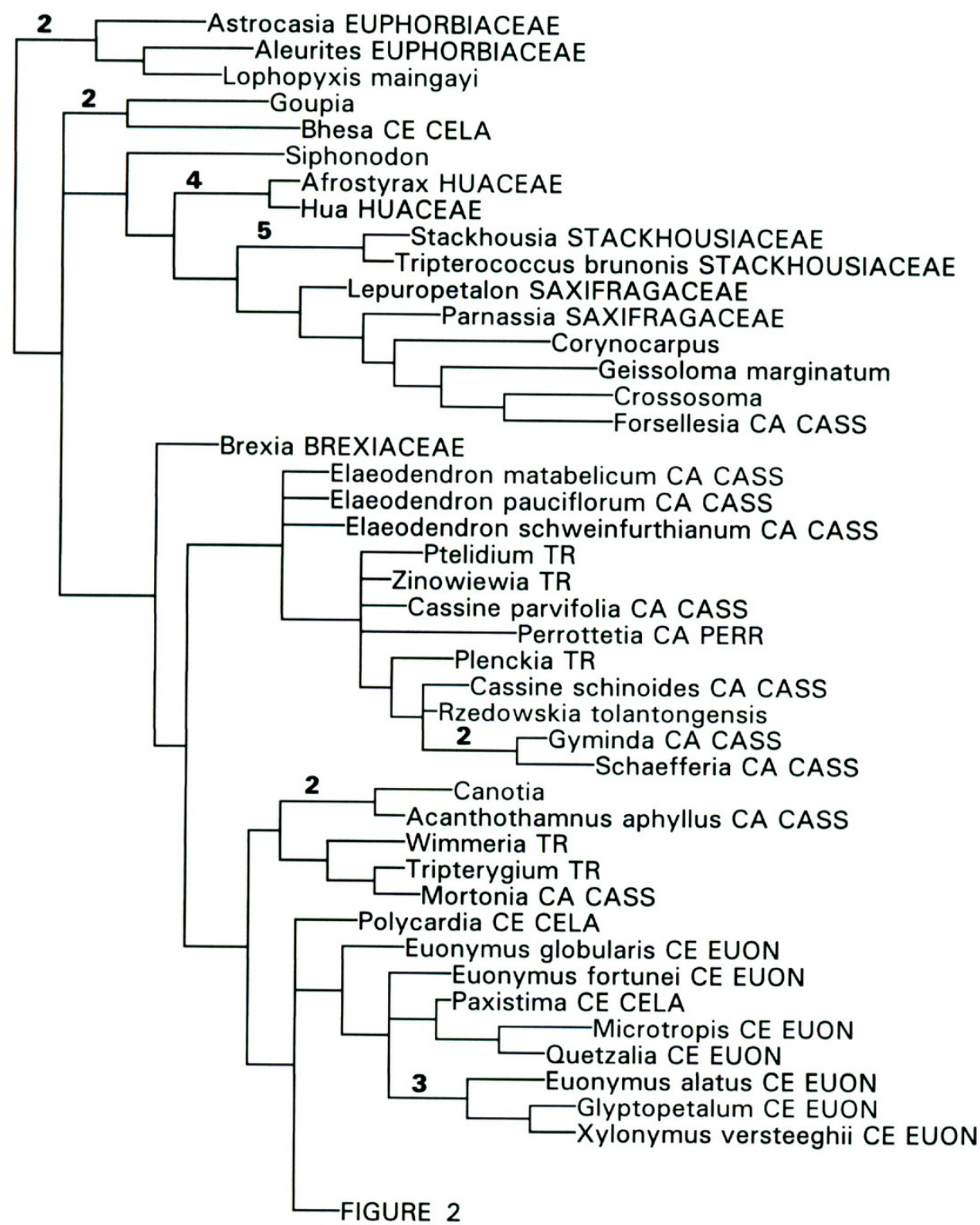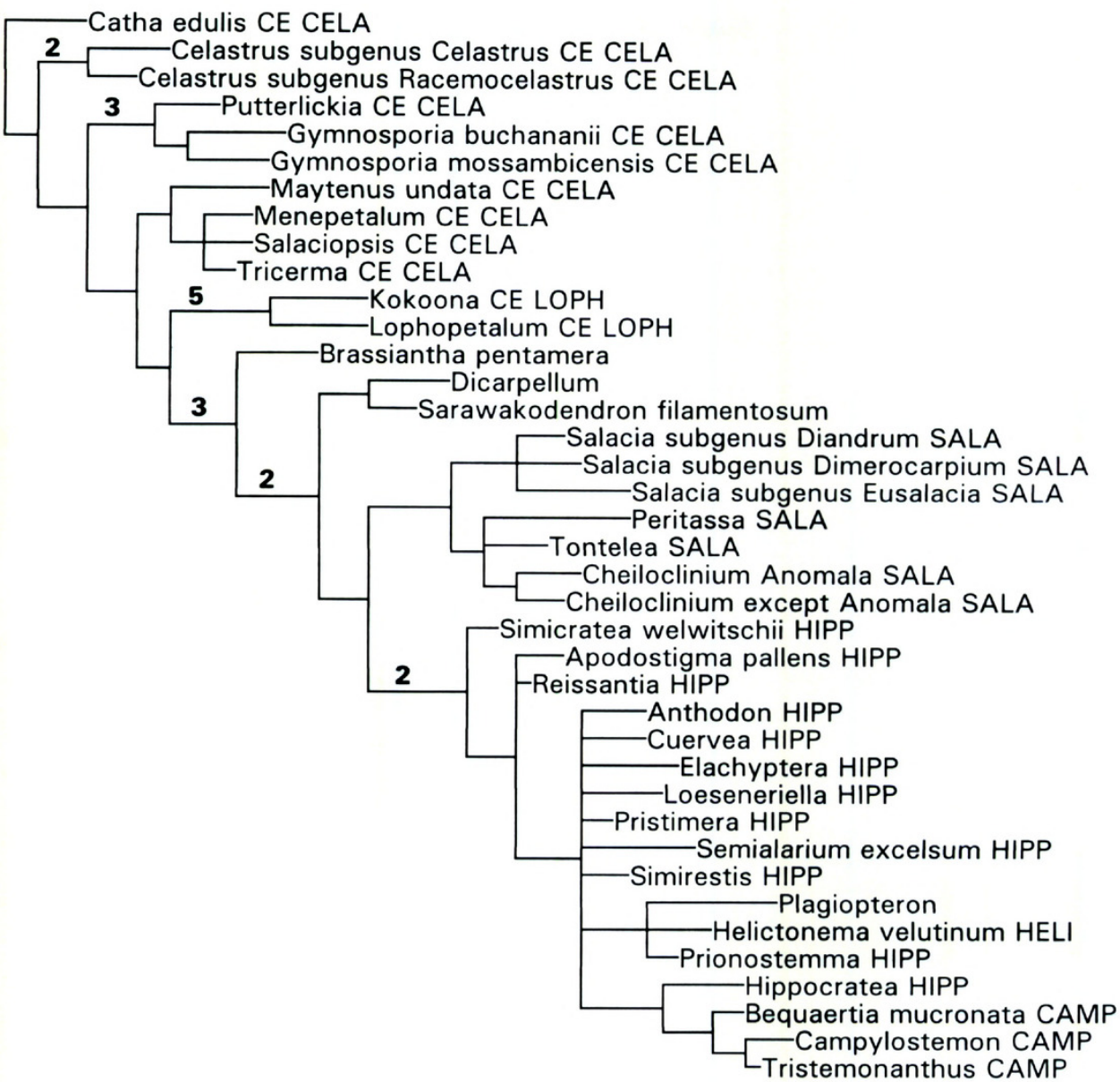
Figure 2. "Distal" portion of strict consensus of 115 most-parsimonious cladograms (309 steps, CI = 0.36, RI = 0.72, excluding uninformative characters; 321 steps including uninformative characters) for 82 taxa of Celastraceae and related families, obtained by equal-weighted analysis of 69 informative characters (Appendices 1, 2). Bremer-support values (Bremer, 1988) greater than 1 are plotted above branches.

1942b), floras, surveys for specific characters, e.g., "Les pollens des Celastrales" by Lobreau-Callen (1977), large-scale taxonomic treatments, e.g., Cronquist (1981), and large-scale anatomical treatments, e.g., Metcalfe and Chalk (1950). The 151 initial potential characters were examined for feasibility of scoring, errors in the literature, independence of characters, distinctness of character states, and constancy of character states within taxa. Material permitting, characters of gross morphology were then examined on herbarium specimens at BH, MO, NY, P, and US. The 79 final characters are described in Appendix 2, which includes comments on distribution of character states, literature sources used, how character states were delimited, and how question-

able character states were scored. The characters that were rejected for inclusion in the cladistic analysis, and the reason(s) for rejection are listed in Appendix 3. The data matrix is in Appendix 4. Literature sources used to code gross-morphological characters are listed in Appendix 1. Herbarium specimens used to code gross-morphological characters are listed in Appendix 5.

If observation of properly annotated herbarium specimens contradicted literature entries, the observations were used instead of the literature entries (e.g., *Elaeodendron* for character 39). However, if the literature described a more general condition than observed in the specimens (e.g., observed only cymose inflorescences, literature de-

scribes the genus as having cymose or paniculate inflorescences), the literature entry was used.

For anatomical characters taken from Solereder (1908), Record (1943), Metcalfe and Chalk (1950), and Den Hartog née Van Ter Tholen and Baas (1978) where multiple taxa are listed as having been studied, but an unusual character state was described for only some of the taxa, the other taxa that were cited as being studied, but which were not described for the unusual character state, were coded as having the "normal" character state. For example, Record (1943) described Celastraceae as having generally simple perforation plates, but cited 2 of the 13 genera he examined as having scalariform perforation plates. Based on this information, the other 11 genera he examined were coded as having simple perforation plates.

Where an older paper described a character state for a given species, the species was referenced in *Index Kewensis* ver. 2.0 (Royal Botanic Gardens, Kew, 1997) to determine if the species has been assigned to a different genus since the publication. An example is Solereder (1908) in which *Salacia calypso* was described for character 70. However, the species has been transferred to *Tontelea*. Therefore, *Tontelea* was coded for this character based on the description, not *Salacia*.

If a character state was described for only one species from a genus that is not monotypic, the entire genus was coded as having that character state. Furthermore, if a genus was divided into subgenera (*Celastrus, Salacia*), species groups (*Cheiloclinium*), or individual species (*Cassine, Elaeodendron, Euonymus, Gymnosporia, Maytenus*), each of these terminals was coded identically for that character state. An example is *Elaeodendron*, which is represented in this study by three species. *Elaeodendron roxburghii* was described in *Index to Plant Chromosome Numbers 1975–1978* (Goldblatt, 1981: 182) as having 17 chromosomes in the gametophyte stage. Based on this, which is the only report of chromosome numbers we know of in *Elaeodendron*, all three species of *Elaeodendron* that were included in the analysis were coded as having a base chromosome number of 17.

Data analysis. The character data matrix (Appendix 4) was created using *Dada* ver. 1.7 (Nixon, 1998b). Cladistic analysis was performed using *Nona* ver. 1.6 (Goloboff, 1993). The analysis was performed through 10,000 searches, each consisting of cladogram construction using a random-taxon entry sequence followed by tree-bisection-reconnection branch swapping with up to 50 most-parsimonious cladograms retained (*hold/50*

mult*10000). The most-parsimonious cladograms retained were then swapped to completion using tree-bisection reconnection (*max**). The strict-consensus cladogram (Schuh & Polhemus, 1980; Sokal & Rohlf, 1981) was calculated by *Nona* (*nelsen*). The most-parsimonious cladograms and the strict-consensus cladogram were examined in and printed from *Clados* version 1.7 (Nixon, 1998a). Bremer-support values (Bremer, 1988) were estimated using *Nona* with 10,000 cladograms retained up to five steps longer than the most-parsimonious cladograms (*hold 10000 bs 5*).

RESULTS

Seventy-nine characters were coded for 82 taxa. Of 6478 cells in the data matrix (Appendix 4), 12.1% of the cells were scored missing (unobserved), 13.2% of the cells were scored as inapplicable (the character is not present in a given taxon), 1.6% of the cells were scored as polymorphic (complete or subset), and 73.1% of the cells were scored with single character states.

Cladistic analysis resulted in 115 most-parsimonious cladograms of length 321 (309 excluding uninformative characters), ensemble consistency index (CI; Kluge & Farris, 1969) of 0.36 (excluding uninformative characters), and ensemble retention index (RI; Farris, 1989) of 0.72. One of the 115 most-parsimonious cladograms was arbitrarily selected and is presented in Figures 3–5 with character state changes mapped on it. Fifty-nine clades are resolved in the strict consensus cladogram (Figs. 1, 2). *Lophopyxis* and the two genera of Euphorbiaceae form a clade. *Bhesa* and *Goupia* are sister groups. *Siphonodon* is the sister group of the clade that consists of the outgroup taxa (except Euphorbiaceae) and *Forsellesia*. Huaceae (*Afrostyrax* and *Hua*) and Stackhousiaceae (*Stackhousia* and *Tripterococcus brunonis*) are monophyletic groups. *Forsellesia* is the sister group of *Crossosoma* (Crossosomataceae). *Brexia* is sister to the clade that consists of Celastraceae s. str. (except *Bhesa* and *Forsellesia*) and Hippocrateaceae.

Subfamily Celastroideae and the Hippocrateaceae are nested within a paraphyletic (Hennig, 1966; Farris, 1974) assemblage of subfamilies Cassinoideae and Tripterygioideae. Genera assigned to subfamily Tripterygioideae are nested among members of subfamily Cassinoideae. *Perrottetia* (subfamily Cassinoideae tribe Perrottetieae) is nested among members of subfamily Cassinoideae tribe Cassineae. Subfamily Celastroideae is a paraphyletic group, in which the Hippocrateaceae are nested. Subfamily Celastroideae tribe Euonymeae is a
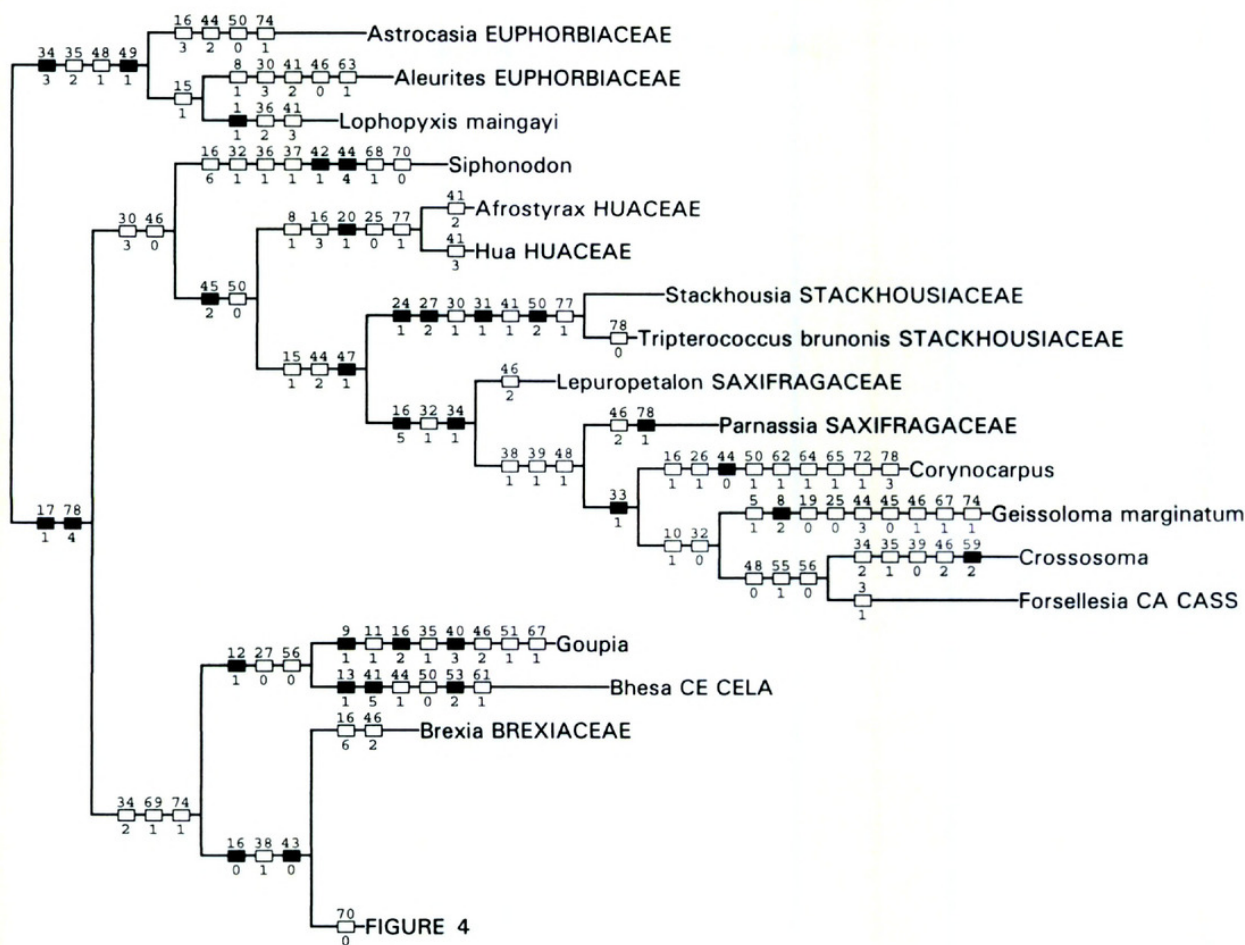
Figure 3. "Basal" portion of one of 115 most-parsimonious cladograms (309 steps, CI = 0.36, RI = 0.72, excluding uninformative characters; 321 steps including uninformative characters as shown) for 82 taxa of Celastraceae and related families, obtained by equal-weighted analysis of 69 informative (79 including uninformative) characters (Appendices 1, 2). Character-state changes, as mapped using slow (DELTRAN) optimization, are marked as bars on internodes, with the number above each bar indicating the character number, and the number below each bar indicating the change to the apomorphic character state (Appendix 2). Solid bars indicate unique origins of character states (regardless of whether or not a reversal occurs) and unshaded bars indicate parallel origins and reversals of character states.

paraphyletic group that includes *Paxistima* of subfamily Celastroideae tribe Celastreae.

Tribe Lophopetaleae is a monophyletic group (Hennig, 1966). The Hippocrateaceae are a monophyletic group (that includes *Plagiopteron*) sister to the clade that consists of *Dicarpellum* and *Sarawakodendron*. Tribe Salacieae is a monophyletic group sister to the clade that consists of tribe Campylostemoneae, tribe Helictonemateae, and tribe Hippocrateeae. Tribe Hippocrateeae is a paraphyletic group with tribe Helictonemateae, tribe Campylostemoneae, and *Plagiopteron* nested within it. Tribe Campylostemoneae is monophyletic.

DISCUSSION

"Basal" groups. *Lophopyxis* is resolved as nested within Euphorbiaceae. Character states grouping *Lophopyxis* with Euphorbiaceae are unisexual flowers, pendulous ovule attachment, and obturators

(only present in this clade). This resolution of *Lophopyxis* is consistent with its placement by Hooker (1887–1888; 1888).

Forsellesia is resolved as the sister group of *Crossosoma* (Crossosomataceae) by two synapomorphies: capsule dehiscence by one side laterally splitting and aril presence. This resolution is consistent with the transfer of *Forsellesia* from Celastraceae to Crossosomataceae by Thorne and Scogin (1978). This transfer has also been supported by leaf and wood anatomy (DeBuhr, 1978).

Bhesa and *Goupia* are resolved as sister groups. Synapomorphies of this clade are distinct crossbar tertiary leaf veins (only present in this clade) and a cupular disk. *Bhesa* has been recognized as unusual, relative to other Celastraceae, based on its gross morphology (Pierre, 1893) and wood anatomy (Metcalfe & Chalk, 1950; Xinying et al., 1990). Xinying et al. (1990: 60) stated, "Significantly,
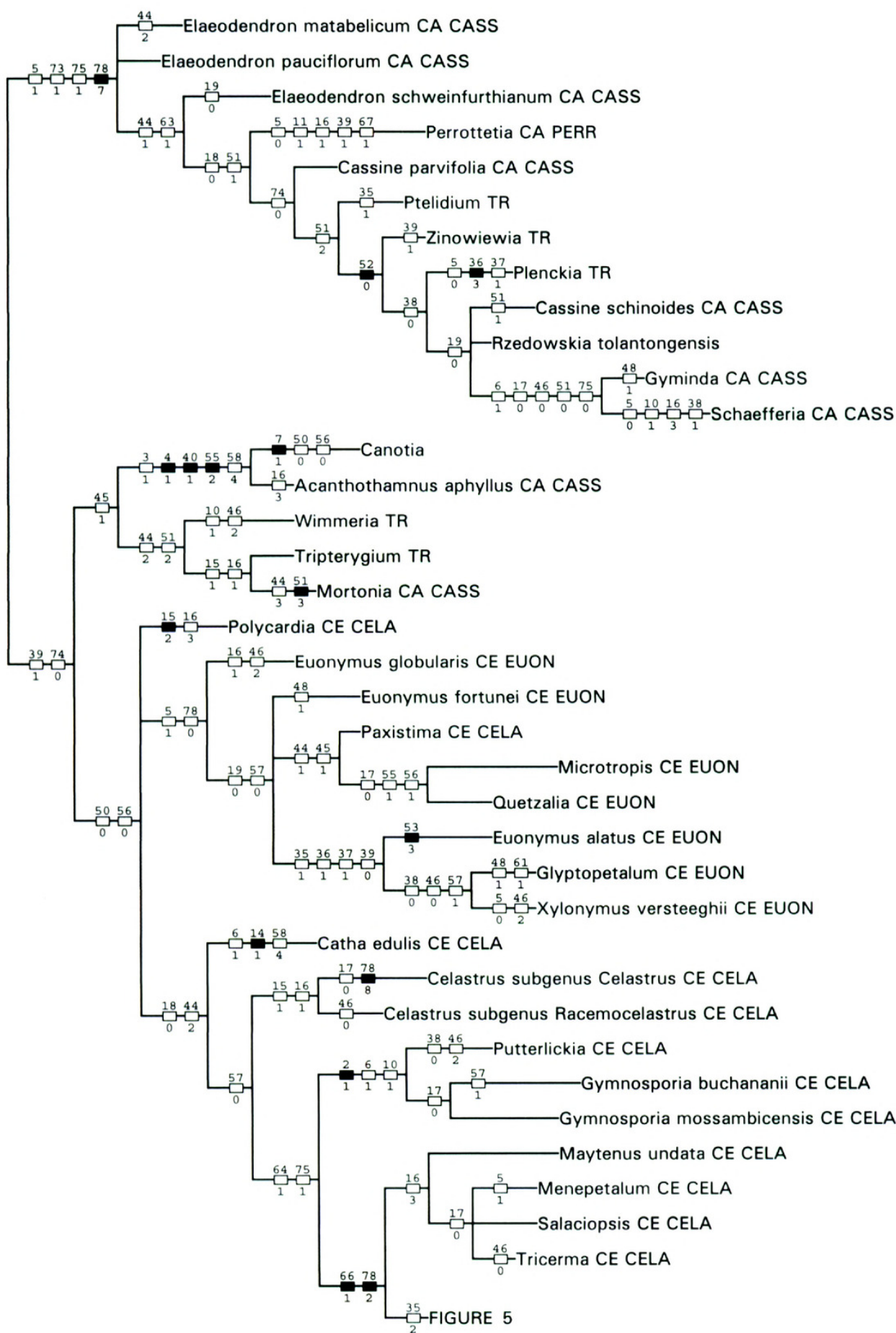
FIGURE 5

Figure 5. Second "distal" portion of one of 115 most-parsimonious cladograms (309 steps, CI = 0.36, RI = 0.72, excluding uninformative characters; 321 steps including uninformative characters as shown) for 82 taxa of Celastraceae and related families, obtained by equal-weighted analysis of 69 informative (79 including uninformative) characters (Appendices 1–4). See legend of Figure 3 for further information.

none of the other genera in [tribe Eucelastreae] bear any wood anatomical resemblance to *Bhesa*." To our knowledge, *Bhesa* and *Goupia* have never been associated with one another in the literature.

Brexia is resolved as sister group of the remaining Celastraceae s.l. (i.e., all other taxa sampled). Synapomorphies for *Brexia* and Celastraceae are dorsifixed anthers and connate styles. Synapomor-

phies for Celastraceae (not including *Brexia*) are an uninterrrupted vascular strand through the petiole and cymose inflorescences. *Brexia* has been variously assigned to Escalloniaceae (Hutchinson, 1967), Brexiaceae (Verdcourt, 1968), and Grossulariaceae (Cronquist, 1981). Close relationship between *Brexia* and Celastraceae was first proposed by Perrier de la Bâthie (1933), rejected by Loese-

←

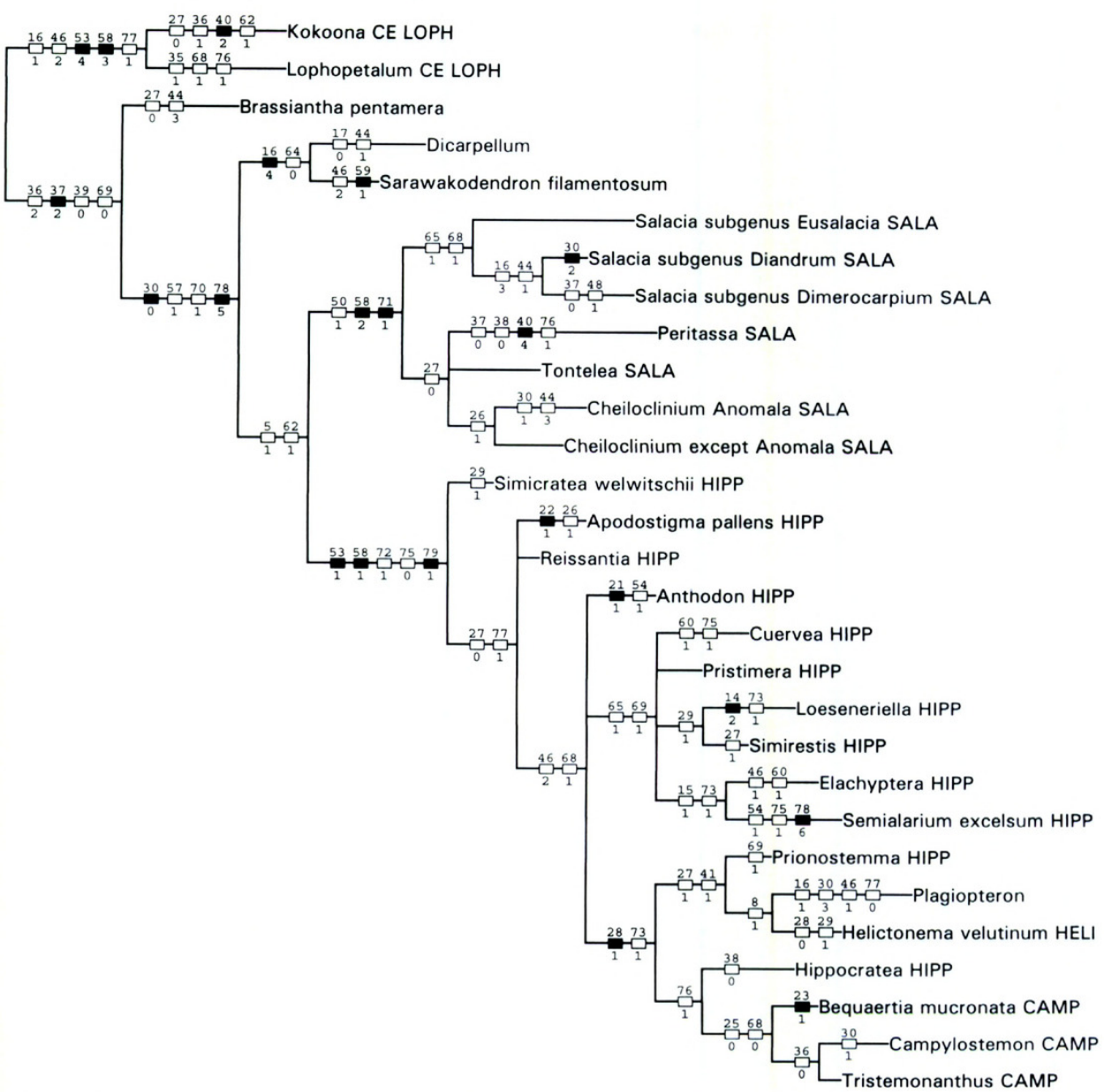Figure 4. First "distal" portion of one of 115 most-parsimonious cladograms (309 steps, CI = 0.36, RI = 0.72, excluding uninformative characters; 321 steps including uninformative characters as shown) for 82 taxa of Celastraceae and related families, obtained by equal-weighted analysis of 69 informative (79 including uninformative) characters (Appendices 1–4). See legend of Figure 3 for further information.

ner (1937), and then retracted, based on Loesener's criticism, by Perrier de la Bâthie (1942). On the basis of embryology, Kamelina (1988) disputed the inclusion of *Brexia* within Escalloniaceae and suggested it be recognized as a separate family, Brexiaceae, in the order Saxifragales. On the basis of embryology and other characters, Tobe and Raven (1993) suggested including Brexiaceae within the order Celastrales, not the order Saxifragales. Based on *rbc*L gene trees (Chase et al., 1993; Morgan & Soltis, 1993), 18S rDNA (Soltis et al., 1997), and *rbc*L 5' flanking sequence gene tree (Savolainen et al., 1997), *Brexia* was resolved as sister group of Celastraceae (when only one taxon of Celastraceae was sampled) or included within Celastraceae (when more than one taxon was sampled; Savolainen et al., 1997) as an early-derived lineage. Based on the resolution of our analysis, *Brexia* may be included within Celastraceae or retained as a separate family.

Celastraceae sensu stricto. The results of this cladistic analysis generally do not support Loesener's (1942a) classification of subfamilies and tribes of Celastraceae. None of the three subfamilies and only one of the four tribes that include more than one genus are resolved as monophyletic. Only tribe Lophopetaleae, represented by two genera in this study, is resolved as monophyletic. Loesener's (1942a) subfamilies and tribes have been found to be heterogeneous based on wood anatomy (Metcalfe & Chalk, 1950), pollen structure (Lobreau-Callen, 1977), and leaf anatomy (Den Hartog née Van Ter Tholen & Baas, 1978). However, all members of Loesener's subfamily Celastroideae (composed of the tribes Celastreae, Euonymeae, and Lophopetaleae) included in the analysis are resolved as a paraphyletic assemblage that includes Hippocrateaceae. Synapomorphies of this group are dehiscent fruits and arillate seeds. The clade of Celastroideae plus Hippocrateaceae is nested within a paraphyletic assemblage of genera Loesener (1942a) assigned to subfamily Cassinoideae and Tripterygioideae.

Two genera (*Campylostemon* and *Cheiloclinium*) that Loesener (1942a) included in Celastraceae are resolved as members of Hippocrateaceae. Loesener (1892b) originally recognized *Campylostemon* as a member of Hippocrateaceae, but transferred the genus to Celastraceae in his 1942 classification, placing it in its own subfamily, Campylostemonoideae. In spite of recognizing the Hippocrateaceae-like growth form of *Campylostemon*, Loesener made this transfer based on its five-merous androecium. All members of Hippocrateaceae, as delimited by Loe-

sener (1942b), have either two or three stamens. Loesener did not have fruits of *Campylostemon* available for examination. Finally, Loesener noted that this genus is transitional between Celastraceae and Hippocrateaceae, which is not supported in this analysis.

Loesener (1942a) transferred Mier's (1872) genus *Cheiloclinium* to Celastraceae, also based on the number of stamens. However, Loesener did have fruit and seed descriptions that described the mucilaginous pulp and lack of albumen, characteristic of Hippocrateaceae. Loesener transferred the genus, then consisting of *C. anomalum* J. Miers and *C. schwackeanum* L. E. T. Loesener, to Celastraceae based on its five-merous androecium.

Due to the lack of resolution at the "basal" node in this analysis, we cannot support or refute Loesener's (1942a) recognition of subfamily Goupioideae as a member of Celastraceae (if *Brexia* is included within Celastraceae). Loesener (1942a) described two genera, *Canotia* and *Siphonodon*, as doubtfully associated with Celastraceae based on the septicidally dehiscent capsules of *Canotia* and the unusual structure of the gynoecium in *Siphonodon*. In this analysis, *Canotia* is supported as a member of Celastraceae. In contrast, *Siphonodon* is resolved among the outgroup taxa, though closely related to Celastraceae. Based on this resolution, *Siphonodon* should be excluded from Celastraceae s.l.

The two tribes and three subtribes proposed by Bentham and Hooker (1862) are no better supported than the subfamilies and tribes delimited by Loesener (1942a). The naturalness of the tribes and subtribes as defined by Bentham and Hooker (1862) is evaluated here. Tribe Hippocrateae is resolved as nested within tribe Celastreae. Tribe Hippocrateae (composed of *Hippocratea* s.l., *Salacia* s.l., *Siphonodon*, and *Llavea*) is not monophyletic though; *Siphonodon* is resolved as not closely related to *Hippocratea* s.l. and *Salacia* s.l. Celastreae subtribe Euonymeae is not a natural group, with genera assigned to this subtribe resolved in many different regions of Celastraceae s. str. Celastreae subtribe Celastreae is not a natural group, as *Kurrimia* (= *Bhesa*) is not resolved as closely related to the other members. Celastreae subtribe Elaeodendreae is not a natural group, as *Forsellesia* (= *Glossopetalon*) and *Goupia* are not resolved as closely related to the other members, among other problems. In contrast to Loesener (1942a), Bentham and Hooker (1862) and Baillon (1880) recognized *Paxistima* as closely related to *Microtropis*. This assertion is supported in our analysis, as *Pax-*

istima is resolved as the sister group of *Microtropis* and *Quetzalia*.

Perrottetia is resolved as a derived member of Loesener's (1942a) subfamily Cassinoideae in our analysis (also among genera assigned to subfamily Tripterygioideae). Loesener recognized the anomalous position of *Perrottetia* by assigning it to its own tribe, Perrottetieae. *Perrottetia* has been recognized as unusual relative to other Celastraceae based on its wood anatomy (Metcalfe & Chalk, 1950) with scalariform perforation plates, paratracheal parenchyma, and lack of fiber tracheids; its seed structure (Corner, 1976) with an exotegmic palisade of lignified malpighian cells; and its leaf anatomy (Den Hartog née Van Ter Tholen & Baas, 1978) with predominately anomocytic stomates, pubescence, and domatia. In our analysis, these characters are generally shared with outgroup taxa. However, synapomorphies of *Perrottetia* and genera that are resolved as closely related to *Perrottetia* include: dioecy, dorsifixed anthers, 2-carpellate ovaries, baccate indehiscent fruits, and presence of parenchyma-like bands of thin-walled septate wood fibers.

Glyptopetalum and *Xylonymus versteeghii* have been described as closely related to *Euonymus* (Hou, 1962). *Glyptopetalum* has also been included within *Euonymus* (Baillon, 1880). Hou described *Xylonymus versteeghii* as closely related to *Euonymus* (Hou, 1962) and *Sarawakodendron* (Hou, 1969). In our analysis, *Glyptopetalum* and *Xylonymus versteeghii* are resolved as sister groups. This clade is nested within a paraphyletic *Euonymus* (represented by three species). This resolution is consistent with Hou (1962), but not Hou (1969); *Sarawakodendron* appears only very distantly related to *Xylonymus versteeghii*. Furthermore, this resolution suggests that the circumscription of *Euonymus* needs to be redefined.

The recognition or reduction of *Cassine* and *Elaeodendron* has been widely debated in the literature. Davison (1927), Hou (1962), Kostermans (1986), and Bornstein (1989) reduced *Elaeodendron* to *Cassine*, whereas Loesener (1942a), Robson (1965), Proctor (1984), Robson et al. (1994), and Archer and van Wyk (1997) recognized *Cassine* as distinct from *Elaeodendron*. A succinct taxonomic history is provided by Hou (1962). Characters distinguishing the genera (to various degrees) have been described from pollen (Archer & van Wyk, 1992), bark (Archer & van Wyk, 1993a), and wood anatomy (Archer & van Wyk, 1993b). Robson et al. (1994) suggested that *Elaeodendron* is derived from *Euonymus*, and that *Elaeodendron* is not closely related to *Cassine* s. str. (as treated by Archer and van

Wyk, 1997). In our analysis, neither *Cassine* (two representative species) nor *Elaeodendron* (three representative species) is resolved as a monophyletic group. However, the two genera are supported as closely related (in contrast to Robson et al., 1994). This result is dependent on sampling; not all the genera Robson et al. (1994) treated are included in this analysis.

Canotia is resolved within Celastraceae, as sister group to *Acanthothamnus aphyllus*. This resolution supports the placement of *Canotia* as a member of Celastraceae by Hutchinson (1969) and Johnston (1975). Synapomorphies that group *Canotia* and *Acanthothamnus aphyllus* are stem apices terminating in sharp points, presence of glands on stems (only present in this clade), and triangular-extended connectives (only present in this clade). Johnston (1975: 119) noted, "In the minutest details of epidermis, bracts, calyx, petals, stamens, gynophore, ovaries, and ovules, *Acanthothamnus* is a diminutive replica of *Canotia*."

Gymnosporia has been treated either as distinct from *Maytenus* (Hou, 1955; Jordaan & van Wyk, in press), or included within it (Exell, 1953; Hou, 1962; Sebsebe, 1985). Loesener (1942a) recognized both genera, but considered the distinction as a stopgap measure with little difference to distinguish between the genera. Jordaan and van Wyk (in press) reinstated *Gymnosporia* to include all "spiny" species of *Maytenus* s.l. (but excluding *Moya*). A thorough taxonomic history of *Gymnosporia* and *Maytenus* is given by Sebsebe (1985). In our analysis, *Putterlickia* is resolved as sister group to two representative species of *Gymnosporia*. This resolution supports the assertion by Jordaan and van Wyk (1998) that *Gymnosporia* and *Putterlickia* (and *Gloveria*) are a natural group. The three synapomorphies supporting this clade are presence of thorns, phyllotaxy alternate on vegetative shoots and opposite on flowering shoots or thorns, and leaves fascicled on short branches. The two species of *Gymnosporia* are recognized as distinct from *Putterlickia* by having unisexual instead of bisexual flowers.

Maytenus, not including *Gymnosporia*, is resolved as a clade separate from the clade of *Gymnosporia* and *Putterlickia*. This resolution supports the recognition of *Gymnosporia* as distinct from *Maytenus*. The two elements of *Maytenus* included in this analysis (*Maytenus undata* and *Tricerma*) are not resolved as sister groups. *Maytenus undata* is resolved as sister group of the clade composed of *Menepetalum*, *Salaciopsis*, and *Tricerma*. This suggests that *Tricerma* should be recognized as distinct from *Maytenus* following Lundell (1971). *Maytenus*

is a large and variable genus; further sampling needs to be conducted to test the resolution found here.

"Transitional" genera between Celastraceae and Hippocrateaceae. Many authors have commented on "transitional" genera and/or characters between Celastraceae and Hippocrateaceae (Smith, 1940; Smith & Bailey, 1941; Loesener, 1942a; Hou, 1962, 1964; Robson, 1965; Robson et al., 1994; Den Hartog née Van Ter Tholen & Baas, 1978; Görts-van Rijn & Mennega, 1994; Mennega, 1997). *Brassiantha* (Den Hartog née Van Ter Tholen & Baas, 1978; Görts-van Rijn & Mennega, 1994), *Campylostemon* (Loesener, 1942a; Hou, 1964), *Elaeodendron* and *Crocoxylon* (Robson, 1965), *Kokoona* (Hou, 1964), *Lophopetalum* (Robson, 1965), and *Sarawakodendron* (Hou, 1967) have been proposed as transitional genera. The bases given for recognizing these genera as transitional have been: 5 stamens with an extrastaminal disk (*Brassiantha, Campylostemon,* and *Kokoona*); an extrastaminal disk and a drupaceous fruit with 3 locules (*Elaeodendron/Crocoxylon*); opposite leaves, 5 stamens located on the disk, a 3-locular ovary, and winged seeds (*Lophopetalum*); or an erect habit, 3 stamens, capsular fruit with 3 locules, and albuminous arillate seeds (*Sarawakodendron*).

Our analysis supports *Kokoona, Lophopetalum, Brassiantha, Dicarpellum,* and *Sarawakodendron* as closely related to the most recent common ancestor of the genera traditionally referred to Hippocrateaceae (*Hippocratea* s.l. and *Salacia* s.l.). In contrast, *Campylostemon* is resolved as a derived genus within Hippocrateaceae (supporting Robson, 1965, in his disagreement with Hou, 1964), and *Elaeodendron* is not resolved as closely related to Hippocrateaceae.

Robson (1965: 43) suggested, "The so-called Hippocrateaceae comprise two groups of genera that have independently evolved a 3-merous androecium arising inside the disk" such that "the *Hippocratea* group (with dehiscent mericarps and winged seeds) and the *Salacia* group (with indehiscent drupaceous fruits) have been derived from different parts of the *Celastraceae*" (Robson et al., 1994: 1). Our analysis supports Hippocrateaceae as a monophyletic group (including *Plagiopteron*), in contrast to Robson's assertion. However, the *Salacia* group and the *Hippocratea* group (including *Plagiopteron*) are each monophyletic, such that the indehiscent drupaceous fruits of the *Salacia* group apparently did not evolve from the dehiscent mericarps and winged seeds of the *Hippocratea* group, or vice versa. The derivation of these fruit types from a cap-

sular fruit, which was not lobed or parted, appears to have been independent of one another.

Kokoona and *Lophopetalum,* the only two representatives of Loesener's (1942a) tribe Lophopetaleae, are resolved as a natural group. The five synapomorphies for this clade are: paniculate to racemose inflorescences, variable number and more than four ovules per locule, capsular fruit flattened along each locule but not parted (only present in this clade), aril modified into a wing surrounding the seed (only present in this clade), and absence of the pollen annulus. *Lophopetalum* has been treated as a section of *Euonymus* (Baillon, 1880); this is not supported by our analysis. *Kokoona* was originally described as a member of Hippocrateaceae by Thwaites (1853). Thwaites (1853: 380) noted, "In habit and general appearance [*Kokoona*] resembles the *Celastraceae,* though it would seem to differ almost as much from members of that natural family as do the *Hippocrateaceae,* from all the genera of which latter Order it differs in having five stamens." It seems that Thwaites was uncertain whether to assign *Kokoona* to Celastraceae or Hippocrateaceae. Based on the resolution of our analysis in which Hippocrateaceae are nested within Celastraceae and *Kokoona* is one of the "transitional" genera, this uncertainty was well justified; the "natural family" Celastraceae does not appear natural at all, if Hippocrateaceae are recognized as distinct. The synapomorphy that groups the clade that consists of *Kokoona* and *Lophopetalum* with Hippocrateaceae is the insertion of filaments inside the inner edge of the disk (only present in this clade [except *Kokoona* in which the filaments are inserted on the disk] and in Euphorbiaceae). Also, of the eight genera scored, only in *Lophopetalum* and *Salacia* do seedlings not become free from all envelopments during growth.

Smith and Bailey (1941: 393), in the original description of *Brassiantha,* noted:

"To summarize, the genus *Brassiantha* appears to have no characters which can be used to exclude it from the Hippocrateaceae. On the other hand, it is so distinct from known genera, in the characters of its disk, stamens, ovary, and fruit, as to make comparison superfluous. It appears to be rigidly excluded from the Celastraceae, as that family is presently constituted, by the position of the stamens within the disk. This, indeed, may be the only fixed character by which the families Hippocrateaceae and Celastraceae may be separated. If so, one must consider the families quite artificial. . . ."

One may interpret this to mean that Smith and Bailey recognized the character states that *Brassiantha* shares with other members of Hippocratea-

ceae are plesiomorphic, but apomorphic relative to members of Celastraceae. Indeed, *Brassiantha* is resolved as sister group of the rest of Hippocrateaceae, and nested within Celastraceae. Synapomorphies for *Brassiantha* and the rest of Hippocrateaceae are three anther characters: anthers not versatile, and transversely dehiscent in the extrorse direction. Extrorsely dehiscent anthers are only present in this clade (though introrse dehiscence occurs in *Campylostemon* and *Tristemonanthus*) and in *Lophopyxis*. Based on this resolution, the distinction between Celastraceae and Hippocrateaceae is indeed artificial.

The first species of *Dicarpellum* was described as *Salacia pancheri* by Baillon (1872). Loesener (1907) named three more species and placed them, and *Salacia pancheri,* into *Salacia* subg. *Dicarpellum.* Smith (1941: 442) elevated subgenus *Dicarpellum* to the generic level and stated, "The genus is not closely related to *Salacia.*" Smith distinguished *Dicarpellum* from *Salacia* based on disk shape and anther dehiscence plane; but neither of these characters excludes *Dicarpellum* from the variable *Salacia* subg. *Eusalacia.* However, based on our analysis, Smith correctly observed that *Dicarpellum* is not closely related to *Salacia.* *Salacia* is resolved as more closely related to *Peritassa,* *Tontelea,* and *Cheiloclinium* than it is to *Dicarpellum,* which is resolved as sister group of *Sarawakodendron.* The synapomorphy for the clade that consists of *Dicarpellum* and *Sarawakodendron* is the inflorescence modified into a condensed bracteate raceme.

Hou (1967: 142–143) described *Sarawakodendron* as "closely allied to *Kokoona* and *Lophopetalum* of the *Celastraceae*" and "one of the transitional links between the two very closely related families, *Hippocrateaceae* and *Celastraceae.*" Both of Hou's assessments are supported by our analysis.

Hippocrateaceae. Our analysis supports the inclusion of Hippocrateaceae within Celastraceae. Traditionally defined members of Hippocrateaceae (*Hippocratea* s.l. and *Salacia* s.l.) are resolved as a clade by two synapomorphies: opposite leaves and loss of albumen (also lost in *Kokoona* and *Corynocarpus* [Corynocarpaceae]). Two other characters supporting this clade (though not unambiguously optimized on the supporting branch) are interrupted vascular strand through petiole in cross section (within Hippocrateaceae, only described in *Salacia,* *Tontelea,* and *Hippocratea*), and base chromosome number of 14 (occurs only in Hippocrateaceae [although the base chromosome number of *Semialarium excelsum* is 15], but only known in *Cuervea,*

Salacia, Campylostemon, Hippocratea, and *Loeseneriella*).

Hallé's division of Hippocrateaceae variously into subfamilies and tribes (1962) and only tribes (1986, 1990) is partially supported by this analysis. Subfamily Salacioideae (= tribe Salacieae) is resolved as a monophyletic group (excluding *Dicarpellum*), sister to subfamily Hippocrateoideae, which includes the tribes Campylostemoneae, Helictonemateae, and Hippocrateeae. The synapomorphies for subfamily Salacioideae are the indehiscent fruit, aril modified into mucilaginous pulp (only present in this clade), and the presence of included phloem (also only present in this clade). This supports Hallé's recognition of the two subfamilies, Hippocrateoideae and Salacioideae. Two synapomorphies for subfamily Hippocrateoideae are some rays greater than ten cells wide (only present in this clade and *Corynocarpus* [Corynocarpaceae]) and loss of parenchyma-like bands of thin-walled septate wood fibers. Three other characters supporting this clade (though not unambiguously optimized on the supporting branch) are capsules strongly parted among locules ("mericarps"; only present in this clade), aril modified into a basal wing with the vasculature of the funiculus along the wing (only present in this clade), and presence of pollen annulus (except in *Simicratea*; also present in *Kokoona* and *Lophopetalum*). However, as Hippocrateaceae are nested within Celastraceae, these subfamilies may not be formally recognized. Tribes Campylostemoneae and Helictonemateae are nested within the paraphyletic tribe Hippocrateeae. Tribe Helictonemateae is monotypic, and tribe Campylostemoneae is monophyletic. Because recognition of tribes Campylostemoneae and Helictonemateae renders tribe Hippocrateeae paraphyletic, recognition of these tribes is not supported.

Note that Hallé (1962: 42) apparently did not interpret his subfamilies or tribes to be monophyletic as indicated in his "Tableau des liaisons intergénériques." In this diagram, which he described as an entirely hypothetical tracing of the evolution of the Hippocrateaceae, the monophyly of the subfamilies is ambiguous, as is the recognition of tribe Helictonemateae as separate from tribe Hippocrateeae. Tribe Campylostemoneae is clearly nested within tribe Hippocrateeae. The synapomorphy for tribe Campylostemoneae is the loss of the disk (which occurs only in this clade).

In this same table (Hallé, 1962: 42), *Simirestis,* *Bequaertia,* and *Tristemonanthus* are illustrated as transitional genera, with *Simirestis* directly giving rise to six different genera independently. These
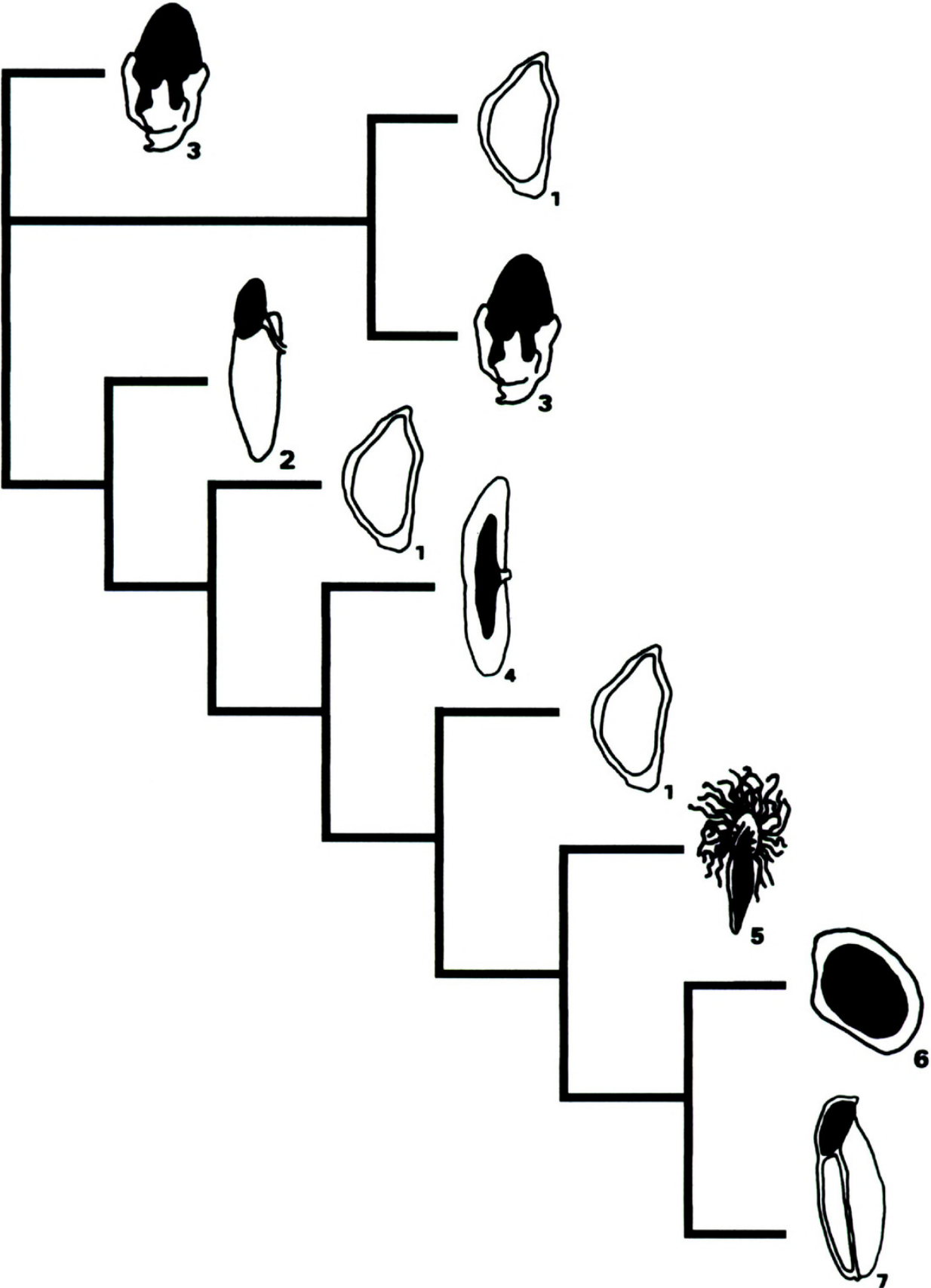
Figure 6. The pattern of aril modification in the clade composed of the most recent common ancestor of *Catha edulis*, *Euonymus*, and *Polycardia*, and their descendents, mapped onto part of a simplified strict-consensus tree from Figures 1 and 2. Embryoniferous portion of seed, when not enveloped by the aril, is shaded. Aril and vasculature of the funiculus are not shaded. —1. Aril entirely enveloping seed (redrawn from Smith & Bailey, 1941). —2. Aril modified into a basal wing with the vasculature of the funiculus attached above the wing (redrawn from Robson et al., 1994). —3. Aril partially enveloping the seed (redrawn from Mueller, 1995). —4. Aril modified into a wing surrounding

transitional genera and narrowly defined segregate genera that Hallé recognized have been criticized by Robson (1965). If Hallé's and Robson's assertion that some of the genera of tribe Hippocrateeae are not monophyletic groups is correct, this would help explain the large polytomy in tribe Hippocrateeae in our analysis. This polytomy reflects character conflict.

Plagiopteron (Plagiopteraceae) is resolved as a derived member of tribe Hippocrateeae, closely related to *Helictonema velutinum* and *Prionostemma*. Characters supporting inclusion of *Plagiopteron* within Hippocrateaceae include: opposite leaves, stellate leaf pubescence, not versatile, transversally dehiscent, extrorse anthers, filaments inserted inside the disk, pilose ovary pubescence, capsular fruit strongly parted among locules, and presence of crystals in leaf epidermal cells.

Evolution of the aril. Characters 56 (aril presence), 57 (aril position on seed), and 58 (aril form) are all coded based on the assertion that the aril may be fleshy (typical of most arils; in *Euonymus*, *Maytenus*, etc.), modified into a basal wing with the vasculature of the funiculus along the wing (in members of *Hippocratea* s.l.), modified into a basal wing with the vasculature of the funiculus attached above the wing (in *Canotia* and *Catha edulis*), modified into a wing surrounding the seed (in *Kokoona*, *Lophopetalum*, and *Peripterygia*), or modified into mucilaginous pulp (in *Salacia* s.l.). This assertion is based on descriptions from the literature and personal observations and inferences. See Appendix 2 for further information on character coding. A brief review of the relevant literature and the basis for the coding follows.

Miers (1872: 323) described the basal wing of the seed in *Hippocratea* as a "very membranous, wing-like support, which is a laminiform expansion of its outer integument: this wing has been supposed to be an expanded funicle; but this I much doubt: one of its margins, that furthest from the sutural line of the cell, is thickened into a narrow coriaceous tube, enclosing a simple chord of numerous spiral threads (the raphe)." We believe that Miers misused the term "raphe." A raphe is defined as a "longitudinal ridge on the outer integument or seed coat in anatropous ovules where the funiculus becomes fused with the integument" (Blackmore & Tootill, 1984: 307). Based on this definition and the

description by Miers, what he described as the raphe is the vasculature of the funiculus. Therefore, there is no basis to conclude that the "laminiform expansion" is not an expanded funicle (i.e., an aril). Hallé (1962) described the wing of *Hippocratea* s.l. as a membranous testa.

The small, thin, flat, basal structures with the vasculature of the funiculus attached above the wing, which occur in *Canotia* and *Catha edulis*, have variously been described as arils or as wings. Loesener (1942a) described the structure in *Catha edulis* as a well-developed white wing-like aril, whereas he described a very similar structure in *Canotia* as a triangular wing, without reference to it being a modified aril. Johnston (1975: 121) described the wing of *Canotia* as a "winglike structure" without further elaboration. Relative to the basal wings found in *Hippocratea* s.l., the basal wings of *Canotia* and *Catha edulis* are much smaller (about the same size as the embryoniferous portion of the seed), and the wing is located immediately below the point of attachment—the vasculature of the funiculus does not run along the wing. No basis was found to code the basal wings of *Canotia* and *Catha edulis* as separate character states.

The vasculature of the funiculus is also medially attached in *Lophopetalum* and *Peripterygia* (basally attached in *Kokoona*), except that the wing surrounds the seed. Loesener (1942a) stated that he was unsure if the wing of *Kokoona* represented a modified aril or a further development of the testa.

The mucilaginous pulp found only in fruits of *Salacia* s.l. was described by Miers (1872: 324) as follows: "In some cases this testa is covered with a white fleshy coating, like that which I formerly described as an *arilline**, and which ultimately forms a sparse pulp in which the seeds are embedded." Miers (1856: 89) defined arilline as an aril "in which the vessels of the raphe are always imbedded." Again, we interpret what Miers described as the "vessels of the raphe" to be the vasculature of the funiculus. Baillon (1880: 15) described the seeds of Salaceae as "nude, or partially enveloped in an aril springing from the umbilicus." Loesener (1942b), in describing the mucilaginous pulp, noted that it is not derived from the ovary walls, but is rather a de novo structure or an outgrowth of the seeds.

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the seed (redrawn from Hou, 1962). —5. Aril partially enveloping the seed with filamentous extensions from base (redrawn from Hou, 1967). —6. Aril modified into mucilaginous pulp (cross section; redrawn from Hallé 1962). —7. Aril modified into a basal wing with the vasculature of the funiculus along the wing (redrawn from Hallé, 1986).

All four character states described above (character 58, states 1–4) have been associated with arils (i.e., modified funiculi) in the literature, as cited above. In all cases, the structures are located at the base of the seed or surrounding the seed, thus establishing positional similarity, which is a basis for a hypothesis of primary homology (de Pinna, 1991). Furthermore, in no case is there an additional structure present in taxa with one of these four character states that could be interpreted as an aril. Therefore, the homology assessment passes Patterson's (1982) test of conjunction.

The following statements are based on the resolution and optimization of unordered character states (Fitch, 1971) on the strict consensus of the most-parsimonious cladograms (Figs. 1, 2), and are applicable only to the taxa included in the analysis. The presence of arils is a derived character state that arose three times in Celastraceae (and once in Crossosomataceae, including *Forsellesia*): once in *Bhesa*, once in *Canotia*, and once in the most recent common ancestor of *Catha edulis*, *Euonymus*, and *Polycardia*. In this latter clade, the aril has been lost only once (although presence/absence of the aril is unknown in *Plagiopteron*), in the clade of *Microtropis* and *Quetzalia*. This suggests that the "thick testa" of *Microtropis* seeds described by Corner (1976: 94) is actually homologous to an aril as cited by Hou (1962). See character 56 in Appendix 2 for further discussion.

In the clade composed of the most recent common ancestor of *Catha edulis*, *Euonymus*, and *Polycardia*, and their descendents, the aril underwent modification from a typical fleshy form (primitive state) to the four above-mentioned forms (derived states). The aril as a basal wing with the vasculature of the funiculus attached above the wing has arisen independently in two terminals, *Canotia* and *Catha edulis*. Each of the three other derived states has arisen only once, and in no case has the derived state been lost (i.e., shown a reversal in the cladogram). Finally, each of the four derived states has arisen independently from the others. The pattern of aril modification in the clade composed of the most recent common ancestor of *Catha edulis*, *Euonymus*, and *Polycardia*, and their descendents is diagrammed in Figure 6. In this cladistic analysis, the aril-homology assessments were tested against homology assessments of other characters (that is to say, tested by congruence; Wiley, 1975; Patterson, 1982). Based on the resolution of this cladogram, in which there is a unique origin for three of the four derived aril character states, these three original homology assessments are supported.

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APPENDIX 1. Taxa sampled for cladistic analysis.

Literature surveyed for gross-morphological characters in parentheses.

Canotia, *Goupia*, *Lophopyxis*, and *Siphonodon* are arranged as separate families following Cronquist (1981). Genera within Celastraceae s. str. are arranged by subfamily and tribe according to Loesener (1942a), except *Campylostemon* and *Cheiloclinium* are arranged in Hippocrateaceae following Hallé (1962, 1986, 1990) and Smith (1940), respectively. Genera within Hippocrateaceae are arranged by tribe according to Hallé (1986, 1990). Capitalized, bold-faced, two- and four-letter abbreviations following subfamilies and tribes, respectively, are used to indicate terminals belonging to these taxa in the strict consensus of 115 most-parsimonious cladograms (Figs. 1, 2). Sixty-two gross-morphological characters were scored for 82 taxa based on literature and/or herbarium specimens. Following the taxon name and author are the literature source(s) examined when coding that taxon.

CORYNOCARPACEAE
  (1) *Cornynocarpus* J. R. Forster & G. Forster (Cronquist, 1981; Guymer, 1984; Philipson, 1987)
CROSSOSOMATACEAE
  (2) *Crossosoma* Nuttall (Nuttall, 1848; Cronquist, 1981)
EUPHORBIACEAE
  (3) *Aleurites* J. R. Forster & G. Forster (Forster, 1996)
  (4) *Astrocasia* B. L. Robinson & Millspaugh (Webster, 1992)
GEISSOLOMATACEAE
  (5) *Geissoloma marginatum* J. Lindley ex K. S. Kunth (Dahlgren & Rao, 1969; Cronquist, 1981)
HUACEAE
  (6) *Afrostyrax* J. R. Perkins & E. F. Gilg (Chevalier, 1947; Baas, 1972)

(7) *Hua* J. B. L. Pierre ex É. A. J. De Wildeman (Chevalier, 1947; Germain, 1963; Willis, 1966; Baas, 1972)

SAXIFRAGACEAE

(8) *Lepuropetalon* C. Elliott (Spongberg, 1972)

(9) *Parnassia* L. (Spongberg, 1972)

STACKHOUSIACEAE

(10) *Stackhousia* J. E. Smith (Barker, 1977, 1984)

(11) *Tripterococcus brunonis* S. F. L. Endlicher (Barker, 1984)

BREXIACEAE

(12) *Brexia* F. Noroña ex L. M. A. P. Thouars (Hutchinson, 1967; Verdcourt, 1968)

CANOTIACEAE

(13) *Canotia* J. Torrey (Johnston, 1975)

GOUPIACEAE

(14) *Goupia* J. B. C. F. Aublet (Aublet, 1775)

LOPHOPYXIDACEAE

(15) *Lophopyxis maingayi* J. D. Hooker (Hooker, 1887–1888, 1888; Willis, 1966)

PLAGIOPTERACEAE

(16) *Plagiopteron* W. Griffith (Airy Shaw, 1965; Willis, 1966; Baas et al., 1979)

SIPHONODONTACEAE

(17) *Siphonodon* W. Griffith (Hou, 1964)

CELASTRACEAE

subfamily Celastroideae L. E. T. Loesener **CE**

tribe Euonymeae L. E. T. Loesener **EUON**

(18) *Euonymus alatus* (C. P. Thunberg) P. F. von Siebold (Ka, 1965)

(19) *Euonymus fortunei* (P. K. N. S. Turczaninow) H. R. E. Handel-Mazzetti (Turczaninoff, 1863; Bailey, 1951)

(20) *Euonymus globularis* Ding Hou (Hou, 1975)

(21) *Glyptopetalum* G. K. Thwaites (Hou, 1962)

(22) *Microtropis* N. Wallich ex C. D. F. Meisner (Hou, 1962; Merrill & Freeman, 1940)

(23) *Quetzalia* C. L. Lundell (Lundell, 1939)

(24) *Xylonymus versteeghii* C. Kalkman ex Ding Hou (Hou, 1962)

tribe Celastreae **CELA**

(25) *Bhesa* F. Buchanan-Hamilton ex G. A. W. Arnott (Hou, 1962)

(26) *Catha edulis* (M. Vahl) S. F. L. Endlicher (Robson et al., 1994)

(27) *Celastrus* L. subg. *Celastrus* (Hou, 1955)

(28) *Celastrus* L. subg. *Racemocelastrus* Ding Hou (Hou, 1955)

(29) *Gymnosporia buchananii* L. E. T. Loesener (Robson et al., 1994)

(30) *Gymnosporia mossambicensis* L. E. T. Loesener (Robson et al., 1994)

(31) *Maytenus undata* (C. P. Thunberg) R. A. Blakelock (Sebsebe, 1985)

(32) *Menepetalum* L. E. T. Loesener (Mueller, 1995)

(33) *Paxistima* C. S. Rafinesque (Navaro & Blackwell, 1990)

(34) *Polycardia* A. L. de Jussieu (Perrier de la Bâthie, 1946)

(35) *Putterlickia* S. F. L. Endlicher (Robson, 1966; Jordaan & van Wyk, 1998)

(36) *Salaciopsis* E. G. Baker (Mueller, 1995)

(37) *Tricerma* F. M. Liebmann (Lundell, 1969, 1971; Correll & Johnston, 1970)

tribe Lophopetaleae L. E. T. Loesener **LOPH**

(38) *Kokoona* G. H. K. Thwaites (Hou, 1962)

(39) *Lophopetalum* R. Wight ex G. A. W. Arnott (Hou, 1962)

subfamily Triperygioideae L. E. T. Loesener **TR**

(40) *Plenckia* S. Reissek (Lourteig & O'Donnell, 1955)

(41) *Ptelidium* L. M. A. P. Thouars (Perrier de la Bâthie, 1946)

(42) *Tripterygium* J. D. Hooker (Ka, 1965)

(43) *Wimmeria* D. F. L. von Schlechtendal & L. K. A. von Chamisso (Lundell, 1939)

(44) *Zinowiewia* P. K. N. S. Turczaninow (Lundell, 1939)

subfamily Cassinoideae L. E. T. Loesener **CA**

tribe Cassineae **CASS**

(45) *Acanthothamnus aphyllus* (F. R. R. Schlechter) P. C. Standley (Brandegee, 1909; Standley, 1923; Loesener, 1942a; Johnston, 1975)

(46) *Cassine parvifolia* O. W. Sonder (Archer & van Wyk, 1997)

(47) *Cassine schinoides* (C. P. J. Sprengel) R. H. Archer (Archer & van Wyk, 1997)

(48) *Elaeodendron matabelicum* L. E. T. Loesener (Robson & Sousa, 1969)

(49) *Elaeodendron pauciflorum* L. R. Tulasne (Perrier de la Bâthie, 1946)

(50) *Elaeodendron schweinfurthianum* L. E. T. Loesener (Robson et al., 1994)

(51) *Forsellesia* E. L. Greene (Ensign, 1942; Thorne & Scogin, 1978)

(52) *Gyminda* C. S. Sargent (Bornstein, 1989)

(53) *Mortonia* A. Gray (Gray, 1852, 1853)

(54) *Schaefferia* N. J. von Jacqin (Bornstein, 1989)

tribe Perrottetieae **PERR**

(55) *Perrottetia* K. S. Kunth (Hou, 1962)

NOT ASSIGNED TO SUBFAMILY OR TRIBE

(56) *Brassiantha pentamera* A. C. Smith (Hippocrateaceae) (Hou, 1964)

(57) *Dicarpellum* (L. E. T. Loesener) A. C. Smith (Hippocrateaceae) (Smith, 1941; Simmons, in press)

(58) *Rzedowskia tolantonguensis* F. G. Medrano (Gonzalez-Medrano, 1981)

(59) *Sarawakodendron filamentosum* Ding Hou (Hou, 1967, 1969; Corner, 1976)

HIPPOCRATEACEAE

tribe Campylostemoneae N. Hallé **CAMP**

(60) *Bequaertia mucronata* (M. A. Exell) R. Wilczek (Hallé, 1986; Robson et al., 1994)

(61) *Campylostemon* F. M. J. Welwitsch (Hallé, 1986; Robson et al., 1994)

(62) *Tristemonanthus* L. E. T. Loesener (Hallé, 1986; Robson et al., 1994)

tribe Helictonemateae N. Hallé **HELI**

(63) *Helictonema velutinum* (A. Afzelius) J. P. L. Pierre (Hallé, 1986; Robson et al., 1994)

tribe Hippocrateeae N. Hallé **HIPP**

(64) *Anthodon* H. Ruíz López & J. A. Pávon (Smith, 1940; Görts-van Rijn & Mennega, 1994)

(65) *Apodostigma pallens* (J. É. Planchon ex D. Oliver) R. Wilczek (Hallé, 1986; Robson et al., 1994)

(66) *Cuervea* Triana ex Miers (Smith, 1940; Hallé, 1986; Robson et al., 1994)

(67) *Elachyptera* A. C. Sm., Smith, 1940; Görts-van Rijn & Mennega, 1994)

(68) *Hippocratea* L. (Smith, 1940; Görts-van Rijn & Mennega, 1994)

(69) *Loeseneriella* A. C. Sm. (Hallé, 1986; Robson et al., 1994)

(70) *Prionostemma* Miers (Smith, 1940; Görts-van Rijn & Mennega, 1994)

(71) *Pristimera* Miers (Smith, 1940)

(72) *Reissantia* N. Hallé (Hallé, 1986; Robson et al., 1994)

(73) *Semialarium excelsum* (HBK) A. C. Smith (Smith, 1940)

(74) *Simicratea welwitschii* (D. Oliver) N. Hallé (Hallé, 1986; Robson et al., 1994)

(75) *Simirestis* N. Hallé (Hallé, 1986; Robson et al., 1994)

tribe Salacieae N. Hallé   **SALA**

(76) *Cheiloclinium* Miers species-group *Anomala* (Smith, 1940)

(77) *Cheiloclinium* Miers except species-group *Anomala* (Smith, 1940)

(78) *Peritassa* J. Miers (Hallé, 1986)

(79) *Salacia* L. subg. *Diandrum* L. E. T. Loesener (Loesener, 1942b; Hou, 1964)

(80) *Salacia* L. subg. *Dimerocarpium* L. E. T. Loesener (Loesener, 1942b)

(81) *Salacia* L. subg. *Eusalacia* L. E. T. Loesener (Loesener, 1942b; Hallé, 1986)

(82) *Tontelea* J. P. C. F. Aublet (Smith, 1940; Görts-van Rijn & Mennega, 1994)

APPENDIX 2. Characters and character states.

Seventy-nine characters were scored for 82 taxa of Celastraceae and related families (Appendix 1). Notes on character coding are given in cases where observations and codings conflict with descriptions in the literature, and when different publications described the taxon scored as having different character states. Also included are discussions of questionable character-state codings, and literature sources (if any) that were used to code each character and/or individual character states. Independence of characters and division of characters into character states are also discussed, and taxa with unusual or infrequent character states are noted. All multistate characters were scored as unordered. The four numbers (or ranges) following each informative character description represent optimization of the character on the 115 most-parsimonious cladograms. The four numbers are: number of steps on most-parsimonious cladograms, number of extra steps beyond minimum required if the character was consistent on the cladograms, consistency index, and retention index. Additional steps implied by polymorphism within terminals are not included in the calculation of steps or consistency indices. Uninformative characters (alternative character state[s] only present in single terminal[s]) are indicated by "UNINF" in place of the four numbers.

STEM AND LEAF

1. *Tendril presence*: absent (0); present (1). Uninformative [UNINF].

Within Celastraceae s.l., tendrils are only present in *Lophopyxis*. Described by Willis (1966: 668) as "watchspring tendrils (modif. infl.)."

2. *Thorn presence*: absent (0); present (1). 1, 0, 1.00, 1.00.

Within Celastraceae s.l., thorns are present in *Gloveria*, *Gymnosporia*, *Moya*, and *Putterlickia*. In the literature (e.g., Robson et al., 1994; Jordaan & van Wyk, 1998), the thorns are generally described as spines. However, we interpret these structures to be modified stems, not modified leaves. Sebsebe (1985) also interpreted these structures to be modified axillary shoots, but incorrectly cited them as

spines. Spines are modified leaves (or parts of leaves), thorns are modified stems (Blackmore & Tootill, 1984). Loesener (1942a) also described these structures as modified shoots, though the German word "Dorn" can be interpreted as either thorn or spine (Artschwager & Smiley, 1925). Evidence favoring the interpretation of the structures (what we term "thorns") in *Gymnosporia* as modified shoots includes leaves generally subtending the structures, and inflorescences and leaves often borne on the structures.

The protuberances on older stems (prickles?) of *Simirestis klaineana* do not appear similar to the thorns of *Gymnosporia*. To our knowledge, these "prickles" only occur in this one species (Hallé, 1962, 1986; Robson et al., 1994).

3. *Stem apices*: not terminating in sharp points (0); terminating in sharp points (1). 2, 1, 0.50, 0.50.

Within Celastraceae s.l., stem apices terminating in sharp points are only present in *Acanthothamnus aphyllus*, *Canotia*, and *Forsellesia*.

4. *Presence of glands on stems*: absent (0); present (1). 1, 0, 1.00, 1.00.

Within Celastraceae s.l., glandular stems are only present in *Acanthothamnus aphyllus* and *Canotia*.

5. *Phyllotaxy on vegetative shoots*: alternate (0); opposite or whorled (1). 9, 8, 0.11, 0.78.

Elaeodendron, which is described as having "leaves all opposite or subopposite to alternate towards the base of the shoot" (Robson et al., 1994: 29), was coded as having opposite or whorled phyllotaxy. No species of *Elaeodendron* we know of has strictly alternate leaves. Specimens we have seen almost always have nodes with opposite leaves and a small minority of nodes that bear subopposite or alternate leaves.

Within Celastraceae s.l., we know of whorled leaves only in *Brexiella*, *Crossopetalum*, and *Evonymopsis*.

6. *Phyllotaxy on plants with alternate leaves*: strictly alternate (0); alternate on vegetative shoots, opposite on thorns or flowering shoots (1). 3, 2, 0.33, 0.50.

Within Celastraceae s.l., phyllotaxy alternate on vegetative shoots and opposite on thorns or flowering shoots occurs in *Catha edulis*, *Gymnosporia*, *Putterlickia*, and *Schaefferia*. Sebsebe (1985: 9) noted, "The leaves are normally alternate in all species [of *Maytenus*, in which *Gymnosporia* was treated], but may be opposite when growing on thorns. These are often seen in *M. obbiadensis*, *M. putterlickioides* and *M. senegalensis*, and more rarely in *M. arbutifolia* and *M. heterophylla*. When growing on short lateral branches the leaves are often clustered." Inflorescences are often, but by no means always, located on the thorns of *Gymnosporia*. Krikorian (1985) made no mention of the similarity between *Catha edulis* and *Gymnosporia*, nor have we found reference to this in any other publication.

7. *Leaf form*: planar (0); sessile delta-shaped scales (1). UNINF.

Within Celastraceae s.l., leaves reduced to sessile delta-shaped scales are present in *Canotia*. The reduced leaves of *Psammomoya* do not appear similar to the reduced leaves of *Canotia*.

8. *Leaf pubescence*: without stellate hairs (0); with stellate hairs (1). 4–5, 3–4, 0.40–0.50, 0.25–0.50.

Most genera of Celastraceae are essentially glabrous. The stellate hairs of *Aleurites* are less dense, smaller, and weaker than the stellate hairs of *Helictonema velutinum*, but were coded as homologous. *Plagiopteron* is the only other taxon in Celastraceae s.l. with stellate hairs.

9. *Leaf venation*: pinnate (0); acrodromous (1). UNINF.

Within Celastraceae s.l., acrodromous leaf venation occurs only in *Goupia* and *Pottingeria acuminata*.

10. *Leaf position*: not fascicled on short branches (0); often fascicled on short branches (1). 4, 3, 0.25, 0.57.

Within Celastraceae s.l., leaves often fascicled on short branches occur in *Forsellesia, Gymnosporia, Putterlickia, Schaefferia,* and *Wimmeria*. The short branches we refer to in *Gymnosporia* and *Putterlickia* are in addition to the thorns, not the thorns themselves. Short branches are also described for *Mystroxylon* (Robson et al., 1994) and occur on *M. burkcanum* O. W. Sonder (A. E. van Wyk, pers. comm. 1998), but not on specimens of *M. aethopicum* (C. P. Thunberg) L. E. T. Loesener that the senior author has examined at NY.

11. *Domatia in axils of midrib and secondary veins*: absent (0); sometimes present (1). 2, 1, 0.50, 0.00.

Within Celastraceae s.l., domatia occur only in *Goupia* and *Perrottetia*. Domatia were described by Hou (1962) for *Perrottetia*, and confirmed on herbarium specimens. The domatia are scattered. They are not present in the axils of the midrib and all secondary veins. Lundell (1985: 239) cited domatia in *Goupia guatemalensis* and stated, "The pitted and barbate domatia are similar to those found in some species of *Perrottetia*, a genus remotely related." We have not examined specimens of *Goupia guatemalensis*.

12. *Distinct-crossbar tertiary leaf veins*: absent (0); present (1). 1, 0, 1.00, 1.00.

Within Celastraceae s.l., distinct-crossbar tertiary leaf veins are only present in *Bhesa* and *Goupia*. The crossbar tertiary leaf veins are not perpendicular to the secondary veins, but rather are perpendicular to the midrib. This character state is most pronounced in *Bhesa* and is a bit less uniform in *Goupia*.

13. *Upper petiole angle*: not geniculate (0); thickened, geniculate (1). UNINF.

Within Celastraceae, thickened, geniculate upper petioles are only present in *Bhesa*.

14. *Stipule morphology on opposite leaves*: intrapetiolar (0); intra- or interpetiolar with tuft of hairs (1); intra- or interpetiolar without tuft of hairs (2). UNINF.

This character was coded as inapplicable for taxa with strictly alternate leaves. Stipules intra- or interpetiolar with a tuft of hairs are present in *Catha edulis*. Stipules intra- or interpetiolar without a tuft of hairs are present in *Loeseneriella*.

INFLORESCENCE AND FLOWER

15. *Inflorescence position*: axillary (0); at least some inflorescences terminal (1); epiphyllous or rarely axillary (2). 6–7, 4–5, 0.28–0.33, 0.66–0.73.

Within Celastraceae s.l., epiphyllous inflorescences are only present in *Polycardia*.

16. *Inflorescence type*: cymose (0); paniculate to racemose (1); umbellate (2); fasciculate (3); condensed bracteate racemose (4); flowers solitary (5); irregularly cymose-umbellate (6). 20, 14, 0.30, 0.53.

Within Celastraceae s.l., umbellate inflorescences are only present in *Goupia*. Condensed bracteate racemose inflorescences are present in *Dicarpellum, Sarawakodendron,* and *Maytenus abbottii* A. E. van Wyk. Irregularly cymose-umbellate inflorescences are present in *Brexia* and *Siphonodon*. *Siphonodon* is described as cymose (e.g., Hou, 1964; Jessup, 1984). The cymes are generally condensed, contorted, and woody. A similar pattern occurs in inflorescences of *Brexia*, which appear almost umbellate,

except the pedicels generally diverge from three areas of the peduncle apex, appearing as reduced cymes.

Fasciculate inflorescences often appear to be sessile cymes (e.g., *Maytenus* has both fasciculate and cymose inflorescences). Through dissections, the second author has found fasciculate inflorescences of *Maytenus* and *Salacia* to be reduced cymes.

17. *Flower sexuality*: unisexual (0); bisexual (1). 7, 6, 0.14, 0.50.

18. *Unisexual-flowered plants*: dioecious (0); monoecious (1). 2, 1, 0.50, 0.83.

19. *Perianth merosity*: four-merous (0); five-merous (1); three-merous (2). 4, 3, 0.25, 0.70.

Within Celastraceae s.l., no taxa have strictly three-merous perianths. However, *Plagiopteron* has a variously three- to five-merous perianth.

20. *Sepal gland presence*: absent (0); present (1). 1, 0, 1.00, 1.00.

Glandular sepals are present in the outgroups *Afrostyrax* and *Hua* (Huaceae).

21. *Petal margins*: entire, ciliate, or irregularly toothed (0); regularly toothed (1). UNINF.

Regularly toothed petal margins occur in *Anthodon*. Initially, attempts were made to code entire, ciliate, irregularly toothed, and regularly toothed petals as separate character states. However, several taxa have two or more of these character states present and also have intermediate states. The only character state that stood out, and was therefore retained, was the regularly toothed petals of *Anthodon*.

22. *Corolla symmetry*: actinomorphic (0); zygomorphic with four of five petals arched (1). UNINF.

Within Celastraceae s.l., zygomorphic corollas with four of five petals arched are only present in *Apodostigma*. This is well illustrated by Hallé (1986). The character state is less obvious in herbarium specimens. The irregularly sized petals (three larger, two smaller) of *Bequaertia mucronata* also make the flower zygomorphic. However, this is not similar to the five equally sized, variously curved petals of *Apodostigma*.

23. *Petal fleshiness*: not fleshy (0); fleshy and irregularly sized (1). UNINF.

Within Celastraceae s.l., fleshy and irregularly sized (three larger, two smaller) petals are only present in *Bequaertia mucronata*. The character state is well illustrated by Hallé (1986) and is obvious on herbarium specimens.

24. *Petal connation*: free (0); free at base, connate above (1). 1, 0, 1.00, 1.00.

Stackhousia and *Tripterococcus brunonis* (Stackhousiaceae) have petals that are free at the base and connate above.

25. *Disk presence*: absent (0); present (1). 3, 2, 0.33, 0.60.

The disk is absent in *Bequaertia mucronata*, *Campylostemon*, and *Tristemonanthus*. All disk descriptive characters were coded as inapplicable for these three genera. What appears to be a disk in *Campylostemon* and *Tristemonanthus*, we interpret (as do Hallé, 1986, 1990; Robson et al., 1994) as flared filament bases.

The disk is inconspicuous, though still present, in some genera (e.g., *Lepuropetalon* [Saxifragaceae], *Microtropis*, and *Schaefferia*). The five nectaries present in *Corynocarpus* (Corynocarpaceae) are interpreted as a discontinuous disk (see discussion by Philipson, 1987).

26. *Disk division*: continuous (0); discontinuous (1). 3, 2, 0.33, 0.33.

A discontinuous disk is present in *Apodostigma* and

Cheiloclinium. The disk in these genera may actually be very deeply lobed, not divided. Smith (1940: 525) described the disk of *Cheiloclinium* as "forming 3 (5 in group *Anomala*) (rarely 4) saccate carnose staminiferous lips." These "staminiferous lips" surround the stamens, with the disk divided between stamens. This is in contrast to some Celastraceae s. str. in which the disk is notched at the point of filament insertion on the disk.

27. *Disk shape*: cupular, not adnate to sepals (0); annular, flat, or margins upturned (1); cupular, adnate to sepals (2). 7–8, 5–6, 0.25–0.28, 0.62–0.68.

A cupular disk that is not adnate to sepals primarily occurs in genera of Hippocrateaceae. Many genera of Celastraceae s. str. have flat disks with the margins upturned, whereas cupular disks do not have a flat inner region.

Cupular disks that are adnate to sepals are present in *Stackhousia* and *Tripterococcus brunonis* (Stackhousiaceae).

28. *Disk pubescence*: glabrous (0); conspicuously puberulent (1). 2, 1, 0.50, 0.50.

The disk is pubescent in *Hippocratea*, *Plagiopteron*, and *Prionostemma*.

29. *Androgynophore presence*: absent (0); present (1). 3–4, 2–3, 0.25–0.33, 0.00–0.33.

This character was scored as inapplicable for taxa that have strictly unisexual flowers. Within Celastraceae s.l., an androgynophore is only present in *Helictonema velutinum*, *Loeseneriella*, *Simicratea*, and *Simirestis*.

30. *Stamen plus staminode number*: three or generally three (0); same as petal number (1); two (2); twice or more than twice petal number (3). 8, 5, 0.37, 0.83.

31. *Fertile stamen length*: equal (0); unequal and monomorphic (1). 1, 0, 1.00, 1.00.

Unequal length monomorphic stamens occur in *Stackhousia* and *Tripterococcus brunonis* (Stackhousiaceae) in addition to some species of *Forsellesia*.

32. *Staminode presence in same flower with functional stamens*: absent (0); present (1). 3, 2, 0.33, 0.33.

Staminodes in the same flower with functional stamens occur in *Corynocarpus* (Corynocarpaceae), *Lepuropetalon* and *Parnassia* (Saxifragaceae), and *Siphonodon*. In all of these genera, five functional stamens alternate individually with five staminodes.

33. *Stamen-petal arrangement*: alternate (0); opposite (1). 1, 0, 1.00, 1.00.

Opposite stamen-petal arrangement occurs in *Corynocarpus* (Corynocarpaceae) and *Forsellesia*.

34. *Numerous stamen arrangement*: unicyclic and twice petal number (0); bicyclic and twice petal number (1); bicyclic and more than twice petal number (2); clustered or connate in center of flower (3). 4, 1, 0.75, 0.75.

35. *Filament insertion relative to disk*: at outer disk margin (0); on disk (1); inside inner edge of disk (2). 7, 5, 0.28, 0.84.

36. *Anther dehiscence direction*: introrse to introrse-latrorse (0); strictly latrorse (1); extrorse (2); apical (3). 7, 4, 0.42, 0.86.

Most Celastraceae s. str. are introrse to introrse-latrorse. Most Hippocrateaceae are extrorse.

Apical dehiscence occurs in *Plenckia* and *Crossopetalum*. *Plenckia* was coded as having apical oblique dehiscence, whereas other obliquely dehiscent genera (e.g., *Glyptopetalum*, *Euonymus alatus*) were coded as strictly latrorse. The difference between *Plenckia* and the other taxa is that *Plenckia* does not have a thick triangular connective that makes the anthers latrorse, while the others do.

37. *Anther dehiscence plane*: longitudinal (0); oblique (1); transverse (2). 6, 4, 0.33, 0.84.

This character may seem to be non-independent with character 29, as longitudinal dehiscent anthers are introrse while transversely dehiscent anthers are extrorse. However, *Campylostemon* and *Tristemonanthus* have transversely dehiscent introrse anthers. *Kokoona* is the only genus with strictly latrorse longitudinally dehiscent anthers.

38. *Anther attachment*: basifixed (0); dorsifixed (1). 8, 7, 0.12, 0.61.

The transversely dehiscent anthers of Hippocrateaceae were scored as dorsifixed, not basifixed. This coding is not immediately obvious as these anthers appear basifixed. However, if the anther locules were folded downward, as occurs in some longitudinally dehiscent species in *Salacia* subg. *Eusalacia*, the anthers would be easily recognized as dorsifixed.

39. *Anther versatility*: not versatile (0); versatile (1). 6–7, 5–6, 0.14–0.16, 0.77–0.81.

Taxa were scored as versatile if, on herbarium specimens, a probe may be used to easily twist the anther on the filament. Stamens with thin, tapered connectives generally have versatile anthers. *Elaeodendron* is described as having versatile anthers (Hou, 1962, as *Cassine*; Robson et al., 1994). However, none of the herbarium specimens of *Elaeodendron* the senior author has examined (in species other than the three included in the analysis) have versatile anthers. This may be due to a difference in versatility in fresh versus dried flowers.

40. *Connective extension shape*: absent or apiculate (0); triangular (1); large ornamented extension (2); bilobed with brush-hairy tip (3); bilobed without brush-hairy tip (4). 4, 0, 1.00, 1.00.

Apiculate extended connectives were not distinguished from connectives without extensions. The presence or absence of an apiculum may vary among flowers of a single specimen. Within Celastraceae s.l., triangular connective extensions are only present in *Acanthothamnus aphyllus* and *Canotia*; large ornamented connective extensions are only present in *Kokoona*; bilobed connective extensions with brush-hairy tips are only present in *Goupia*; bilobed connective extensions without brush-hairy tips are only present in *Peritassa*. These various forms of connective extensions are not coded as homologous because of their striking differences in shape or pubescence.

41. *Ovary pubescence*: glabrous (0); completely pilose (1); stellate (2); tomentose (3); densely hirsute (4); apex pilose (5); stellate (6). 7, 2, 0.57, 0.50.

42. *Apical hollow in ovary center*: absent (0); present (1). UNINF.

With Celastraceae s.l., an apical hollow in the center of the ovary occurs only in *Siphonodon* (see Croizat, 1947, for discussion of this structure). This structure is not the same as found in *Brassiantha*, which is described by Smith and Bailey (1941: 393) as ". . . the stigmas are obscure, apparently reduced to minute radiating lines in the hollow of the ovary-summit." *Siphonodon*, in contrast, has a deep circular cavity with a narrow column arising from the base.

43. *Style connation*: connate (0); not connate (1). 1, 0, 1.00, 1.00.

Bhesa, in which the two styles are free or connate only at the very base, was coded as uncertain. This character was coded as inapplicable for taxa without styles (e.g., *Brassiantha*). For *Siphonodon*, we follow Croizat (1947) in which the narrow column in the apical cavity is not in-

terpreted as a style; rather, the styles are around the margin of the cavity (see his fig. 4). *Lophopyxis* was coded based on Hooker's (1888) description "stigmas 5, sessile, subulate, recurved," in conjunction with the illustration of Hooker (1887–1888) plate 1714 numbers 8 and 9 where stigmas (or styles?) are obviously distinct from one another.

44. *Ovary carpel number*: one (0); two or modifications thereof (1); three (2); equals perianth merosity (3); many irregularly superposed (4); four, when not equaling perianth merosity (5). 16, 11, 0.25, 0.61.

Within Celastraceae s.l., many irregularly superposed carpels occur only in *Siphonodon*, which is very different from all other taxa sampled.

45. *Ovary septa walls*: complete (0); incomplete (1); absent (2). 4, 2, 0.50, 0.77.

This character is based on whether or not ovary septa walls meet in the center of the ovary (complete) or not (incomplete). *Stackhousia* and *Tripterococcus brunonis* (Stackhousiaceae), in which the carpels are basically separate from one another, were coded as inapplicable for this character.

Brexia was coded as polymorphic based on the description by Verdcourt (1968: 1) in which the genus was described as ". . .completely or imperfectly 5–7 locular."

46. *Ovule number per locule*: one (0); two or four (1); variable and more than four (2). 21, 19, 0.09, 0.42.

47. *Placentation*: axile (0); parietal (1). 1, 0, 1.00, 1.00.

Parietal placentation occurs in *Lepuropetalon* and *Parnassia* (Saxifragaceae).

48. *Axile ovule attachment*: basal to axile, erect or horizontal (0); pendulous (1). 7, 6, 0.14, 0.25.

49. *Obturator presence*: absent (0); present (1). 1, 0, 1.00, 1.00.

Obturators are present in *Aleurites*, *Astrocasia* (Euphorbiaceae), and *Lophopyxis*. *Lophopyxis* was scored based on Willis (1966: 668), who described ovules of Lophopyxidaceae as ". . .each surmounted by an obturator-like appendage." Pfeiffer (1951: 6) also cited this as an "anomalous appendage." However, note that Hooker (1888) cited *Lophopyxis* as "obturator 0." Hooker (1887–1888) also cited "obturatore 0." We are making the assumption that Pfeiffer and Willis saw something Hooker did not, which does in fact exist. Willis (1966) cited no other taxa included in this study (outside of Euphorbiaceae) as having an obturator.

FRUIT

50. *Fruit type*: dehiscent (0); indehiscent (1); cocci (2). 8, 6, 0.25, 0.79.

51. *Indehiscent fruit type*: drupaceous (0); baccate (1); samara (2); nut (3). 7–8, 4–5, 0.37–0.42, 0.37–0.50.

All samaroid indehiscent fruits were coded as homologous, regardless of wing position. This assertion is based on the observation that in fruits with apical wings (see character 52), the wing begins at the base along the side of the fruit; the wing is not confined to the apex of the seed.

52. *Fruit wing form*: at apex (0); at side along each locule (1). 2, 1, 0.50, 0.50.

This character was coded as inapplicable for taxa without winged fruits to avoid non-independence among characters. Within Celastraceae s.l., an apical fruit wing occurs only in *Plenckia*, *Rzedowskia tolantonguensis*, and *Zinowiewia*. A wing along the side of each locule occurs in *Ptelidium*, *Tripterygium*, *Wimmeria*, and also *Platypterocarpus* and some *Euonymus*.

53. *Capsular fruit shape*: not lobed or parted (0); strongly parted among locules (1); lobed but not parted among locules (2); lobed to base but not parted among locules (3); flattened along each locule but not parted (4). 4, 0, 1.00, 1.00.

Within Celastraceae s.l., capsular fruits that are strongly parted among locules occur only in *Hippocratea* s.l. Each of these three-parted segments is generally termed a mericarp in the literature. A capsular fruit that is lobed but not parted among locules occurs in *Bhesa*. A capsular fruit that is lobed to the base but is not parted among locules occurs in *Euonymus alatus* and several other *Euonymus* species. A capsular fruit that is flattened along each locule but is not parted occurs in *Kokoona*, *Lophopetalum*, and *Peripterygia*. States two, three, and four are quite distinct from state one.

54. *Mericarp connation*: separate (0); connate (1). 2, 1, 0.50, 0.00.

This character was coded only for taxa with state one (capsules strongly parted among locules) in character 53. The character was scored as inapplicable for all other taxa. Within Celastraceae s.l., connate mericarps are only present in *Anthodon* and *Semialarium excelsum*.

55. *Capsular fruit dehiscence*: loculicidal (0); one side laterally split (1); septicidal (2). 3, 2, 0.66, 0.66.

This character was scored only for taxa with dehiscent fruit (character 50 state 0). The character was scored as inapplicable for all other taxa. Capsular fruits that split laterally along one side occur in *Crossosoma* (Crossosomataceae), *Forsellesia*, *Microtropis*, and *Quetzalia*. Within Celastraceae s.l., septicidal capsule dehiscence is only present in *Canotia*. Note that the fruit of *Canotia* also splits, although less strongly, loculicidally (there are twice as many splits as there are locules).

Sarawakodendron was described by Corner (1976) as having capsules with septicidal dehiscence. However, in the original generic description by Hou (1967), *Sarawakodendron* was described and illustrated as having capsules with loculicidal dehiscence. We followed Hou (1967) in our coding.

SEED

56. *Aril presence*: absent (0); present (1). 5, 4, 0.20, 0.86.

The small wings of *Canotia* and *Catha edulis* seeds are interpreted as modified arils. The large apical and circular wings of *Kokoona* and *Lophopetalum* (also present in *Peripterygia*) are interpreted as modified arils. The large basal wings (or flanges) of *Hippocratea* s.l. are also interpreted as modified arils. Finally, the mucilaginous pulp surrounding seeds of *Salacia* s.l. (Salacieae) is also interpreted as a modified aril.

Helictonema velutinum was described by Robson et al. (1994: 43) as having "no pocket-like structure at the point of attachment (such as occur in *Simirestis* and *Pristimera*) but sometimes with the vestiges of arils." However, in examining the well-preserved mature fruiting holotype specimen (*R. P. Klaine 1316*), the senior author found no evidence of any such "vestiges of arils." He did, however, note a "pocket-like structure" at the point of seed attachment. Therefore, based on these observations, this "vestiges of arils" character was not coded into the matrix.

Corner (1976) contradicted Hou (1962) in describing seeds of *Microtropis* and *Perrottetia* as exarillate. For *Microtropis*, Corner (1976: 94) stated, "It appears that the thick testa has been mistaken for an aril (Hou, 1962)." Lundell (1970) described *Quetzalia*, which he segregated from *Microtropis*, as exarillate. However, in observing

Breedlove 55604 (NY) the senior author thought he observed an aril, apparently making the same mistake Hou did, in misinterpreting the orangish red fleshy seed coat. We followed Corner (1976) in coding *Microtropis* and *Perrottetia* as exarillate.

57. *Aril position on seed*: entirely enveloping seed (0); partly enveloping seed (1). 5, 4, 0.20, 0.55.

The wings (modified arils) of *Kokoona* and *Lophopetalum* are interpreted as entirely enveloping the seed. This coding was based on the descriptions and illustrations of Hou (1962) in which the primarily apical wing of *Kokoona* also extends around the base of the seed, and the circular wing of *Lophopetalum* completely encircles the seed. The basal wings of *Canotia*, *Catha edulis*, and *Hippocratea* s.l. were coded as partly enveloping the seed. The mucilaginous pulp (modified aril) of *Salacia* s.l. (Salacieae) was coded as entirely enveloping the seed.

58. *Aril form*: fleshy (0); basal wing with vasculature of the funiculus along wing (1); mucilaginous pulp (2); wing surrounding seed with medial or basal attachment of the vasculature of the funiculus (3); basal wing with vasculature of the funiculus attached above wing (4). 5, 1, 0.80, 0.95.

Within Celastraceae s.l., a basal wing with vasculature of the funiculus along the wing occurs only in *Hippocratea* s.l. Mucilaginous pulp occurs only in *Salacia* s.l. (Salacieae).

An aril modified to be a wing surrounding the seed with medial (or basal in *Kokoona*) attachment of the vasculature of the funiculus occurs only in *Kokoona*, *Lophopetalum*, and *Peripterygia*. A basal wing with vasculature of the funiculus attached above the wing occurs in *Canotia* and *Catha edulis*.

59. *Fleshy aril form*: without filamentous extensions (0); with filamentous extensions from base (1); with filamentous extensions from apex. UNINF.

This character was only coded for taxa with fleshy arils (character 58 state 0). *Sarawakodendron filamentosum* has fleshy arils with filamentous extensions from the base. *Crossosoma* (Crossosomataceae) has fleshy arils with filamentous extensions from the apex. Taxa with laciniate arils (e.g., *Maytenus abbottii* van Wyk) were not interpreted as having filamentous extensions from the apex of the aril.

60. *Basal seed wing form*: membranous, papyraceous, or thin coriaceous (0); membranous or a flange (1). 2, 1, 0.50, 0.00.

This character was only coded for those taxa with a basal seed wing with the vasculature of the funiculus along the wing (Campylostemonae, Helictonemateae, and Hippocrateeae). A membranous or flange-like basal seed wing occurs in *Cuervea* and *Elachyptera*. Both genera have species with a large membranous wing and other species in which the wing is a flange. A similar state also occurs in *Hylenaea*.

61. *Raphe branching*: unbranched (0); branched (1). 2, 1, 0.50, 0.00.

A branched raphe (postchalazal vascular branches) is present in *Bhesa* and *Glyptopetalum*. A branched raphe also occurs in *Brexiella*. All three genera with branched raphes were observed by the senior author; the branched raphes of *Bhesa* and *Glyptopetalum* are also described by Corner (1976).

62. *Endosperm presence*: present (0); absent (1). 3, 2, 0.33, 0.85.

Many codings were taken from Miers (1872), Hou (1962, 1964), and Robson et al. (1994). The coding for *Dicarpellum* was taken from Baillon (1872) and observations by the senior author. The coding for *Sarawakodendron* was taken from Hou (1967) and Corner (1976).

63. *Exotegmic palisade of lignified malpighian cells presence on seed*: absent (0); present (1). 2, 1, 0.50, 0.00.

An exotegmic palisade of lignified malpighian cells occurs in *Aleurites* (Euphorbiaceae) and *Perrottetia*. This character was coded from Corner (1976).

64. *Seed tegmen composition*: fibrous (0); not fibrous (1). 3, 2, 0.33, 0.71.

This character was coded from Corner (1976) and Tobe and Raven (1993).

65. *Seed germination type*: epigeal (0); hypogeal (1). 4, 3, 0.25, 0.50.

Codings were taken from Hallé (1962, 1986) and de Vogel (1980).

66. *Seedling growth*: becoming free from all envelopments (0); not becoming free from all envelopments (1). 1, 0, 1.00, 1.00.

Codings were taken from de Vogel (1980). This character appears independent from character 57, as *Lophopetalum* has epigeal germination with the seed not becoming free from all envelopments, whereas *Salacia* has hypogeal germination with the seed not becoming free from all envelopments.

LEAF ANATOMY

67. *Mucilaginous leaf epidermal cells*: absent (0); present (1). 3, 2, 0.33, 0.00.

This character was coded from Solereder (1908). Solereder (1908: 875) stated, "Mucilaginous epidermal cells have only been recorded in *Goupia glabra*, Aubl., *Perrottetia alpestris*, Loes. and *P. sandwicensis*, Gray." Metcalfe and Chalk (1950) did not note mucilaginous cells in any Celastraceae s.l. Mucilaginous leaf epidermal cells are also present in *Geissoloma marginatum*.

68. *Presence of crystals in leaf epidermal cells*: absent (0); present (1). 5, 4, 0.20, 0.73.

Codings for this character and character 69 were taken from Den Hartog née Van Ter Tholen and Baas (1978).

69. *Crystal type*: druses (0); solitary rhomboidal crystals (1). 5, 4, 0.20, 0.33.

Only taxa that were coded as having crystals in leaf epidermal cells present (character 68) were coded for this character. This character was coded as inapplicable for all other taxa to avoid non-independence among characters.

70. *Vascular strand through petiole in cross section*: uninterrupted (0); interrupted (1). 3, 2, 0.33, 0.85.

Codings were taken from Solereder (1908), Metcalfe and Chalk (1950), Baas et al. (1979), and Mueller (1995). *Aleurites* and *Astrocasia* (Euphorbiaceae) were coded as interrupted based on Metcalfe and Chalk (1950: 1213) who stated, "Petiole examined in 125 genera by Dehay (557), according to whom 3 leaf-traces enter the base in most species, although higher numbers (up to 8 in *Ricinus*) were observed in a few instances." *Lepuropetalon* is coded as interrupted based on Metcalfe and Chalk (1950), in which all Saxifragaceae were described and illustrated as having an interrupted vascular strand through the petiole in cross section. *Lepuropetalon* was one of the genera of Saxifragaceae cited as examined by Metcalfe and Chalk (1950).

WOOD ANATOMY

71. *Included phloem presence*: absent (0); present (1). 1, 0, 1.00, 1.00.

Character-state codings were taken from Brown (1922),

Record (1943), and Mennega (1994, 1997). Mennega (1997: 335) stated, "Included phloem is restricted to the Salacieae where it is found in all genera, though not in all species, as it is usually not present in trees, *Cheiloclinium cognatum* excepted." Therefore, this character was only coded for taxa in which some members are scandent or are lianas, unless they are found to have included phloem in the trees (which has not been reported except in *Cheiloclinium cognatum*). For taxa in which some species are lianas and have included phloem, whereas other species in the taxon are erect shrubs or trees and do not have included phloem, this character was coded as included phloem present, not as polymorphic, because only scandents or lianas are being coded. It is expected that Record (1943) would have described any Celastraceae he examined as having included phloem, were it present. He did not describe included phloem in any of the Celastraceae examined. Therefore, those taxa that he studied which include scandent members were coded as included phloem not present.

72. *Ray width*: one to six cells (0); some greater than ten cells (1). 2, 1, 0.50, 0.93.

Within Celastraceae s.l., very wide rays are only present in *Hippocratea* s.l. Most taxa coded as having narrow rays have only uniseriate and biseriate rays. Most codings were taken from Record (1943) and Mennega (1972, 1997). *Bhesa* was coded based on Xinying et al. (1990), and *Stackhousia* was coded based on Carlquist (1987). Solereder (1908: 884) cited "the absence of medullary rays in the wood" in Stackhousiaceae. However, Carlquist (1987) described rays as one to three cells wide in *Stackhousia*. We followed Carlquist (1987) in our coding of *Stackhousia*.

73. *Unlignified ray cells on the growth ring border presence*: present (0); absent (1). 3–5, 2–4, 0.20–0.33, 0.20–0.60.

Codings were taken from Mennega (1997). This character was only coded for taxa with state one in character 72. This is based on Mennega (1997: 335): "A striking feature of the wide rays in certain genera of the Hippocrateae (Table 2 [sic]) is constituted by the rows of unlignified cells forming a V-shaped figure at the growth ring margins (Fig. 21, 24)." As Salacieae (Mennega only examined genera of Hippocrateaceae) do not have wide rays, they were coded as inapplicable for this character. *Reissantia* was coded as uncertain because Mennega (1997: 366) cited unlignified ray cells at the growth ring border in *Reissantia* as "only noticed as rare cells in *R. indica* var. *loeseneriana*." This may be due to growth rings being inconspicuous or absent in the genus (Mennega, 1997).

74. *Perforation plate type*: simple (0); scalariform (1). 5, 4, 0.20, 0.50.

Codings were taken from Record (1943), Metcalfe and Chalk (1950), Den Hartog née Van Ter Tholen and Baas (1978), Xinying et al. (1990), Archer and van Wyk (1993b, 1997), and Mennega (1994). *Aleurites* and *Astro-*

casia (Euphorbiaceae) were coded from Metcalfe and Chalk (1950) where they cited Crotonoideae as having simple perforation plates and Phyllanthoideae as having scalariform (their group A) or simple perforation plates (their group B). *Aleurites* is a member of Crotonoideae, and *Astrocasia* is a member of Phyllanthoideae (Webster, 1975). As we do not know if *Astrocasia* would be included in Metcalfe and Chalk's group A or B, the genus was coded as uncertain for this character.

75. *Parenchyma-like bands of thin-walled septate wood fibers presence*: absent (0); present (1). 5–6, 4–5, 0.16–0.20, 0.33–0.78.

Codings were taken from Brown (1922), Smith and Bailey (1941), Record (1943), Xinying et al. (1990), Archer and van Wyk (1993b), and Mennega (1994, 1997). *Elaeodendron* was coded as polymorphic following Archer and van Wyk (1993b).

POLLEN MORPHOLOGY

76. *Pollen aggregation*: monads (0); tetrads or polyads (1). 3, 2, 0.33, 0.60.

This character was scored primarily from Lobreau-Callen (1977). *Sarawakodendron* was scored from Hou (1967); *Corynocarpus* (Corynocarpaceae) was scored from Nowicke and Skvarla (1983); *Lophopyxis* and Euphorbiaceae were scored from Erdtman (1952); and *Plagiopteron* was scored from Baas et al. (1979). All genera scored as having "tetrads or polyads" have tetrads, though *Hippocratea* and *Lophopetalum* also sometimes have polyads.

77. *Pollen annulus presence*: absent (0); present (1). 5, 4, 0.20, 0.78.

This character was scored from Lobreau-Callen (1977). *Plagiopteron* was scored from Baas et al. (1979), and *Sarawakodendron* was scored from Hou (1967). The annulus is a thickening on the interior of the pore (Lobreau-Callen, 1977, plate 14 number 10).

KARYOTYPE

78. *Base chromosome number*: 8 (0); 9 (1); 10 (2); 11 (3); 12 (4); 14 (5); 15 (6); 17 (7); 23 (8). 10, 2, 0.80, 0.85.

Chromosome numbers are quite variable within Celastraceae s. str. Within Hippocrateaceae, however, the base chromosome number stabilizes at 14 (15 for *Semialarium excelsum*). This character was coded from Bolkhovskikh et al. (1969) and *Index to Plant Chromosome Numbers* (Cave, 1958, 1961, 1964; Ornduff, 1967, 1968; Moore, 1971, 1973, 1977; Goldblatt, 1981, 1984, 1985, 1988; Goldblatt & Johnson, 1990, 1991, 1994).

79. *Haploid chromosome number of plants with base chromosome number of 14*: 14 (0); 28 (1). 1, 0, 1.00, 1.00.

This character was coded only for those taxa with a base chromosome number of 14 in character 78. All other taxa were coded as inapplicable (if their chromosome numbers are known).

APPENDIX 3. Rejected characters for cladistic analysis. List of 80 characters rejected for inclusion in cladistic analysis and reason(s) for rejection. "1" = unable to score from herbarium specimens; "2" = unable to confirm description from literature with observations from herbarium specimens; "3" = unable to distinguish distinct character states; "4" = lack of independence from other character(s); "5" = developmental stage that may or may not appear present on herbarium specimens depending on when collected or where on plant specimen was collected; "6" = invariant.

Character	Reason for rejection
Plant habit: herbaceous, woody	3
Woody plant habit: scandent, erect	3
Presence of buttressed trunks	1
Presence of thin, papery orange layer on older bark	2
Presence of deep furrows filled with parenchyma on old stems	2
Presence of swollen and/or slightly flattened nodes	3
Presence of branchlets drying blackish	3
Presence of darkened branchlets	3
Presence of zigzag branchlets	4
Presence of striate branchlets	3
Presence of subpersistent bracts at terminal node	5
Presence of elastic or resinous threads	4
Vegetative plant pubescence	3
Opposite leaf arrangement: opposite, opposite or subopposite	5
Opposite leaf arrangement: decussate, distichous	3
Alternate leaves: spiral, distichous	5
Presence of convex midrib so blades fold in herbarium specimens	2
Presence of heteromorphic leaf sizes	5
Presence of decurrent leaves	2
Presence of shiny adaxial leaf blades	3
Presence of black dots on abaxial surface of leaf blade	1
Leaf margin: entire, toothed or crenate, dentate-thorned	3
Presence of stipules	6
Stipule persistence	3
Stipule margin: simple, laciniate, or fimbriate	3
Structure subtending inflorescence: leaves, leaves or only bracts	5
Presence of cauliflorous inflorescences	1
Presence of accessory branches in axils of leaves subtending inflorescences	2
Presence of quadrangular internodes	3
Presence of bracts in inflorescence	6
Color of bracts in inflorescence	3
Inflorescence bract persistence	3
Pedicel bract number at articulation	5
Inflorescence flower number	3
Flower pubescence	4
Petal color	3

APPENDIX 3. Continued.

Character	Reason for rejection
Corolla aestivation: imbricate, valvate	3
Presence of irregularly cleft inner petals	2
Size of inner relative to outer calyx lobes	3
Sepal margin: entire, fringed, ciliate	3
Sepal connation	2
Petal connation	2
Presence of contorted petals	2
Presence of petals with two longitudinal grooves	1
Presence of clawed petals	3
Petal margin: entire, erose, ciliate, denticulate	3
Petal adnation to staminal disk	3
Disk conspicuousness	3
Disk texture: fleshy, membranous	3
Presence of notch in disk opposite stamens	3
Disk margin: entire, lobed, or angular	3
Disk surface: smooth, rugose, or papillate	3
Stamen position relative to disk lobes: between, within	6
Stamen position at anthesis: inflexed, erect, reflexed	3, 5
Stamen persistence	3, 5
Stamens ± connivent around ovary	2
Presence of pappillae on filaments	2, 5
Presence of thick dorsal connective on stamens	3, 4
Pollen surface	6
Pollen aperture type	2
Ovary position relative to disk	3
Ovary adnation to disk	3
Style shape: obscure, short and stout, long and slender	3
Stigma division: lobed, unlobed	3
Stigma with central depression	3
Position of stigmas relative to stamens: alternate, opposite	1
Presence of disk subtending fruit	6
Perianth subtending fruit: none, calyx, calyx and corolla	5
Inner capsule pubescence: glabrous, densely pubescent	4
Columella persistent after capsule dehiscence	2
Seed color: black, red or red-brown, brown	3
Testa surface texture: smooth, wrinkled	5
Seed pubescence: glabrous, pubescent	4
Presence of angular seeds	3
Presence of elongated funiculus	3
Presence of elevated bilobed structure subtending seeds	4
Aril color: white, orange, or red	3
Cotyledon connation	1
Radicle prominence: prominent, very reduced	3
Leaf gap number: unilacunar, trilacunar	4

Appendix 4. Character data matrix. Data matrix for 79 characters (Appendix 2) scored for 82 taxa of Celastraceae and related families (Appendix 1). Complete and subset polymorphisms are indicated as signified as: A = [0,1]; B = [0,1,2]; C = [0,2]; D = [0,1,3]; E = [0,1,2,3]; F = [1,2]; G = [1,2,3]; H = [1,4]; I = [1,2,4]; J = [2,3]; K = [2,5]. "-" = character inapplicable for a taxon; "?" = character state unobserved for a taxon.

Character number

Taxon	1 / 1 5	2 1 / 2 5	3 1 / 3 5	4 1 / 4 5	5 1 / 5 5	6 1 / 6 5	7 1 / 7 5
(1)	0000000000 000-111-10	0000011003	?111-00110	00-0-0-101	0----1----	0101120?21	-1200023-
(2)	0000000001 000-151-10	0001010003	00-2100100	0012-2--00	--0-10102-	?0002?0???	-02A0024-
(3)	0000000100 000-110?10	00001010-3	00-3200000	201E000111	0----1----	?010007??1	-??0?023-
(4)	0000000000 000-030A10	000010A0-A	00-32?0000	0012010110	--0-01----	00000??2?1	-??12002-
(5)	00001-0201 0000151-00	0000101001	00-1-00110	001301-100	--0-01----	?0???1??2?	-0210002?
(6)	0000000100 000-031-11	00000---03	00-0-?00?0	20?320-00?	?-0-?1----	?0???200-1	-??0?022?
(7)	0000000100 000-031-11	00000---03	00-0-?0000	30-320-000	--0-?1----	?0???200-1	-??0?01??
(8)	0000000000 000-151-10	---010-003	0101000000	0012221-00	--0-01----	?000?????1	-??0?00H-
(9)	00000000?0 000-151-10	000010-003	0101-00110	001K221-00	--0-01----	?A??0?????	-??0?021-
(10)	0000000000 000-111-10	0001102001	100-000000	101J-0-002	-----1----	?000??0???	-0?0?011-
(11)	0000000000 000-111-10	0001102001	100-000000	1012-0-002	-----1----	?000??0???	-0?0?010-
(12)	0000000000 000-061-10	0000101001	000-000100	0003A20001	0----1----	?000??????	-0?1?????
(13)	0011001000 0---001-10	0000101001	000-000111	00031F0000	---2014-0	?000??????	-??0?022?
(14)	0000000010 110-021-10	0000100001	000-100003	0013?20001	1----????	?000??????	-0210002?
(15)	1000000?00 ???-1A0110	00001012-1	000-2????0	3013?10111	??--????	?????????	?????????
(16)	00001-0100 0000011-B0	0000101103	00-2222100	1002010000	--10??????	0??????1?1	0??0?002?
(17)	0000000000 000-061-10	0000101003	0100011000	0114?00A01	0----1----	?0??000100	-??0?002?
(18)	00001-0000 000000A100	0000101001	000-111100	000J010000	--3-00000-	000A?000-0	-0?00000-
(19)	00001-0000 000000A100	0000101001	000-000110	0003010100	--0-00000-	000A?000-0	00?00000-
(20)	00001-0000 0000011-10	0000101001	000-000120	0003020000	--0-00100-	000A?000-0	-0?00000-
(21)	00001-0000 0000001-00	0000101001	000-111000	0003000100	--0-00100-	1?0??2?0-0	-??0?022?
(22)	00001-0000 000000A1A0	000010A001	000-0C0110	0001A10000	--0-11----	?000??00-0	-??0?022?
(23)	00001-0000 00000001A0	0000101001	000-000110	00011A0000	--0-11----	?0??????-?	-??0?022?
(24)	0000000000 000-001-00	0000101001	000-111000	00-3020000	--0-00100-	?0??????-?	-??0?022?
(25)	0000000000 011-011-A0	0000100001	000-0C0000	50?1?10000	-2-A0A00-	1000000-1	-0-12002?
(26)	0000010000 0001001-10	0000101001	000-000110	00?2A10000	--0-0014-0	00?0?00-0	-??0?022?
(27)	0000000000 0000110010	000010A0-1	000-000110	0002A10000	--0-00000-	0000?000-0	00?000008-
(28)	0000000000 0000111-10	0000101001	000-000110	0002A00000	--0-00000-	0000?000-0	00?000002-
(29)	0100010001 000-000A10	0000101001	000-000110	0002A10000	--0-00100-	0A012?00-0	-??0100H-
(30)	0100010001 000-000A10	0000101001	000-000110	0002A10000	--0-00000-	0A012?00-0	-??0100H-
(31)	0000000000 000-031-10	0000101001	000-000110	0002A10000	--0-00A00-	0A??000-0	-??A100I-

Appendix 4. Character data matrix. Continued.

Taxon	1 / 5	11 / 15	21 / 25	31 / 35	41 / 45	51 / 55	61 / 65	71 / 75
(32)	00001-0000	0000030010	00001010-1	000-000110	0002010000	--0-00A00-	00????????0	-??????0??
(33)	00001-0000	0000001-00	0000101001	000-000110	0001110000	--0-00?00-	?0????0???	00?00000-
(34)	000000000	000-231-10	0000101001	000-000110	0003010000	--0-00100-	?A?????0??	-??????0??
(35)	0100010001	000-001-A0	0000101001	000-000010	0002220000	--0-00000-	00????0???	-????????
(36)	0000000000	000-030010	00001010-1	000-000110	0002010000	--0-00A00-	00?????A	-????????
(37)	0000000000	0000000000	00001010-1	000-000110	0002?00000	--0-00000-	?0?????0-?	-????????
(38)	0000A-0000	000-030010	0000100001	000-210112	00-2020000	--4-0003--	?1012?00-?	-????????
(39)	0000A-0000	0000011-10	0000101001	000-100110	0002020000	--4-0003--	0A01010110	-??0?112-
(40)	0000000000	000-001-10	0000101001	000-031000	0001?10001	20---1----	00????00-?	-0?010???
(41)	00001-0000	0000001-A0	0000101001	000-100100	0001010001	21---1----	?0?????0??	-????????
(42)	0000000000	000-11A110	0000101001	000-000110	0002110001	21---1----	0????0??0	????004?
(43)	000000001	000-001-A0	0000101001	000-000110	000F120001	21---1----	00????00-?	-0?00???
(44)	00001-0000	0000001-10	0000101001	000-000110	0001010001	20---1----	?0?????0??	-????????
(45)	0011000000	000-031-10	0000101001	000-000111	0003?10001	0----1----	?000??????	-????????
(46)	00001-0000	0000001-10	0000101001	000-000100	0001?10001	1----1----	?0?????A10	-01010???
(47)	00001-0000	0000001-00	0000101001	000-000000	0001?10001	1----1----	?0?????A10	-01010???
(48)	0000010000	0000001-10	0000101001	000-000100	0002010001	0----1----	00????A10	-0111007-
(49)	0000100000	0000001-10	0000101001	000-000100	0003010001	0----1----	00????A10	-0111007-
(50)	0001000000	000000A100	0000101001	000-000100	0001010001	0----1----	00????A10	-0111007-
(51)	001000001	000-151-A0	000010100G	A011000110	00-B2A-000	--0-10100-	00????0???	-??0?0???
(52)	00001-0000	0000001-10	0000101001	000-000000	0001000101	0----1----	?0?????0??	-????????
(53)	0000000000	0000000000	0000101001	000-000110	0003110001	3----1----	00????0???	-0?000???
(54)	0000010001	000-030000	00001010-1	000-000100	0001000001	0----1----	00?????0??	-0?000???
(55)	0000000000	100-01A0A0	0000101001	000-000110	0001010001	1-0-1----	0010?1?00	-0?1100??
(56)	0000000000	000-0A1-10	0000100001	000-222100	00-30F0000	--0-00000-	?0?????0-?	-??210???
(57)	0000000000	000-040010	000010A000	00--22C100	0001010000	--0--0100-	00?????0??	-?-??0???
(58)	00001-0000	0000001-00	0000101021	000-??00?0	0001?10001	20---1----	00?????0??	-????????
(59)	0000000000	020-041-10	0000101000	00--22100	0002020000	--0-00101-	000??00-?	-??????0??
(60)	00001-0000	0000001-10	00100---00	00--22100	00-2020000	--100011-0	0??????0-?	011001??
(61)	00001-0000	0000A1-10	00000---01	000--02100	00-2020000	--100011-0	0??0?00-?	011001151
(62)	00001-0000	0000001-10	00000---00	00--02100	0002020000	--100011-0	0??0?00-?	011001??
(63)	00001-0100	0000001-10	0001101010	00--222100	1002020000	--100011-0	0??????10?	011000112
(64)	00001-0000	0000001-10	1000100000	00--222100	0002020000	--110011-0	0?????10?	010000012
(65)	00001-0000	0000001-10	0100110000	00--222100	00-2010000	--100011-0	0??0?00-?	010000012

Appendix 4. Character data matrix. Continued.

Taxon	1 — 5	1 1 — 1 5	2 1 — 2 5	3 1 — 3 5	4 1 — 4 5	5 1 — 5 5	6 1 — 6 5	7 1 — 7 5
(66)	00001-0000	0000001-10	0000100000	00--222100	00020F0000	--100011-1	01??1??11?	010010151
(67)	00001-0000	00001A1-10	0000100000	00--222100	0002010000	--100011-1	0??????11?	0110001??
(68)	00001-0000	00000A1-10	0000100100	00--222000	0002020000	--100011-0	010???1?101	01100115A
(69)	00001-0000	0002001-10	0000100010	00--222100	0002020000	--100011-0	01??1??11?	01100015A
(70)	00001-0000	0000001-10	0000101100	00--222100	1002020000	--100011-0	01??1??11?	0110001??
(71)	00001-0000	0000001-10	000010A000	00--222100	0002020000	--100011-0	0??????11?	0100001??
(72)	00001-0000	0000001-10	0000100000	00--222100	0002010000	--100011-0	01??0?0-?	01?0001??
(73)	00001-0000	00001A1-10	0000100000	00--222100	0002020000	--110011-0	01??0?11?	01101016-
(74)	00001-0000	0000001-10	0000101010	00--222100	0002010000	--100011-0	0????????	010000???
(75)	00001-0000	0000001-10	0000101010	00--222100	0002020000	--100011-0	0??1??11?	010000???
(76)	00001-0000	0000001-A0	0000110001	00--222100	00-3010001	0----0?2--	?1?????0-?	10-0100??
(77)	00001-0000	00000A1-A0	0000110000	00--222100	00-2010001	0----0?2--	?1?????0-?	10-0100??
(78)	0000A00000	00000A1-10	0000100000	00--220004	00020A0A01	0----0?2--	?1?????0-?	10-0110??
(79)	00001-0000	0000031-10	0000101002	00--222100	0001010001	0----0?2--	?101112101	10-010050
(80)	00001-0000	0000031-10	0000101000	00--220?00	000F010101	0----0?2--	?101112101	10-010050
(81)	0000A00000	00000D1-10	000010A0A0	00--22C100	00020F0001	0----0?2--	?101112101	10-010050
(82)	0000A00000	0000001-A0	0000100000	00--222100	00020F0001	0----0?2--	?1?????0-1	10-0100??

APPENDIX 5. Specimens examined for gross-morphological characters.

Sixty-two gross-morphological characters were scored for 82 taxa based on literature and/or herbarium specimens. The numbering of taxa follows that of Appendix 1. Following the taxon name and author are the specimens examined, if any (some taxa were scored entirely based on the literature). If the taxon entered in the data matrix is a genus or subgenus, the species of each herbarium specimen examined is listed. Herbarium specimens were examined at BH, NY, P, and US (Holmgren et al., 1990).

(1) *Cornynocarpus laevigata* J. R. Forst. & G. Forst., *Hitchcock 15173* (US). (2) *Crossosoma bigelovii* Wats., *Dearing 4022* (BH), United States. (3) *Aleurites moluccana* (L.) Willd., *Bailey 604* (BH), Panama; *De Winter 2931* (BH), South Africa (Cultivated); *Zanoni 18848* (BH), Dominican Republic. (4) None examined. (5) *Geissoloma marginatum* Lindl. ex Kunth, *Carlquist 4558* (BH), South Africa. (6) None examined. (7) None examined. (8) *Lepuropetalon spathulatum* Ell., *Blake s.n.* (NY). (9) *Parnassia fimbriata*, *Jones 23924* (BH), Canada; *Perkins s.n.* (BH), Canada. (10) *Stackhousia monogyna* Labill., *Conn 2282* (NY). (11) *Tripterococcus brunonis* Endl., *Morrison s.n.* (US). (12) *Brexia madagascariensis* Thouars ex Ker-Gawl., *Degener 36588* (BH), United States (Cultivated); *Houghton 1104* (BH), United States (Cultivated); *Wikoff 1390* (BH), United States (Cultivated). (13) *Canotia holacantha* Torr., *Collom s.n.* (NY); *Landrum 6151* (NY). (14) *Goupia glabra* Aubl., *Silva 2401* (NY); *Wurdack 40961* (NY); *Zanderij 73* (NY). (15) None examined. (16) None examined. (17) *Siphonodon celastrineus* Griff., *Kostermans 9647* (NY); *Poilane 3054* (P); *Wenzel 3255* (NY). (18) *Euonymus alatus* (Thunb.) Siebold, *Unknown s.n. 8 May 1921* (BH), United States (Cultivated); *Unknown s.n. October 1933* (BH), United Kingdom (Cultivated); *Simmons 1772* (BH), United States (Cultivated). (19) *Euonymus fortunei* (Turcz.) Hand.-Mazz., *Simmons 1778* (BH), United States (Cultivated). (20) None examined. (21) *Glyptopetalum feddei* (Lév.) Ding Hou, *Esquirol 4007* (P); *G. gracilipes* Pierre, *Kerr 20323* (P); *G. poilanei* Tardieu, *Petelot 6874* (P). (22) *Microtropis fokiensis* Dunn., *Kanehira 3067* (US); *Rock 7536* (US); *M. japonica* Hallier f., *Murata 21451* (US); *Sonohara 44* (US); *Wilson 8194* (US); *Yokoyama 1152* (US); *M. wallichiana* Wight. ex Thwaites, *Waas 883* (US). (23) *Quetzalia occidentalis* (Loes. ex Donn.) Lundell, *Magana 5343* (US); *Smith P3299* (US); *Standley 48169* (US). (24) None examined. (25) *Bhesa* Buch.-Ham. ex Arn.; *B. archboldiana* (Merr. & Perry) Ding Hou, *Brass 25551, 28105* (US); *B. paniculata* Arn., *Beaman 9527* (US); *Boeea 7215* (US); *Toroes 3923* (US). (26) *Catha edulis* (Vahl) Endl., *Bailey 9036* (BH), United States (Cultivated); *Gander A321* (BH), United States (Cultivated); *Moran 2410, 7172* (BH), United States (Cultivated). (27) *Celastrus scandens* L., *Fernald 13973* (US); *Knowlton s.n.* (US); *Lix 569* (US); *Moiser s.n.* (US); *Smith 882* (US); *Waugh 129* (US). (28) *Celastrus pringlei* Rose, *Hinton 3506, 9020* (US); *King 5040* (US); *McVaugh 10308* (US); *Smith 4437* (US); *C. racemosus* Turcz., *Silva 1609* (US). (29) None examined. (30) None examined. (31) None examined. (32) *Menepetalum salicifolium* Loes., *Compton 1476* (BH), New Caledonia; *M. schlechteri* Loes., *McPherson 4821* (BH), New Caledonia; *Schlechter 15630* (BH), New Caledonia. (33) *Paxistima myrsinites* (Pursh) Raf., *Dress 4273* (BH), United States (Cultivated); *Muenscher 910, 17016* (BH), United States (Cultivated). (34) *Polycardia aquifolium*

Tul., *Harder 1700* (P), Madagascar; *Villiers 4952* (P), Madagascar; *P. lateralis* O. Hoffm., *Dorr 3031* (P), Madagascar. (35) None examined. (36) *Salaciopsis eocaledonica* Baker F., *Compton 1692, 1944* (BH), New Caledonia; *S. sparsiflora* Hürl., *Guillaumin & Baumann-Bodenheim 8948* (A), New Caledonia. (37) None examined. (38) *Kokoona ochracea* Merr., *Soejarto 7021* (NY). (39) *Lophopetalum beccarianum* Pierre, *Jacobs 5546* (BH), Borneo; *L. javanum* Turcz., *Kostermans 5894* (BH), Borneo; *L. rigidum* Ridl., *Jacobs 5519* (BH), Borneo. (40) *Plenckia populnea* Reissek, *Anderson 10036* (NY); *Heringer 5678* (NY); *Ratter et al. 2582, 3794* (NY). (41) *Ptelidium ovatum* Poir., *Caprun 22742* (P), Madagascar; *P. scandens* H. Perrier, *Leandri 2193* (P), Madagascar. (42) *Tripterygium regelii* Sprague & Takeda, *Davis 80–220* (BH), United States (Cultivated); *Elsik 3290* (BH), United States (Cultivated); *Michener 4682* (BH), United States (Cultivated). (43) *Wimmeria persicifolia* Radlk., *Conralli 4273* (US); *Kirkby 2795* (US); *Pringle 6210* (US). (44) *Zinowiewia costaricensis* Lundell, *Skutch 4028* (US); *Jiménez 1538* (US); *Z. integerrima* Turcz., *Calzada 01799* (US); *Nee 29403* (US); *Purpus 2386* (US). (45) *Acanthothamnus aphyllus* (Schltr.) Standl., *Lundell 12520* (US), Mexico. (46) *Cassine parvifolia* Sond., *Burchell 5769* (P). (47) *Cassine schinoides* (Spreng.) R. H. Archer (none examined). (48) None examined. (49) None examined. (50) None examined. (51) *Forsellesia spinescens* Gray, *Clokey 8514* (BH), United States; *Constance 1002* (BH), United States; *Duran 548* (BH), United States. (52) *Gyminda latifolia* Urb., *Correll 47427, 47672* (NY); *Zanoni 39340* (NY). (53) *Mortonia scabrella* A. Gray, *Powers s.n.* (BH), United States; *Wentworth 118* (BH), United States; *Wolf 2495* (BH), United States; *M. utahensis* A. Nelson, *Thorne 44536* (BH), United States. (54) *Schaefferia cuneifolia* A. Gray, *Chiang 10136* (US); *S. frutescens* Jacq., *Acevedo-Rdgz. 5357* (US); *Britton 3328, 5972* (US); *Crosby 1026* (US); *Ekman 10605* (US); *Jak 6938* (US). (55) *Perrottetia longistylis* Rose, *Breedlove s.n.* (NY); *Calderón 486* (NY); *Utley 3082* (NY); *P. ovata* Hemsl., *Fernandez 4076* (NY). (56) None examined. (57) *Dicarpellum pancheri* (Loes.), A. C. Sm., *Balansa 1354* (BH), New Caledonia; *Bamps 5927* (BH), New Caledonia; *Compton 1664* (BH), New Caledonia. (58) *Rzedowskia tolantonguensis* Medrano, *Rzedowski 38344* (US), Mexico. (59) None examined. (60) *Bequaertia mucronata* (Exell) R. Wilczek, *Andoh 5494* (P); *Chevalier 19055* (P); *Tisserant 1197* (P). (61) *Campylostemon angolense* Welw. ex Oliver, *Asonganyi 293* (P); *C. laurentii* W. J. de Wilde, *Louis 10273* (NY); *Tisserant 1189* (P); *C. warneckeanum* Loes. ex Fritsch, *Troupin 6308* (NY). (62) None examined. (63) *Helictonema velutinum* (Afzel.) Pierre, *Benoît 455* (P); *Letouzey 5531* (P); *Reitsma 2271* (P); *Rlaine 1316* (P). (64) *Anthodon panamense* A. C. Sm., *Croat 8426, 11734, 12622* (NY); *Hayden 139* (NY); *A. decussatum* Ruíz & Pav., *Liesner 5400* (NY). (65) *Apodostigma pallens* (Planch. ex Oliv.) R. Wilczek, *Heudelot 341* (P); *Jansen 1662* (P); *Pobéguin 815* (P). (66) *Cuervea kappleriana* (Miq.) A. C. Sm., *Cid 1110* (NY); *Oliveira 4772* (NY); *Rabelo 3699* (NY). (67) *Elachyptera bipendensis* (Loes.) R. Wilczek, *Bos 3581* (P); *Rlaine 1505* (P); *Sita 1526* (P); *E. holtzii* (Loes. ex Harms) R. Wilczek, *Fleury 26299* (P); *E. parvifolia* (Oliver) N. Hallé, *Dubois 202* (P). (68) *Hippocratea volubilis* L., *Goodland 946* (US); *Henkel 2441, 4586* (US); *Jansen-Jacobs 3203* (US). (69) *Loeseneriella clematoides* (Loes.) R. Wilczek, *Louis 13499* (NY); *L. apiculata* (Welw. ex Oliv.) R. Wilczek, *Reitsma 2276* (NY); *L. concinna* A. C. Sm., *Tsang 21743* (NY). (70) *Prionostemma aspera* Miers, *Davidson 10645* (NY); *Ek 770* (NY); *Steyermark 107744*

(NY). (71) *Pristimera andongensis* (Welw. ex Oliv.) N. Hallé, *Hladik 2854* (P); *Wild 6611* (P). (72) *Reissantia indica* (Willd.) N. Hallé, *Corbisier-Baland 1637* (NY); *R. angustipetala* (H. Perrier) N. Hallé, *Keraudren 438* (P). (73) *Semialarium excelsum* (HBK) A. C. Sm., *Ayala 730* (NY); *Molina 13698* (NY); *Walker 422* (NY). (74) *Simicratea welwitschii* (Oliv.) N. Hallé, *Klaine 177, 1001* (P); *Lock 46710* (P). (75) *Simirestis dewildemaniana* N. Hallé, *Tisserant 938, 2125* (P). (76) *Cheiloclinium anomalum* Miers, *Ferreira 6309* (NY); *Wurdack 2379* (NY). (77) *Cheiloclinium belizense* (Standl.) A. C. Sm., *Ferreira 7374* (NY); *C.*

cognatum (Miers) A. C. Sm., *Dionizia 37* (NY); *Irwin 10935, 17633* (NY); *Maguire 56441* (NY). (78) *Peritassa campestris* (Cambess.) A. C. Sm., *Eiten 1628* (NY); *Irwin 7010, 16847* (NY); *Mimura 427* (NY); *P. laevigata* (Hoffmg.) A. C. Sm., *Irwin 17468*; *Maguire 56092* (NY). (79) *Salacia erythrocarpa* K. Schum., *Schlechter 18864, 47003* (NY). (80) None examined. (81) *Salacia prinoides* DC, *Merrill 371, 2044* (NY); *Ramos 44109* (NY). (82) *Tontelea attenuata* Miers, *Cid 748* (NY); *Little 9535* (NY); *Vásquez 2950* (NY); *T. brachypoda* Miers, *Goodland 886* (NY); *Harley 10138* (NY); *Hassler 5030, 9667* (NY); *Ratter 390* (NY).